

AN ECOLOGICAL STUDY OF THE CRICKET FROG, ACRIS CREPITANS,
IN NORTHEASTERN KANSAS

by

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CONTENTS

	Page
INTRODUCTION	1
DESCRIPTION OF STUDY AREAS	3
METHODS	8
THE LIFE CYCLE	11
Annual and Diel Cycles of Activity	11
The Breeding Season	12
Chorus Structure	15
Eggs	18
Larvae	19
Growth Rate	19
POPULATION STRUCTURE	27
Sex Ratio	27
Estimation of Post-Metamorphic Density and Survival	29
Reproductive Potential	49
Polymorphism and Its Significance	52
PREDATION AND PARASITISM	64
MOVEMENTS	67
DISCUSSION	90
SUMMARY	103
ACKNOWLEDGMENTS	108
LITERATURE CITED	108

INTRODUCTION

The cricket frog, Acris crepitans, is a useful subject for population studies since it is generally present in large numbers throughout most of the year near permanent and semipermanent bodies of water and tends to form separate and distinct populations. Populations of this species were studied in and near Lawrence, Douglas County, Kansas, in the autumn of 1961 and from autumn, 1963, through spring, 1966. Two populations were studied intensively: one at the University of Kansas Natural History Reservation, about seven miles northeast of Lawrence, and the other at the University of Kansas Fish Laboratory on the southwestern part of the campus in Lawrence. A total of 2492 frogs was marked at the Natural History Reservation, and 1077 frogs were marked at the Fish Laboratory. The importance of the Kansas River (which lies between the two populations) as a barrier to gene flow is uncertain. Cricket frogs are found on both sides of the river and occasionally may cross it either intentionally or accidentally. Crossing of the river by adults probably occurs mainly during flooding, as Acris generally will not voluntarily swim more than a few feet from shore. These two populations (hereinafter referred to as the Reservation population and the Fish Lab population) were permitted to exist naturally, except that a few small samples of unmarked frogs were taken from them occasionally for preservation. Samples also were taken periodically from the Rockefeller Experimental Tract, adjacent to the Reservation on the north; two miles west of the Reservation; Lone Star Lake, 12 miles southwest of Lawrence; Baldwin Woods, 15 miles south of Lawrence; and three miles south of Denison,

Jackson County, Kansas.

The main objective of this study was to determine if there were any differences in the ecology of populations of cricket frogs in different habitats separated by only a few miles. Morphological variations have been used as criteria for taxonomic studies for years, but ecological criteria have come into use only recently. However, little is known concerning ecological variation within a local area. Since Acris crepitans lives in a variety of habitats, it is suitable for this kind of study. Since morphological variation often reflects ecological conditions, it was assumed that ecological variation might shed light upon morphological differences in populations.

The biological implications of wide ecological variation in a species scarcely need mentioning, yet ecological data are missing all too often in studies of various organisms. For instance, a taxonomist may assume that morphological differences in two samples had a genetic basis and name such populations as subspecies; in actuality these differences may be the result of a different sex ratio or size composition at the time of sampling. Or, an ecologist might assume he understood the ecology of a species as a whole or in a limited area after studying it at only one locality. The conditions at that locality may be sufficiently different from other localities that the ecology is significantly altered from that of most populations.

The genus Acris includes two species of small, non-arboreal, hylid frogs. A. crepitans occurs throughout most of the United States east of the Rocky Mountains and south from the southern portions of South Dakota, Minnesota, Michigan, Pennsylvania, and New York to the Gulf Coast, excluding peninsular Florida. A. gryllus is found along the

southeastern coastal plains from Virginia to the Mississippi River. An area of sympatry between the two species covers slightly more than 50 per cent of the range of A. gryllus.

Until recently both species have been studied but casually; knowledge of their ecology has been based mainly on short notes, most of which have been well summarized by Wright and Wright (1942). Recent studies include those by Turner (1960b) and Ferguson, Landreth, and Turnipseed (1965) on Acris gryllus; and those by Ferguson, Landreth, and McKeown (1967), Pyburn (1958, 1961a, 1961b) and Blair (1961) on Acris crepitans. Gerald T. Regan is presently studying distribution of A. crepitans and the factors limiting to it in the Missouri River drainage; Dr. Eviator Nevo is studying geographical variation of both species; and Dr. Laurence E. Bayless has recently completed an ecological study of sympatric populations of both species in southeastern Louisiana.

Studies of populations of animals have become increasingly important as knowledge of evolutionary processes has grown. With the increase in knowledge of animal populations numerous studies of each species throughout its geographical range are needed, so that ecological variation may be compared, along with other parameters. Such studies have rarely been made except on certain game animals and other species of economic importance. Noteworthy studies of populations of anurans include those by Fitch (1956), Jameson (1955), Thornton (1960), and Turner (1960a).

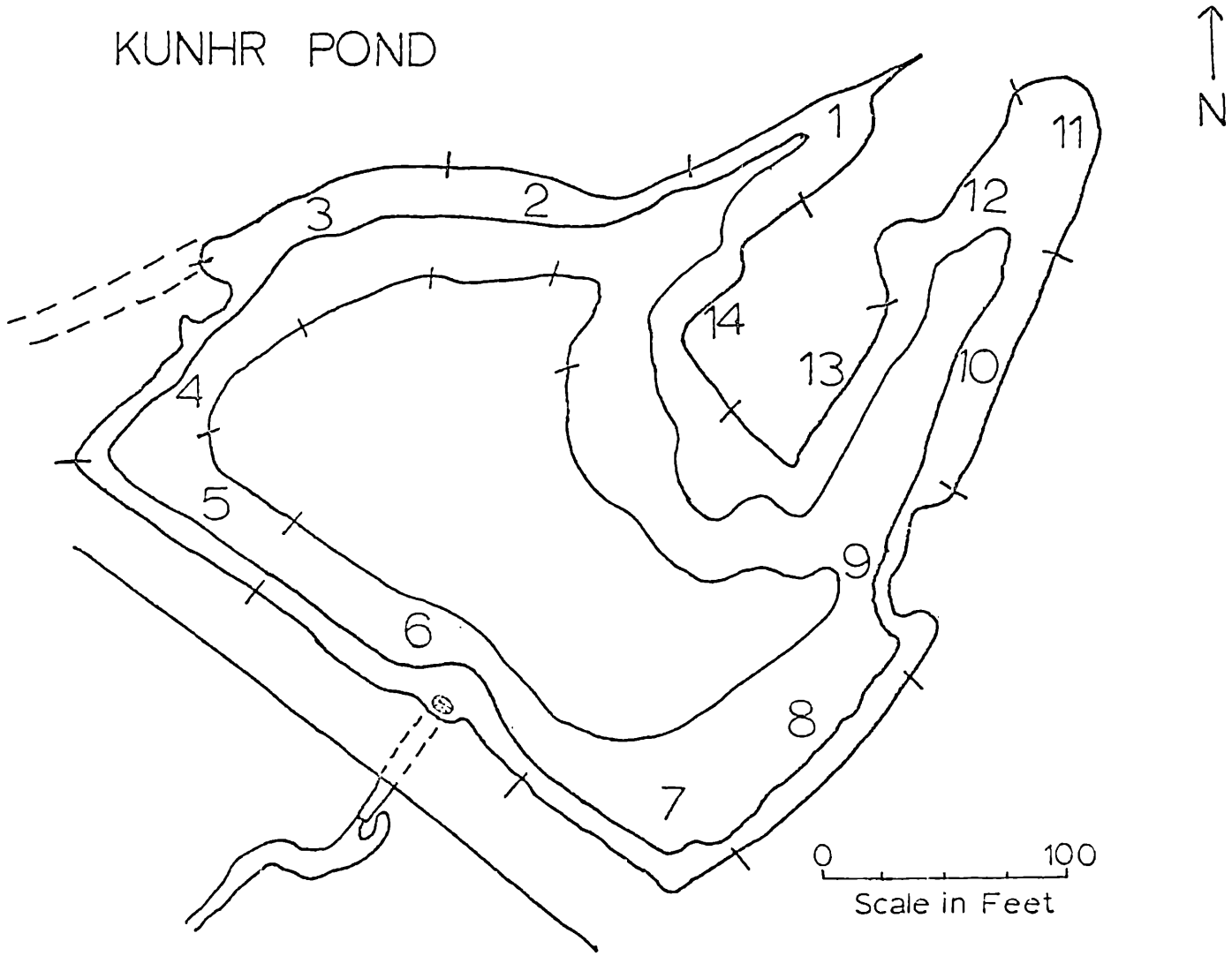
DESCRIPTION OF STUDY AREAS

The pond at the University of Kansas Natural History Reservation

lies near the upper end of a narrow valley and is bordered by hills to the northwest, northeast, and southeast. It was created by the construction of an earthen dam impounding water on its northeast side. A drainage pipe covered by an iron grid is situated near the center and a few feet below the top of the dam. When the pond overflows, its water drains down a stream to the southwest and into a small creek, "Mud Creek", that empties into the Kansas River about two and one-half miles east of Lawrence. A diversion ditch carries water from the northwest corner of the pond after excessive rains. The pond has a maximum circumference of about 1425 feet (Fig. 1). The front half of the pond has a slope of about 30° with no "beach" area when water is flowing through the drain. Only areas 3 to 6 receive much sunlight, except when the pond is low or when there are no leaves on the trees. The northeastern (or upper) end of the pond is shallow and swampy, with numerous willows (Salix) along its edge. Honey locust (Gleditsia triacanthos) borders much of the northern edge and the northwestern end of the dam. The southeastern border of the pond is almost always shaded by several large oaks (Quercus velutina), elms (Ulmus americana), and ash (Fraxinus americanus). Much of the northwestern edge of the pond and the dam are bordered by small trees, shrubs, herbs, and grasses. The most abundant of these are Vitis vulpina, Bidens bipinnata, Rubus flagellaris, Polygonum coccineum, Echinochloa crus-galli, and Ambrosia trifida. Also common are: Rhus radicans, Rosa setigera, Commelina communis, Smilax hispida, Cornus drummondii, Ulmus americana, Populus deltoides, and Carex. Typha latifolia and Sagittaria latifolia are found in the water. Algae are usually common in the water in a zone from about one foot to three feet from shore.

Fig. 1.—Pond at the University of Kansas Natural History Reservation showing location of the 14 designated areas, each 100 feet in length. The two inner lines indicate the approximate location of one-foot and six-foot depths when the pond is full. In the autumn of 1963 the water level was at the six-foot contour line. (Areas 1 through 5, each 50 feet in length, are indicated by hatch marks). Throughout the remainder of the study period, the pond did not recede beyond the one-foot level.

KUNHR POND



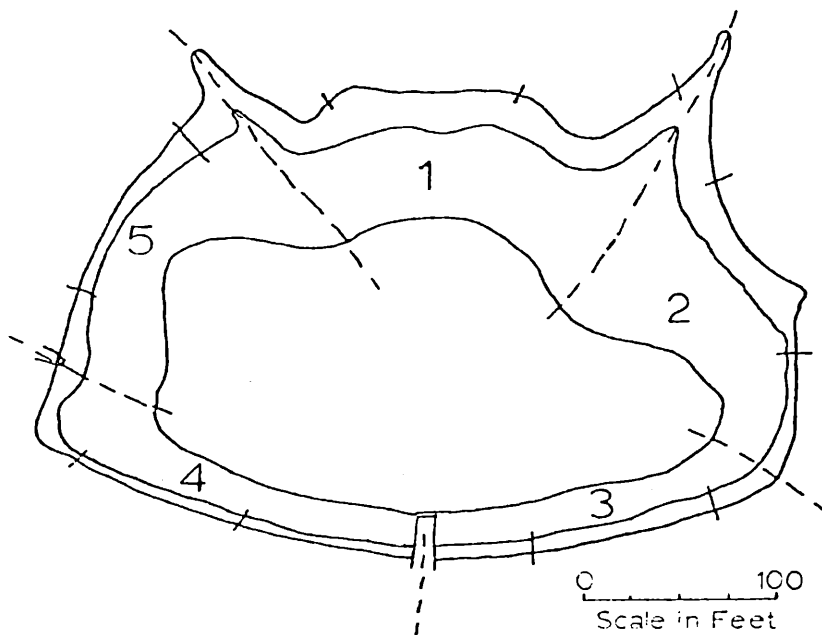
A small intermittent stream that drains into the pond from the north receives overflow from a pond one-half mile away in a heavily grazed pasture. This pond is less than half the size of the pond on the Reservation when it is full and is much shallower than the latter. For a more complete description of the Reservation, see Fitch (1952, 1965) and Fitch and McGregor (1956).

At the University of Kansas Fish Laboratory there is a reservoir on a south-facing slope, and eleven rectangular ponds are located about 100 yards south of the reservoir (Fig. 2). Through an underground system of pipes, water is drained from the reservoir into the ponds each spring when studies on fish begin. Each pond is drained through pipes that empty into a small stream south of the ponds. About 100 yards downstream is still another small pond with a swampy area nearby. The stream continues south until it reaches the Wakarusa River, which enters the Kansas River about seven miles east of Lawrence.

The reservoir fluctuates considerably in depth since the water is used to fill the fish ponds. Also it tends to diminish in circumference each fall but fills with the coming of rain each spring. If it does not fill naturally, water is pumped in from the Lawrence mains. The maximum circumference of the reservoir during my study was about 1200 feet, and the minimum was about 750 feet. During the winter months little direct sunlight strikes the southern shore because it is shaded by the steep slope of the dam. Three small gullies drain into the reservoir. Stakes were driven into the ground every 20 feet around the reservoir; and five study areas, varying in length from 175 to 300 feet, were designated. The only trees around the reservoir are a few small saplings of Populus and Salix, which occur in about equal numbers.

Fig. 2. The University of Kansas Fish Laboratory showing location of the ponds and of the five designated study areas at the reservoir. The two inner lines indicate the approximate location of one-foot and six-foot depths when the reservoir is full.

FISH LAB RESERVOIR



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Abundant herbaceous plants include: Lippia lanceolata, Ammannia coccinea, Xanthium strumarium, Setaria viridis, and S. faberii. Other less common plants are: Ambrosia trifida, Echinochloa crus-galli, Helianthus, Cyperus, Convolvulus arvensis, Panicum capillare, Physalis, Polygonum, and Lespedeza.

The eleven ponds are arranged in two rows, the western row containing five ponds and the eastern, six. When the ponds are in use, the depth of water in each one varies from one to five feet. The banks of the ponds are steep (about 45°) and approximately four feet high. However, erosion has caused the formation of narrow beaches around portions of some of the ponds (Numbers 1 and 6 to 10). Distance from the top of the bank of one pond to the bank of another is roughly 10 feet, and distance between the two rows of ponds is nearly 70 feet. Each pond measures approximately 48 x 122 feet at the top of the bank and 40 x 114 feet at water level. Ponds 10 and 11 have fences dividing them into six sections; therefore, six sections were assigned to each pond so that the location of each frog captured could be recorded more exactly. Plant life is similar to that around the reservoir with the addition of grasses between the ponds. There was only one small tree (Salix), at the edge of pond 7. Cattails (Typha) were usually found in ponds 1 and 10.

METHODS

Frogs were captured by hand or with the aid of a small net. Each individual was measured to the nearest millimeter on a rule which was taped to a clipboard. It was not feasible to make more accurate measurements, as tests showed variations of nearly one-half millimeter

in successive measurements of several individuals. Sex was recorded when it could be determined. Adult males were recognized by presence of a dark vocal pouch and adult females by presence of eggs and their larger size. Juvenile males sometimes could be distinguished by dark spots on the chin, but these are present on some females, too. Characteristics of each individual that made it easier to recognize (such as missing toes or limbs, scars, number of chiggers, pattern, or color) were recorded. Color and pattern were especially notable because of the polymorphism exhibited in most populations of Acris. A vertebral stripe of green, rust, dark brown, light brown, or gray appears on some individuals; in most, however, the stripe was absent or difficult to detect. There was considerable variation in the pattern and size of the stripe. For purposes of this paper, the stripes will be referred to as green, brown, or gray (see section on Polymorphism for explanation).

Frogs were marked by toe-clipping with small scissors. Hundreds of individuals were sometimes present in a population surrounding one pond; and if each frog had been marked individually, excessive time would have been consumed in the field. Therefore, new individuals captured in each area on the same date were marked alike. Areas (not exceeding 330 feet long and 15 feet wide) were marked off at each locality, and all individuals captured in each area were marked on the left hind foot by amputating the one toe designated for that particular area. Thus, the area of original capture could be determined by examination of the left hind foot of a recaptured frog. In the second sampling period the first toe on the right hind foot (1-RH) was clipped on all frogs recaptured, and all new frogs were marked

with the area-marking on the left hind foot and the second toe of the right hind foot (2-RH) was clipped. In each subsequent sampling period the marking representing the area of capture was given by clipping a toe on the left hind foot, and a marking different from any used in other periods was made on the right hind foot. This method allowed the dates of 15 sampling periods and the differentiation of 15 areas to be indicated by clipping no more than two of the toes on each hind foot.

Frogs that were marked in the first period and recaptured in the second period were marked individually (by clipping toes on the front feet) the third time they were captured. All other frogs were marked individually the second time they were captured. The place of capture, precise to the nearest linear foot, was recorded whenever frogs were given individual markings and at subsequent times when they were recaptured. Whenever groups were being marked, they were captured in an area of pond-margin up to 20 feet in length, then released in the center of the area. Any frogs marked in the first period but not recaptured in the second period were given individual markings whenever they were recaptured and also were given the group marking, 1-RH. Thus, frogs with the 1-RH mark were not always those recaptured in the second period. The data on each individual were coded onto marginally punched tabulating cards, eliminating the possibility of confusing the dates on which each individual was marked.

In this report the sample-size mentioned for a particular date may differ under the separate discussions of different topics. These differences do not reflect errors or inconsistencies in the presentation of data, because on almost every occasion that I carried on field work

at least one frog escaped before I had recorded all pertinent data. In a few instances frogs were captured in which the original marking had been altered by loss of toes or limbs. Adjustments in certain calculations were made to account for these individuals.

THE LIFE CYCLE

Annual and Diel Cycles of Activity

Acris crepitans is one of the most common anurans in its habitat and geographic range throughout most of the year. Fitch (1956c:426) stated that Acris is active at temperatures from slightly above freezing to summer heat, and is the only frog commonly seen in winter in northeastern Kansas. Two or three warm days in winter will usually cause a few cricket frogs to appear. These are probably individuals "hibernating" close enough to the surface to be warmed by rising temperatures. Ordinarily for the population as a whole, activity does not begin until mid-March. Cold fronts after this time cause most individuals to disappear again for a few more days. Activity is restricted more or less to daylight hours in cool weather, but lengthens to include both day and night as temperatures rise. Cricket frogs again disappear, retiring into hibernation, from mid-November to mid-December, depending on temperatures. In contrast, Pyburn (1958:341) reported activity in every month in central Texas, where temperatures seldom remain below freezing for more than a few days.

Cricket frogs apparently make burrows or use those of other animals for retreats in cold weather. Although I have never observed them digging, I have seen them sitting in small depressions and burrows or emerging from such shelters on several occasions.

Fitch (op. cit.:428) recorded body temperatures of 102 Acris between 8.3° and 34.8° C.; more than half were between 28.0° and 31.7° C. On November 11, 1964, I tested the critical thermal maximum and minimum of 18 Acris. Nine frogs were heated first and nine were chilled first; then the process was reversed for the survivors. A jar containing three frogs and about one-half inch of water was warmed in a bath of hot tap water. Cooling was accomplished by immersing a jar, in similar fashion, into a mixture of salt, crushed ice and water. At 37.7° C. (100° F.) all frogs began to jerk spasmodically. Three of those exposed died and one remained almost completely paralyzed. When chilled, 14 frogs continued to move slowly and right themselves until the temperature reached -0.28° C. (31.5° F.).

Under natural conditions in northeastern Kansas, the low temperature at which Acris become inactive is reached more often than the high temperature. Presumably more Acris freeze to death than die from exposure to lethally high temperatures. When air temperatures exceed 100° F., water temperatures are likely to be somewhat lower and evaporative cooling would tend to keep frogs' temperatures lower. Most frogs that die in hot weather probably succumb from desiccation rather than heat per se.

The Breeding Season

The breeding season of Acris varies somewhat with geography and weather. Periods of calling near Austin, Texas, have been reported as early as January 30 and as late as September 10 (Blair, 1961:106). Smith (1961:79) stated that in Illinois calling occurs from late April until late summer. Smith (1956:89) reported that breeding occurs from

early April until May 9, in Kansas, but that calling continues until July 15.

Somewhat different dates for the same events were recorded in my study (Table 1). Large choruses were heard as early as late April in 1965 and mid-May in 1964 and 1966, and as late as June 23, 1964. Each year calling began in the daytime, but later as temperatures increased there was calling at night. Blair (1961:106) reported that evening calling began only after temperatures exceeded those of the preceding days when afternoon calling was heard. Daytime calling does not cease after night calling begins but continues until all calling ceases in mid-summer. Blair (loc. cit.) found little correlation between rainfall and calling in Acris, and stated that calling was heard between temperatures of 41° and 95° F.

The relationship between calling and spawning is not well known in the populations studied herein, since amplexus was not observed. However, observation of gravid and post-partum females indicates that most spawning occurred from late May to early July. Eggs became fully developed about mid-April, and almost all females remained gravid until the end of May. Post-partum females first appeared in the populations on June 6, 1964, May 31, 1965 (NHR), and June 29, 1965 (FL). In the sample taken on July 13, 1965 (NHR), some females were fully gravid, but most had only a few eggs remaining on one or both sides. One female containing only a few eggs was found as late as August 3. The number of eggs laid during each spawning is unknown. However, judging from the number of females containing only a few eggs, it appears that females may mate at least twice during the breeding season. In Texas Pyburn (see Blair, loc. cit.) also found evidence that females may lay

TABLE 1.—Reproduction in Acris crepitans at the University of Kansas Natural History Reservation and the University of Kansas Fish Laboratory.

	Year	Gravid females first found	50 to 100% of females gravid	Post-partum females found	Earliest calls heard	Last calls heard	Tadpoles found	Young with tails found
KUNHR	1964	4/25	--	6/6	4/24	--	--	7/10 - 9/29
	1965	4/20	4/29 - 6/11	5/31 - 7/13	4/20	--	--	7/13 - 8/21
	1966	4/24	--	--	4/24	--	--	--
Fish Lab	1963	--	--	--	--	7/25	9/18	9/18
	1964	--	--	--	±5/2	before 7/30	7/15 - 7/30	7/15 - 7/30
	1965	4/17	4/17 - 6/23	6/29	4/16	7/28	--	7/15 - 8/26
	1966	--	5/7	--	between 4/17 and 5/7	--	--	--

eggs twice; in Kansas, however, there is definitely no second breeding season involving young-of-the-year as found by Pyburn in Texas.

Females become mature in late April when their eggs enlarge, but males mature earlier. In northern Texas, I have found motile sperm in males in early September. In northeastern Kansas in late September the sperm were all grouped in clumps. By early October nearly all males had well-formed sperm. A few of the males also develop chin spotting in the autumn, but the vocal pouch is formed in late March or April, preceding the breeding season.

Chorus Structure

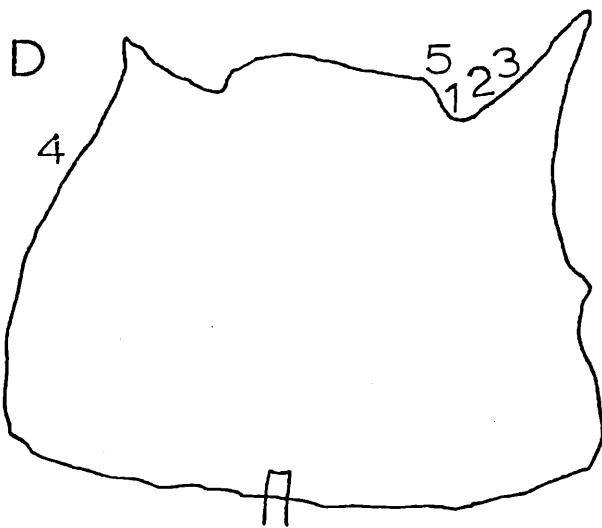
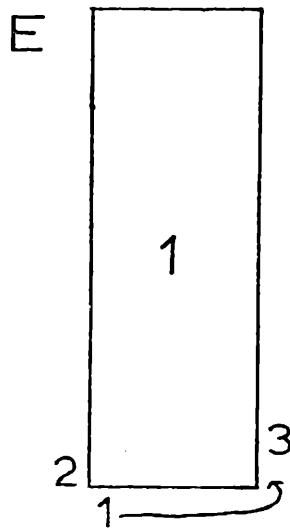
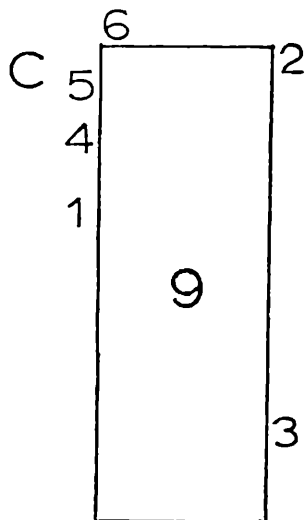
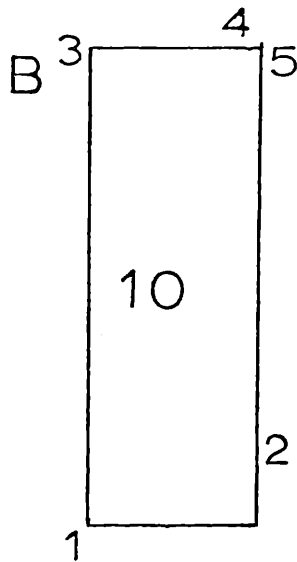
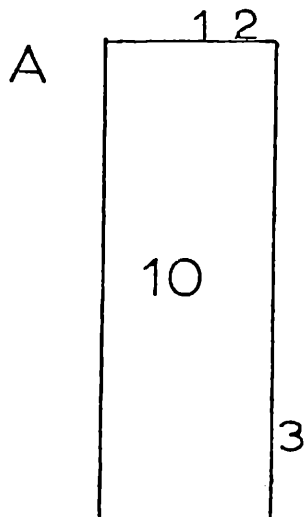
Smith (1956:89) stated that the rhythm of a small chorus of Acris crepitans is suggestive of a call order like that recorded for Hyla crucifer. My observations on calling groups are shown in Table 2.

These data suggest that there is an imperfect tendency for ordered sequence in choruses of Acris. Groups of two or three frogs may follow a pattern, but larger choruses seem chaotic. Certain individuals appear to be "leaders" and others "followers". There seems to be no correlation between loudness and answering as found in Hyla regilla and other species (Foster, 1967:101). However, Acris often answers close calls more rapidly than distant ones. Spacing of the individuals mentioned in Table 2 can be seen in Figure 3. Both calling and rate of repetition of calls are stimulated by calling of other frogs. I have started many choruses by imitating the call with my voice but do not know if other sounds will stimulate Acris to call. In a few instances the calls of grackles and red-winged blackbirds seemed to stimulate choruses. It is noteworthy that one participant in the chorus on July 28

TABLE 2.—Sequences of calling in several choruses of Acris crepitans at the University of Kansas Fish Laboratory. Numbers designate individuals and are listed in the order in which individuals called. Hyphens (-) between numbers indicate relative length of time of call. Each line is a new sequence after a relatively long period of silence. Letters A to E refer to Fig. 3, where spacing of frogs around ponds is given.

Date	Location	Calling sequence
A. 6/21/64	Pond 10	1-2-3 several times
B. 6/23/64	Pond 10	1--2---3--4-5 1-2 1-2 3-4-5- 3-1-2-4-5- 5-----
C. 5/06/65	Pond 9 Pond 10	1-2---3-4-5 (10:54 a.m.) 5-6 (12:28 p.m.) 1-2 1-2
D. 7/28/65	Reservoir	1-2 1-2 1-2-3---- 3--1 and 2-- 1 and 2 (8:30 p.m.) 4--- 4-5-1-- 5-1-3-- 5-1-3-2-- 3-2- 3-2-5- 3-2-5-1- 4--5-1-2-3 4--2-- 2-3-5--- 2-3-5-1-- 4---1--2-- 1-2-3-- 2-3-- 1-2-5-3-- (ended 9:00 p.m.)
E. 7/28/65	Pond 1	1-2 (9:20 p.m.) 1-3 (1 moved nearer to 3) (10:05 p.m.)

Fig. 3.—Positions of calling males represented in Table 2. Small numerals represent individual frogs. Large numerals refer to pond numbers.



was a newly metamorphosed male, 19 mm. in snout-vent length. This was the only immature frog that I heard calling, and it had a very soft and high-pitched voice with no detectable vocal pouch. Calling did not seem to serve for spacing of individuals; or, if it did, the distances maintained were small--as little as one foot. However, mature males that were not calling were sometimes found within three inches of one another.

Eggs

Livezey (1950:139) described the eggs of Acris crepitans (from Walker County, Texas) as slightly larger than those of A. gryllus, having a vitellus averaging 1.13 (1.06 to 1.17) mm. in diameter and two gelatinous envelopes (rather than one as in A. gryllus) averaging 2.60 (2.34 to 2.74) mm. and 3.34 (2.98 to 3.70) mm. in diameter. Smith (1956:63) reported an envelope diameter of 2.4 to 3.6 mm. and vitellus of 0.9 to 1.0 mm. in specimens from Kansas. Eggs are laid singly or in small clusters of two to seven (Livezey, loc. cit.; Smith, 1956:89; Smith, 1961:79).

Number of eggs produced per female has been reported on the basis of a few specimens, but no study has yet been made on this subject. Numbers reported in the literature are: over 200 (Smith, 1961:79); about 250 (Smith, 1956:89); 225, 315, and 340 (Livezey, 1950:139-140). In three females that I examined, the counts were 279, 277, and 395. The first count represents eggs laid; the latter two only approximate the number of ovarian eggs in preserved frogs, as the eggs often broke into small pieces upon removal.

Larvae

Tadpoles of A. crepitans have a distinctive black tail-tip. Mouthparts are illustrated and/or keys for identification are presented in Smith (1956:59), Smith (1961:66), and Stebbins (1966:213).

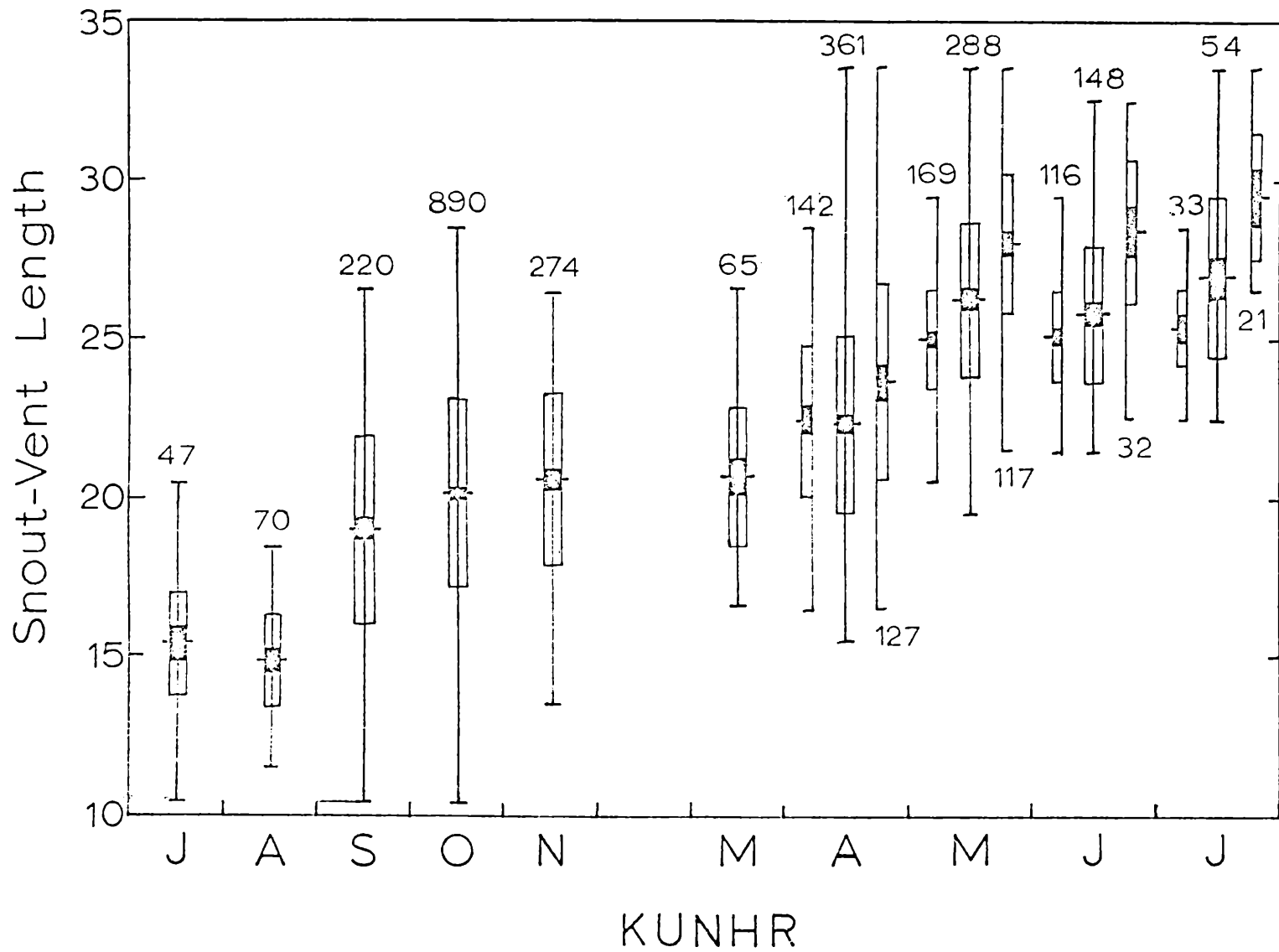
The tadpoles of Acris seem more secretive and solitary than those of most other anurans in northeastern Kansas. Few were seen, and a survey of the literature indicates that little is known about their ecology. Pyburn (1961a:238) reported that in the laboratory hatching usually took place between three and four days after fertilization and that the tadpole stage lasted from 29 days to more than three months.

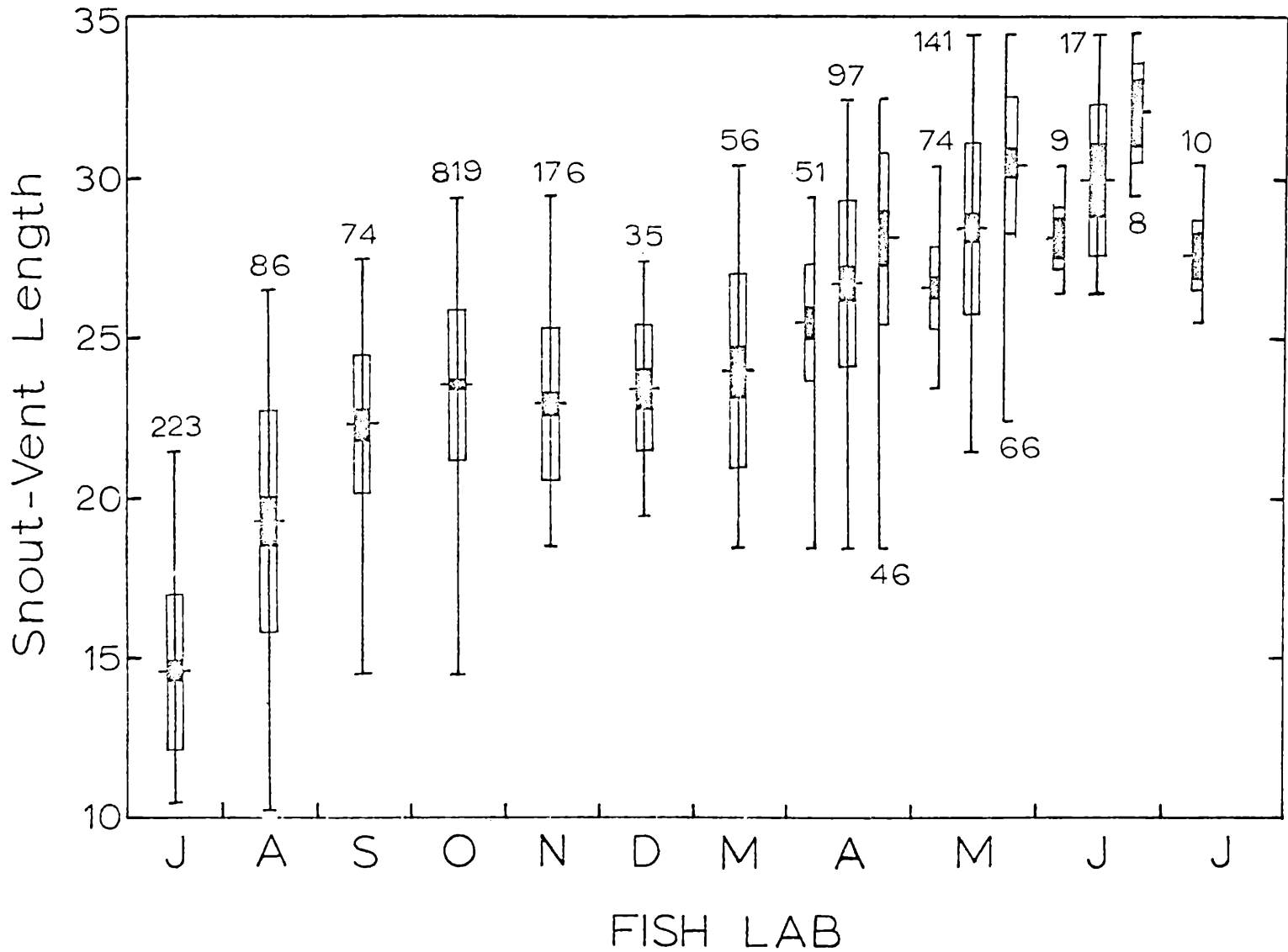
Tadpoles were seen only between July 15 and September 18; but, since metamorphosed young appeared about July 10, tadpoles must have been present at least as early as June 10, and probably in mid-May. Incompletely metamorphosed frogs still retaining tails were observed on September 29. Transformation into frogs takes about two days (Wright and Wright, 1942:227). My data (Table 1) indicate that larval development generally requires five to ten weeks in northeastern Kansas.

Growth Rate

There are two periods of rapid growth in Acris: from July until late September (juvenile period of growth) and from March through the breeding season (adult period of growth). Growth is minimal from October until March, as would be expected owing to scarcity of food and low temperatures. Figure 4 shows the composite growth rates for the entire study period in the Reservation and Fish Lab populations.

Fig. 4.—Growth rate of two populations of Acris crepitans. The KUNHR graph (A) includes the combined samples from the 1961, 1963, 1964, and 1965 year classes. The Fish Lab graph (B) includes the combined samples from the 1963, 1964, and 1965 year classes. Vertical lines indicate range; horizontal lines, the mean; dark bars, two standard errors on either side of the mean; light bars, one standard deviation on each side of the mean; and numbers above or below each line, the number of individuals in each sample. The April-through-July samples are subdivided down to show the above statistics for the entire sample, center; males, left; and females, right. Sex was not ascertained for some adults, especially in April (KUNHR). In September and October a few individuals were captured that were difficult to classify into age groups; they were either extremely large juveniles or small female adults that had lived past the usual life span. None of them were marked and examination of the ovaries revealed only small eggs. Because of the overlap in size and the small number of suspected adults, these individuals were not represented in the figure.





Although the two populations have similar growth patterns, the growth rate and average sizes at any given time differ considerably. In almost every instance the minimum, maximum, and mean size of frogs in the Fish Lab population exceeded those in the Reservation population. The growth rate in millimeters per month also was generally greater at the Fish Lab (Table 3). Factors contributing to these differences are elaborated upon in the "Discussion" section.

TABLE 3.—Mean monthly growth rates of *Acris crepitans* illustrated in Fig. 4. Numbers indicate millimeters of growth per month for the period indicated.

Population	July to Oct.	Oct. to March	March to June	♂	♀	Total
				(Apr. to July) 1.30	(Apr. to June) 1.33	
KUNHR	1.59	0.10	1.71	2.40		(July to July) 0.96
Fish Lab	3.02	0.08	2.00	1.96		(July to June) 1.40

The sizes and growth rates of females exceeded those of males. Since this study was based chiefly on populations of living frogs, sex could not be recognized in most individuals until April. At that time females were, on the average, three millimeters longer than males. Difference in growth rate between the sexes begins at an early age, as indicated in Table 4. The differences in size were slight; but, nevertheless, females were larger than males in all samples.

Spotting on the chin of males sometimes appears as early as October, and tentative allocations as to sex were made whenever possible. These estimates also indicated that females were larger than males at an early age.

TABLE 4.—Lengths of juvenile *Acris crepitans* in three populations, indicating difference in size associated with sex. Sex was determined by dissection of frogs. In each pair the upper figures represent males and the lower figures, females.

Date	Locality	Range (mean)	No. of frogs
7/30/64	Fish Lab	12-18 (14.6)	8
		12-20 (15.7)	25
9/22/65	Fish Lab	20-24 (21.9)	15
		18-27 (23.5)	13
9/25/65	KUNHR	13-19 (15.4)	19
		13-20 (15.9)	20
10/03/65	RET	16-23 (19.2)	20
		17-23 (19.7)	14
10/15/65	Fish Lab	20-25 (23.1)	12
		20-28 (23.4)	10
11/11/64	Fish Lab	22-24 (22.8)	4
		23-27 (25.3)	3

Cricket frogs, because of their high surface-to-volume ratio, can be warmed rapidly in sunlight. This may account in part for their long season of activity. They are seen in the fall later than any other species of frog and are among the first to appear in spring. If slight size differences affect activity, the larger individuals may become inactive early in fall and may not appear until later in spring. If this occurs, error will be introduced into estimates of growth rates, as smaller individuals will be sampled in colder weather. This could explain why the apparent growth rate tapers off suddenly in autumn and increases suddenly in spring. Perhaps there is a differential sexual behavior, which would give the same result, since females are larger. Additional studies are needed to determine

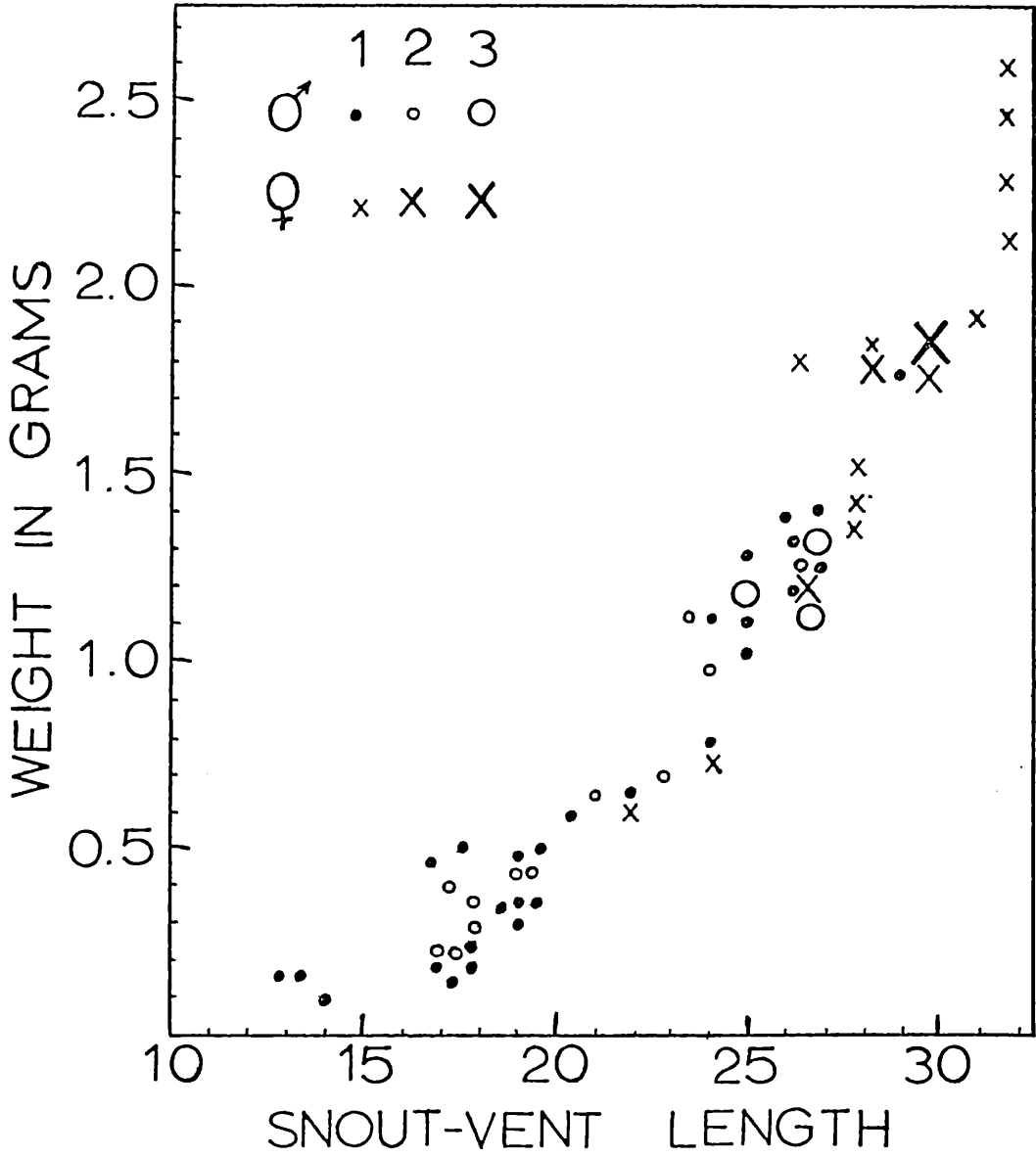
whether there are differences in behavior due to size and/or sex and how extensive these differences are.

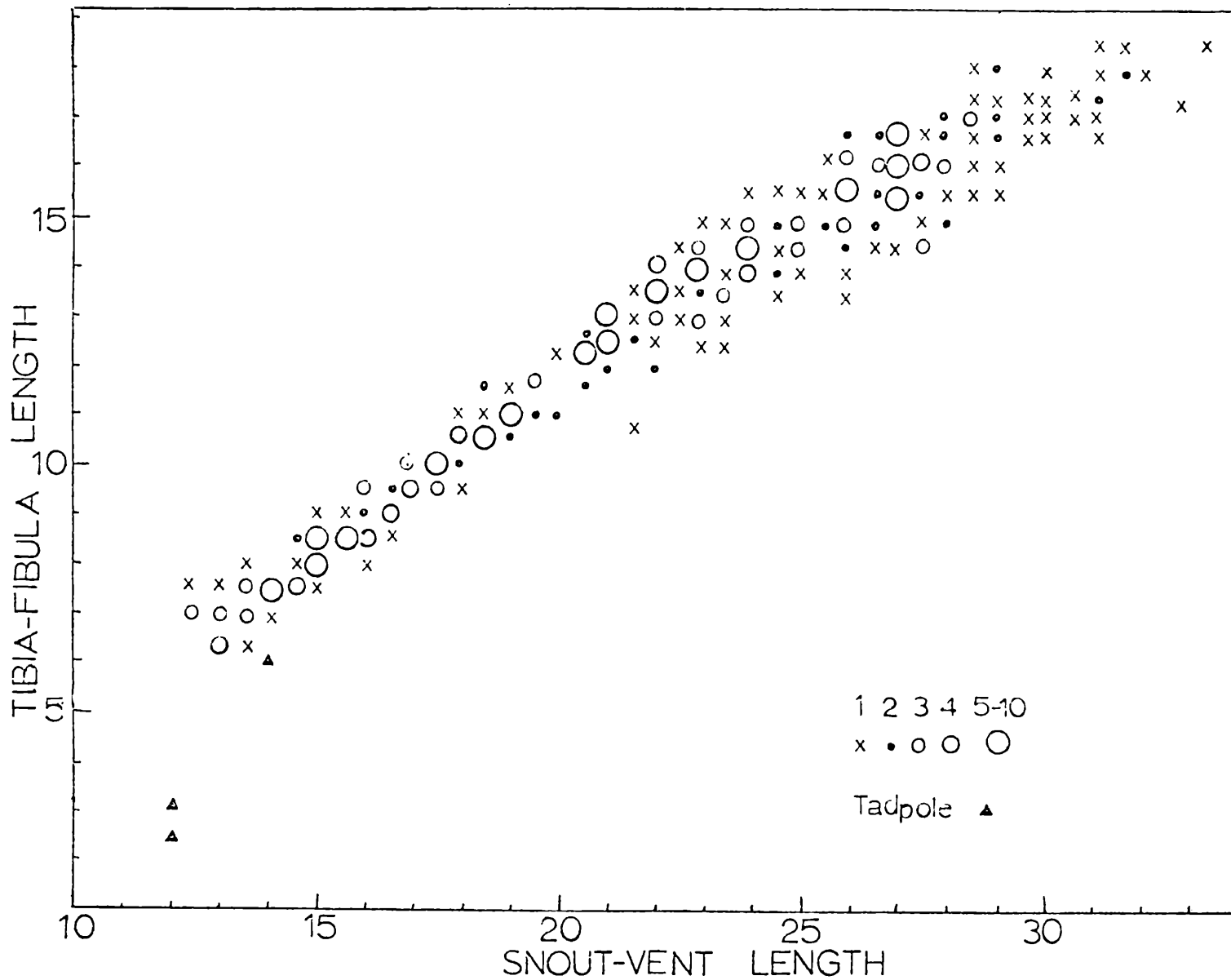
The weight of adult cricket frogs is usually between 1.0 and 2.5 grams. Females tend to be larger, and they also are heavier, especially when they are gravid. Figure 5 shows length and weight relationships for a group of Acris varying in length from 13 to 32 mm. As frogs grow larger, the range of weight for a particular length increases, as the bulk increases proportionately much faster than length.

The relationship between tibia length and snout-vent length is a curvilinear one reflecting allometric growth (Fig.6). Tibia length as a percentage of snout-vent length increases until frogs reach 24 mm., then decreases as the line curves to the right. Mean values increase from 52.7 per cent at 13 mm. to 60.7 per cent at 24 mm. and then decrease to 54.5 per cent at 33.5 mm. Large cricket frogs of the same length vary over a range of 2.5 mm. in length of the tibia, while the small ones show a variation of 1.5 mm. There is no difference in this character between males and females of the same size. However, since females are larger than males, these values will most likely differ in any sample. Ratios involving characteristics which show allometric growth are often used in comparing populations of anurans, especially in studies of geographical variation, as employed by Smith (1961). Differences in growth rate such as those found in the two populations here reported upon result in quite different ratios for any two samples taken at the same time, even though in this instance the two populations involved are only seven miles apart. Unless sizes, sex ratio, and date of collection are given for each sample, or unless samples are identical in size, such comparisons are useless. Large

Fig. 5.—Length versus weight in Acris crepitans.

Fig. 6.—Snout-vent length versus tibia length (left) in 336 Acris crepitans from northeastern Kansas. Δ - tadpoles; x - one individual; circles (increasing in size) represent 2, 3, 4, and 5 to 10 individuals, respectively.





samples including all sizes of frogs must be utilized before comparison of populations can have significance.

POPULATION STRUCTURE

Sex Ratio

Determinations of sex ratio have been made in only a few species of anurans. Turner (1960:259) reviewed much of the literature on the genus Rana and stated that most species seem to have a preponderance of females. Jameson (1955:359) found males to be slightly more numerous than females in Syrrophus marnocki but attributed this to difficulties in sexing and to differences in activity between the sexes. In adult frogs males are certainly more conspicuous because of their calling, and undistorted sex ratios are difficult to obtain. Little information is available concerning sex ratios of tadpoles and young frogs. Tadpoles and juveniles of Acris are easy to sex if killed and examined under a dissecting microscope; the testes are well formed and black. However, in my study, few tadpoles were found. The sex ratio in newly metamorphosed Acris was found to be about four females per male, but in frogs three months old and older males usually were predominant (Table 5). From September until the following July, males averaged between 47 and 78 per cent of samples. The overall percentage for males was 57.6. This figure is highly significant in its deviation from the expected 1:1 ratio, as were most of the monthly samples. Whether or not this difference is real or the result of differences in behavior of the sexes is unknown. Pyburn (1958:340) obtained a ratio near 1:1 in a sample of 152 Acris from Texas in April, 1954. He obtained more males than females at night

TABLE 5.—Sex ratios of Acris crepitans in northeastern Kansas. Figures represent the totals of several samples from populations near Lawrence. Frogs in each sample are approximately the same age.

Month	Number in sample Males:Females	Percentage of males
July	11:50	16.4
Sept.	34:33	50.7
Oct.	160:181	46.9
Nov.	4:3	57.2
March	75:25	75.0
April	310:258	54.5
May	344:260	58.0
June	241:70	77.5
July	48:24	66.7

but obtained more females than males on the following morning, and he stated that females probably moved away from the water at night. Almost all of my own samples were obtained during the day, and I caught the frogs by moving slowly along the edge of ponds and streams. Most frogs were seen and captured only after they had hopped in an attempt to escape, but many were captured that had not yet moved as I approached. No differences in behavior were noticed. Females may tend to remain motionless relying on their cryptic coloration to go unnoticed, but this, to me, seems unlikely. Another possibility, and a more likely one, is that females, because of their larger size, may be more sluggish and more easily seen and, hence, are preyed upon more heavily than males. Thus, the percentage of males may actually

increase as time elapses.

Estimation of Post-Metamorphic Density and Survival

Before discussing the methods used in determining estimates of density and survival in the populations that were studied, some of the peculiar traits of this species in northeastern Kansas affecting those estimates should be reviewed. Some of these characteristics have been discussed heretofore, while others will be presented subsequently in more detail. These traits are:

1. A tendency toward linear concentration of the population in its riparian habitat with seasonal expansion and contraction of the habitat correlated with changing weather conditions.
2. Populations that are usually rather sedentary but have explosive dispersals in wet weather.
3. Tendency of most frogs to burrow into the ground in the colder months of the year, leaving few individuals exposed to capture.
4. A high and fairly steady mortality rate resulting in almost complete turnover of populations every year.
5. Limited annual breeding season (May through July) with most adults dying soon after appearance of newly metamorphosed young.
6. Mortality and recruitment cause population composition to shift continuously during summer. Discrete size and age groups occur only from July until September or October, when small, surviving adults are difficult to distinguish from large juveniles that metamorphosed early in July.
7. Appearance of young over a period of only about three months results in populations with a relatively stable composition during

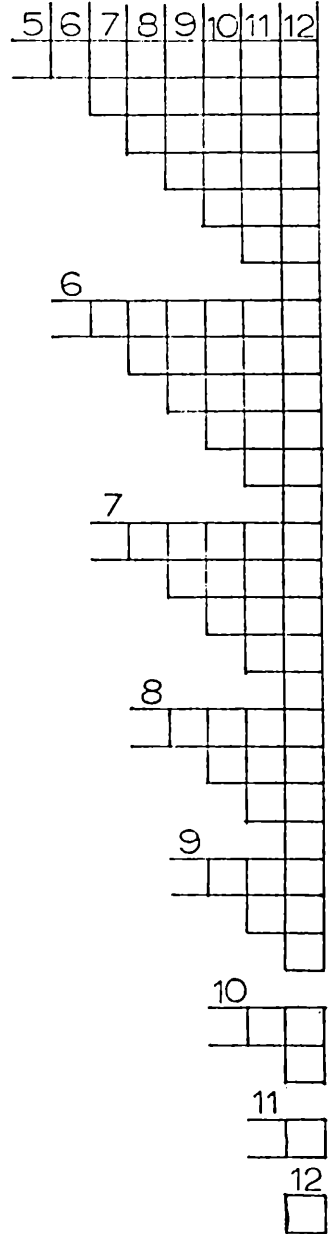
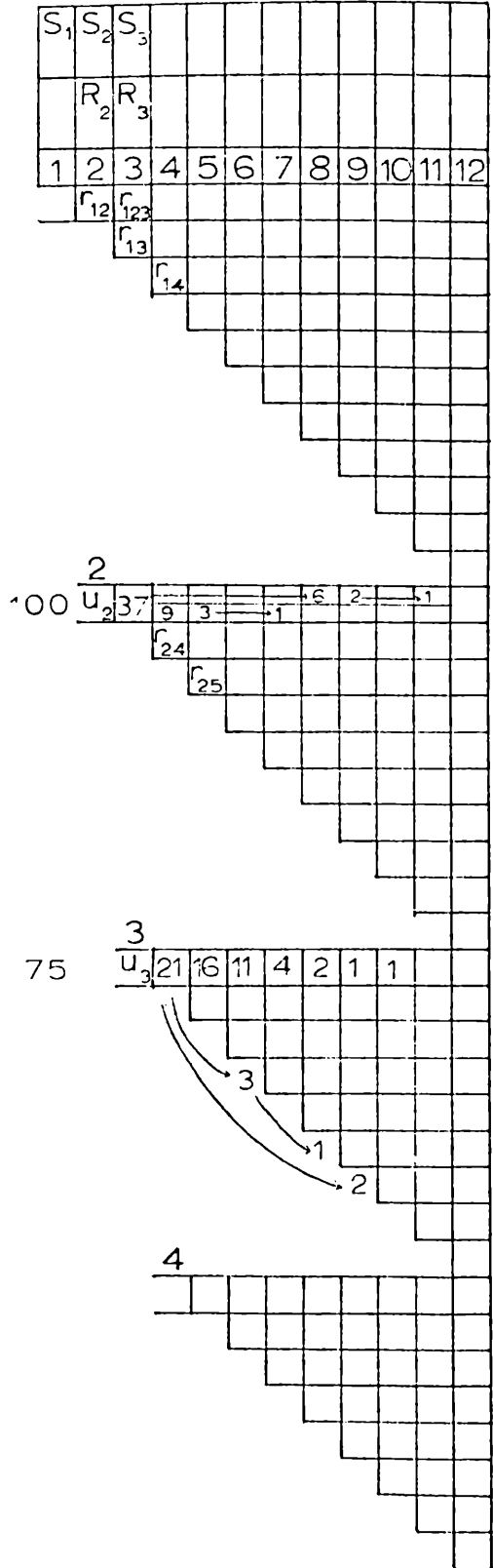
the remaining nine months.

8. Large numbers of individuals present in the populations during most of the year, making marking of the population a formidable task. An entire population usually cannot be sampled in one day.

Data concerning number of individuals in the populations were recorded on trellis diagrams that were designed to keep accurate records of recapture data for each individual (Table 6). From this diagram one can calculate density by several methods.

In the diagram, the number of new (unmarked) individuals is recorded in the first space of the respective trellis for each sampling period. Thus, in sample 1, the number of individuals captured is recorded in the first space of the upper trellis and S_1 ; in sample 2, new individuals are recorded in u_2 of the second trellis, and recaptures are recorded under r_{12} of the first trellis and R_2 . This system is followed for each successive sampling period. Each horizontal line on each trellis is used to record successive recaptures from the first of the sampling periods through the last. Hence, the number of individuals captured in every sample from the first to the twelfth would fill the top row. Those individuals first recaptured in the third or fourth sampling period are recorded under r_{13} or r_{14} respectively. Since individuals are not always captured in successive samples, but may "skip" a period or two, the data may be recorded in one of two ways: (1) each line may be subdivided and arrows drawn through the squares representing samples in which no recaptures were made; or (2) the number of individuals may be entered below the column for the period in which they were recaptured and an

TABLE 6.—Trellis diagram used for recording capture-recapture data. Numbers across top of diagram and above first square of each trellis represent sampling periods. 'S' denotes total sample for each period; 'R', total recaptures in each sampling period; recapture data are indicated by 'r' and subscripts. The letter 'u' and subscript refer to new or unmarked individuals captured in each sampling period. Subscripts refer to sampling period or periods involved. See text for explanation of numbers in trellises 2 and 3.



arrow drawn from the square that designates their last time of recapture. These methods are illustrated in trellises 2 and 3.

Calculations now can be made using a number of different methods. These figures can be applied to the trellis diagram devised by Dowdeswell, Fisher, and Ford (1940); or, captures and recaptures may be accumulated and the Schnabel method used (see Smith, 1966:653). The Lincoln Index or Modified Lincoln Index (which reduces positive bias) may be calculated by the following formulae:

$$\frac{S_1 \times S_2}{R_2} \quad \text{and} \quad \frac{S_1 \times (S_2 + 1)}{(R_2 + 1)} \quad \text{These formulae also may be applied to}$$

any subgroup within a trellis. The Hayne method involving percentage of recaptures and accumulative number marked also is easy to calculate from the diagram (see Hayne, 1940).

The equation developed by Leslie and Chitty (1951) for calculation of survival rate (P) can be set up from Table 6 by means of the following formula: $P = \frac{r_{12} R_3 + u_2 r_{13}}{r_{23} S_1}$ Subscripts may be changed

and the same formula applied on any sample from a later period.

This method was generally unsatisfactory in my study, as erroneous results often were obtained (i.e., $P = > 1.00$).

The greatest advantage of the method of recording data outlined above, aside from the ease of manipulating data for different purposes, is that the minimum living population (MLP) can be calculated for any date. The MLP is the minimum number of individuals known to be alive at any one time, and can be calculated because the approximate age of all frogs is known. It is based on the number of individuals captured in any sample plus all other individuals captured in later

samples. The MLP for the last sample (S_{12}) is simply S_{12} . The MLP for Sample 11 is: $MLP_{11} = S_{11} + S_{12} - r_{11,12}$. Therefore, MLP_{10} may be expressed as: $MLP_{10} = S_{10} - r_{10\dots n} + MLP_{11}$. And the MLP for the x^{th} sample is expressed as: $MLP_x = S_x - r_{x, x+1, x+2, \dots, x+n} + MLP_{x+1}$. These figures, added in reverse order, equal the total number of individuals marked in any population. The MLP, then, serves as a basis for comparing other estimates of population density; if they are lower than the MLP, they are known to be too low (unless there has been uncompensated immigration); if higher, they may be more difficult to interpret. Since the MLP is based upon number of individuals captured, it reflects degree of activity of the frogs as well as effort of the collector (s). Only when almost all of the population has been marked will the MLP approach the actual number in the population.

Capture-recapture data and estimates of the number of frogs in each population are given in Table 7. Several methods were used to estimate the size of the populations throughout each season. Some of the basic assumptions regarding estimations of populations by most of these methods are: (1) that mortality, recruitment, emigration and immigration are negligible; (2) that mortality and emigration are equal in marked and unmarked groups; (3) that the population is essentially stationary; (4) that all members of the population have an equal chance of being captured. In my study, mortality and/or emigration definitely were significant factors influencing the results obtained over the long periods of time involved. Even from one sampling period to the next, the effects of mortality and/or emigration often could be observed. Appearance of young frogs in the population

TABLE 7.—Capture-recapture data and various estimates of population density for the University of Kansas Natural History Reservation (A) and the University of Kansas Fish Laboratory (B) populations. The mean date was recorded for each sample when sampling periods included from one to twelve days. The number of recaptured frogs on each date are from all preceding samples. "Total percentage recaptured of group marked" indicates total recaptured at all subsequent dates. Estimates based on Lincoln Index and Schnabel method are placed in the row corresponding to the first sample upon which these estimates are based. Calculations were not recorded where data were inadequate or estimates appeared unreasonable (i.e., extremely higher or lower than the M.L.P.). See text for explanation of other columns. Asterisks indicate samples in which fewer frogs were captured than expected. Primary explanation is as follows: *rain; **rain and low temperature, ***low temperature.

A. KUNHR

Date	Number marked	Number recaptured	Total % recap. of group mkd.	Minimum Living Population	Lincoln Index (Modified)	Schnabel Method	Density (frogs/foot)	Population estimate based on density	Hayne Method	Per cent of fall catch recaptured in spring
Pond										
9/05/63	313	--	6.4	1,260	47,889 (32,030)	47,576	--	--	1,450-1,700	2.17 (7,697)
10/01/63	304	2	40.2	956	2,430 (2,307)	77,042	1.780	1,105		
10/06/63	112(-4) ^a	19	36.1	774	545	1,592	--	--		
10/08/63	158(-10)	148	?	685	576	924	1.240	772		
10/15/63	135	250	?	633	--	943	1.565	970		
*10/22/63	65	63	?	311	--	924	0.532	330		
***11/10/63	34	47	2.9	230	359	1,000	0.432	267		
4/10/64	67	19	10.4	170	163		0.258	360		
4/18/64	10	9	0	105	--		--	--		
* 4/25/64	4	9	50.0	92	172 (88)		0.170	238		
6/06/64	42	19	7.1	86	147 (112)		0.155	217		
* 6/12/64	5	3	0	41	--		0.080	112		
7/06/64	8	7	12.5	27	64 (36)		0.066	92		
7/16/64	7	6	--	13			--	--		

(continued)

A. KUNHR (continued)

Date	Number marked	Number recaptured	Total % recap. of group mkd.	Minimum Living Population	Lincoln Index (Modified)	Schnabel Method	Density (frogs/foot)	Population estimate based on density	Hayne Method	Per cent of fall catch recaptured in spring
Stream										
9/29/64	50	--	68.0	256	227 (220)	177	--	--	375	6.64 (6,406)
10/06/64	78	22	38.4	240	413 (395)	232	--	--	--	
10/13/64	73	35	41.1	186	234 (227)	217	--	--	--	
10/20/64	55	55	7.3	120	536 (440)	297	--	--	--	
Pond										
** 3/15/65	35	0	48.6	423	336	437	0.350	490	465-585	
4/18/65	69	10	47.8	411	562 (500)	521	0.132	185		
4/29/65	50	15	40.0	367	172	590	0.285	399		
5/09/65	49	18	34.7	318	265	586	0.187	262		
5/21/65	75	59	18.7	263	--	769	0.116	163(278) ^b		
5/31/65	80	5	13.8	163	526 (470)	750	0.109	153		
6/10/65	39	37	2.6	91	390 (214)		0.066	92		
* 7/13/65	10	10	--	20	-- --		0.014	20		

(continued)

A. KUNHR (continued)

Date	Number marked	Number recaptured	Total % recap. of group mkd.	Minimum Living Population	Lincoln Index (Modified)	Schnabel Method	Density (frogs/foot)	Population estimate based on density	Hayne Method	Per cent of fall catch recaptured in spring
Stream										
10/07/65	100	--	56.0	553	482	382	--	--	900	5.32 (1,812)
10/12/65	145	38	20.7	509	1,378 (1,200)	458	--	--		
10/19/65	51	21	27.4	383	1,194 (1,000)	578	--	--		
10/22/65 ^c	30	--	0	--	315		1.200	1,680		
10/26/65	112	45	25.9	335	468 (453)	580	--	--		
11/02/65	73	51	?	216			--	--		
11/19/65 ^c	19	2	0	--			0.210	294		
4/24/66	72	21	--	93	-- --		--	--		

^aNot marked

^bAll areas in which no frogs captured were eliminated

^cPond

B. FISH LAB

Date	Number marked	Number recaptured	Total % recap. of group mkd.	Minimum Living Population	Lincoln Index (Modified)	Schnabel Method	Density (frogs/foot)	Population estimate based on density		Hayne Method	Per cent of fall catch recaptured in spring
								Reservoir	Ponds		
Ponds											
** 3/15/65	19	--	47.4	115	247 (202)				104	165	29.9 ^a (228)
*** 3/31/65	0	1	--	101				--			
*** 4/14/65	48	4	31.3	100	154 (147)	182		106			
** 4/26/65	0	1	--	69				--			
5/08/65	33	20	9.1	68	55 (50)	120		86			
** 5/28/65	2	4	0	19		111		44			
* 6/07/65	4	1	0	14				22			
6/26/65	4	0	0	9				18			
* 7/28/65	4	0	0	5				18			
8/03/65	1	0	--	1				9			

(continued)

B. FISH LAB (continued)

Date	Number marked	Number recaptured	Total % of recap. of group mkd.	Minimum Living Population	Lincoln Index (Modified)	Schnabel Method	Density (frogs/foot)	Population estimate based on density		Hayne Method	Per cent of fall catch recaptured in spring
								Reservoir	Ponds		
Reservoir											
*** 4/01/65	11	--	0	75			0.044	52			
4/19/65	10	0	0	64			0.034	40			
** 4/26/65	7	0	14.3	54			0.010	34			
5/10/65	41	1	2.4	47	294 (150)		0.043	51			
** 5/28/65	1	1	0	6	82 (62)		--	--			
* 6/07/65	1	0	0	5			--	--			
* 7/28/65	4	0	--	4			0.003	4			
Reservoir											
7/15 to 8/26/65	205	--	6.3	887	4,450 (3,390)	4,237	0.960	1,116		875	6.42 (1,043)
8/03/65	11 ^b								825		
9/22/65	28 ^c	--	--	695	--	--					
9/28/65	62	3	72.5	667	2,195 (2,095)	1,039	0.285	331			
10/06/65	38	19	79.0	649	750 (705)	1,723	0.242	281			
10/08/65	25 ^b								275		

(continued)

B. FISH LAB (continued)

Date	Number marked	Number recaptured	Total % recap. of group mkd.	Minimum Living Population	Lincoln Index (Modified)	Schnabel Method	Density (frogs/foot)	Population estimate based on density		Hayne Method	Per cent of fall catch recaptured in spring
								Reservoir	Ponds		
Reservoir (continued)											
10/12/65	281	41	62.6	633	680 (675)	866	0.284	330			
10/15/65	22 ^c	--	--	514	--	--					
10/27/65	224	214	28.6	492	315 (312)	707	0.403	469			
11/21/65	13	77	7.7	163	39 (26)	677	0.078	90			
12/07/65	2	24	0	86	--	606	0.024	28			
*12/11/65	8 ^b								40		
3/12/66	1	39	0	66	--	596	0.032	37			
4/07/66	0	7 ^d	--	30	--	598	0.001	1	70		
4/16/66	0	2 ^b							20		
5/07/66	11	13	--	24	--	--	0.026	30			

^a Per cent of March and April catch recaptured in May and thereafter

^b Captured at ponds

^c Removed from population

^d Six of these seven were captured at ponds

occurred only from July to September, and these individuals usually were detectable by their small size. Thus, natality (or recruitment) may have influenced estimates of population size only for a short time, whereas other factors influenced estimates of population size throughout the year.

Perhaps the greatest problem encountered in this study was that of large numbers of frogs and mobility of the populations. The extremely large populations at certain times often made sampling of the total habitat impossible within a day's time. Thus, with only a small portion of the population sampled each day, frogs that moved from area to area might not be captured during the entire sampling period. Also, because all of the available habitat (pond and stream at the Reservation; reservoir and ponds at the Fish Lab) could not be sampled adequately in a short time, movement of frogs between these areas undoubtedly affected the results.

Changing weather conditions greatly affected activity and movements and in this way influenced the number of frogs captured at any one time. Rains and cold weather had the greatest influence on sample-size. Usually, when collections were made within two days following rain, the number of frogs caught was lower than in dry periods. Temperature, relative humidity, and cloudiness also influenced dispersion and activity. Whenever clouds provided cover and/or when humidity was high, frogs seemingly remained dispersed following rains, and relatively few were captured. However, when rains were followed by clear, dry, warm weather, more frogs were captured, indicating an early return to the water's edge. The amount of time spent collecting cricket frogs, the number of persons of

varying skill and experience who helped, and the precise weather conditions were not recorded for all of the samples, statistical comparisons cannot be made.

Seasonal changes in activity, when compared with climatic records reported by Visher (1954), showed that cessation and beginning of activity in autumn and spring were correlated with normal average daily minimum and maximum temperatures of 32° and 56° F. Weather conditions thus affected estimates of density (frogs per linear foot of shore line) more than they affected estimates made by other methods, since the ratio of marked to unmarked frogs presumably remained essentially the same regardless of the number of frogs captured. However, in small samples each frog represents a large percentage of the sample, thus increasing experimental error.

The Schnabel method was found to be almost totally unacceptable in this study. Since this method does not take mortality into consideration and is based upon cumulative number marked, population estimates sometimes increased as the populations actually decreased. Although the total number of marked frogs increased steadily, the accumulated number of recaptures tended to be disproportionately low, causing population estimates to be extremely high. To be reliable this method must be used with rather stable populations. In Acris, even weekly samples seemed to yield poor results. Perhaps if this method were applied to daily samples within an extremely short period of time, it would be more accurate.

The Lincoln Index also tends to overestimate the population, but its major advantage is that it can be used on any two samples and it

is not necessarily based upon cumulative numbers. The Modified Lincoln Index tends to reduce positive bias, and in this way it is probably more realistic. The Lincoln Index also was calculated using the actual number of marked individuals known to be alive during the second sampling period (based upon their capture at a subsequent time) rather than the number recaptured. In almost every instance the population estimate was below the MLP for that date.

Density was estimated as number of frogs per foot of shore line of the pond on which they were captured. For the ponds at the Fish Lab, density was estimated as frogs per pond. The total number of frogs in the population was then calculated on the assumption that distribution was even around the margin of the pond and that every frog was captured in the area(s) being sampled. Distribution of frogs around the ponds was uneven; but the percentage of frogs captured in each area in each sample was highly variable, making it difficult, in most instances, to establish trends. Whenever only part of a pond was worked in a sampling period (usually areas of greater density), the number of frogs that escaped capture served to equalize the number of frogs occurring in areas of lesser density. Acceptable estimates of density (\geq MLP) for most samples indicate that this assumption was fairly reasonable. Attempts were made to calculate density on the basis of uneven distribution, and almost without exception these estimates were below the MLP for the population at the time they were made. In many instances the entire pond was sampled and the resulting figure of population density was based upon an actual count of the frogs captured. These estimates, as expected,

tended to be lower than the MLP since invariably some frogs escaped detection in each sampling period.

The total percentage of recaptures (at all subsequent times) of each group of frogs marked was recorded in Table 7 in order to estimate the success obtained in recapturing each group. Percentage of frogs recaptured from each group ranged from 0 to 79 with an average of 25.5. Percentages are low toward the end of each group of samples representing a yearly population, not only because mortality may have increased with increasing activity but also because fewer subsequent samples were taken in which individuals could be recaptured. Thus, the first sample of young individuals each year has the most time remaining in which recaptures can be made. However, the first sample, if taken before mid-September, has a very low percentage of recaptures. This indicates one of two possibilities: an extremely large population (as evidenced by the Lincoln Index and Schnabel method for this period), or an unusually high mortality rate in small frogs caused either by natural causes and/or by handling and toe-clipping. If the former were true, estimates of density would be much higher, since more frogs would have been captured per linear foot of shore line. The latter possibility appears to be the most likely for the following reasons: (1) Small, young frogs are more susceptible to desiccation than larger individuals because of a higher surface-to-volume ratio. (2) Increased density at the time of metamorphosis may have attracted predators that normally feed on a wider variety of species. (3) The young of most predators appear at approximately the same season, resulting in heavier predation on small frogs. (4) Greater density at the time of

metamorphosis may enhance the spread of disease. (5) Cricket frogs tend to jerk violently when held in an attempt to escape. Injuries were noticed occasionally, and in many instances these frogs were not recaptured. It is quite likely that small frogs received more fatal injuries due to handling than did large frogs. (6) Toe-clipping alone may have caused an increase in mortality rate, or pathogenic organisms may have been spread through the population by the scissors.

Of the above possibilities, the first three are probably more important in accounting for the rapid disappearance of young frogs in late summer and early autumn. Although most metamorphosis occurred in July and August, few frogs were captured at this time. Most field work in July was concerned with study of adults rather than juveniles; vegetation became dense, especially at the Reservation pond, causing parts of the pond to become inaccessible and allowing more frogs to escape detection; and increased rainfall, high temperatures, and the usual swarms of arthropod pests resulted in decreasing efficiency in collecting. The populations at this time undoubtedly were at their greatest density, and mortality rates also may have been greater. By September, more favorable conditions for collecting revealed what was believed to be the "tail-end" of a trend in high mortality rate. Desiccation is believed to be the major cause of the high mortality rate in young frogs because of the climatic conditions in the first three months of their life on land. Average rainfall per month from July through September is more than two inches; relative humidity is usually low (47 to 69 per cent); and daytime high temperatures usually are above 80° F. and often are above 90° F. The combination of frequent rains (which allow dispersal), high temperatures and low

relative humidity are extremely dangerous to small frogs. Numerous species of predators are not only active at all hours during summer months, but they also have reached population peaks with the appearance of their young at this time. Intensified predation is influenced not only by large numbers of prey and predators, but also by some predators which may be feeding their young.

Very few dead or dying frogs were found throughout this study, indicating that disease and/or injury were minor causes of mortality. Most of the dead frogs found were partially eaten, making it even more difficult to ascertain the cause of death.

Few recaptures were obtained from the samples of 11/10/63 (KUNHR) and 11/21/65 to 12/7/65 (Fish Lab), suggesting that few of the frogs still active in late fall are destined to survive the winter. However, the total percentages for all frogs marked in autumn and recaptured in spring are even lower, indicating that winter weather contributes appreciably to mortality. These percentages were used to estimate the population in autumn, assuming that the number of unmarked individuals captured in spring represents the same percentage of the individuals living in autumn as is found among the marked frogs. Thus, $\frac{\text{Number unmarked frogs captured in spring}}{\text{Percentage recaptures from autumn}} + \text{total marked in autumn} = \text{total living in autumn}$. From March to July the importance of predators as a factor in mortality increases, because frogs are increasingly exposed to more predators as activity increases and because their larger size enables them to survive under climatic conditions that are more detrimental to smaller frogs. The role of natural death in post-reproductive Acris is not known.

Comparison of the methods used in Table 7 generally indicates two

tendencies: (1) the Lincoln Index, Schnabel Method, and percentage of autumn catch recaptured in spring are generally high; and (2) the MLP, density method, and Hayne Method are generally low.

Regardless of the method used to calculate population density, the reduction in number of individuals from one month to the next reveals a "type 2" survivorship curve for this species. Approximately 50 per cent of the frogs alive in early September die before mid-October. Almost 95 per cent do not survive winter, and the survivors are reduced even more as the breeding season progresses. Less than one tenth of one per cent may live into the following September or October. Bayless (in litt.) reported that a few Acris crepitans in southern Louisiana live through two breeding seasons.

Since widely disparate figures were obtained with the different methods utilized, a few remarks about each year class may clarify some of the reasons for these discrepancies.

University of Kansas Natural History Reservation:

1963: Extremely high estimates from the Lincoln Index and Schnabel Method in the first few samples result from the low number of recaptures. Only areas 1 through 5 (on the six-foot contour line of Fig. 1) were sampled in the fall. Areas 6 through 8 were sampled for the first time on April 10, 1964. The high estimates obtained by the Lincoln Index and Schnabel Method for the previous sampling period result from the large number of new individuals captured in previously unsampled areas. Since only about one half of the pond was studied this year, the various population estimates apply only to part of the pond. The estimates based on density and the Hayne Method seem most reliable for the population of the entire pond.

1964: The first four estimates refer only to frogs living in the stream within 500 feet of the pond; 256 individuals were marked there, but probably at least 400 were present in the area when the first sample was taken. All sampling in spring was done around the pond. Only the estimate by the Lincoln Index seems unreliable for the number of frogs in the pond in early spring. All others seem relatively consistent (423 to 490). The last two estimates by the Lincoln Index and the last four by the Schnabel Method seem unreasonably high. On May 31, only areas 8 to 2 were sampled. Few frogs had been marked previously on the back side of the pond, thereby favoring new frogs over recaptures. Therefore the Lincoln Index was not calculated for the previous sampling period. This influx of newly marked frogs also accounts for the high estimates determined by the Schnabel Method in the last two instances. Nearly every estimate based on density was below the MLP, indicating low activity or low success in finding and capturing the frogs present when each sample was taken. On August 27, seventy frogs were captured in area 5. All were juveniles, none of which were subsequently recaptured.

1965: Sampling was primarily along the stream for a distance of 600 feet. Two small samples taken in the pond were not recorded in the MLP but were used to make estimates of density. Population estimates based on density were not calculated for samples from along the stream because they would have been almost identical to sample size in nearly every instance. Estimates obtained by the Modified Lincoln Index are probably most reliable for the population inhabiting the stream. Since sampling began in October and terminated in April, the MLP was low.

University of Kansas Fish Laboratory:

1964: Sampling was done at the ponds and the reservoir. More frogs were captured at the ponds than at the reservoir, but recaptures were scarce in both situations, making estimates of the population extremely difficult. Density at the ponds was calculated by multiplying the number of frogs captured by the number of ponds containing water and then dividing by the number of ponds in which frogs were captured. Hence, it was assumed that frogs were distributed evenly among the ponds. All estimates but the first by this method were slightly above the MLP. All other estimates for the first sampling period seemed reasonable, since they were somewhat higher than the MLP. No suitable estimates were obtained at the reservoir. The last estimate at the reservoir was based upon four males which were calling at night. A sample of 29 frogs obtained the following morning included only juveniles. It seems that more adult frogs were inhabiting the ponds than were inhabiting the reservoir.

1965: This population was sampled perhaps more extensively than any other. In the majority of the samples, recaptures comprised more than 50 per cent; by early November, more than 85 per cent of each sample were recaptures. Judging from these results, I am inclined to accept the MLP calculated as being close to the actual number of individuals in the population. In the first sample, I caught about three-fourths of the individuals seen, so the first estimate should be at least 1200. Almost every estimate based upon density was lower than the MLP and, hence, unacceptable. The reservoir was partially drained in early April, and many of the frogs moved to the ponds. In May, some of them returned to the reservoir, and it appears that some

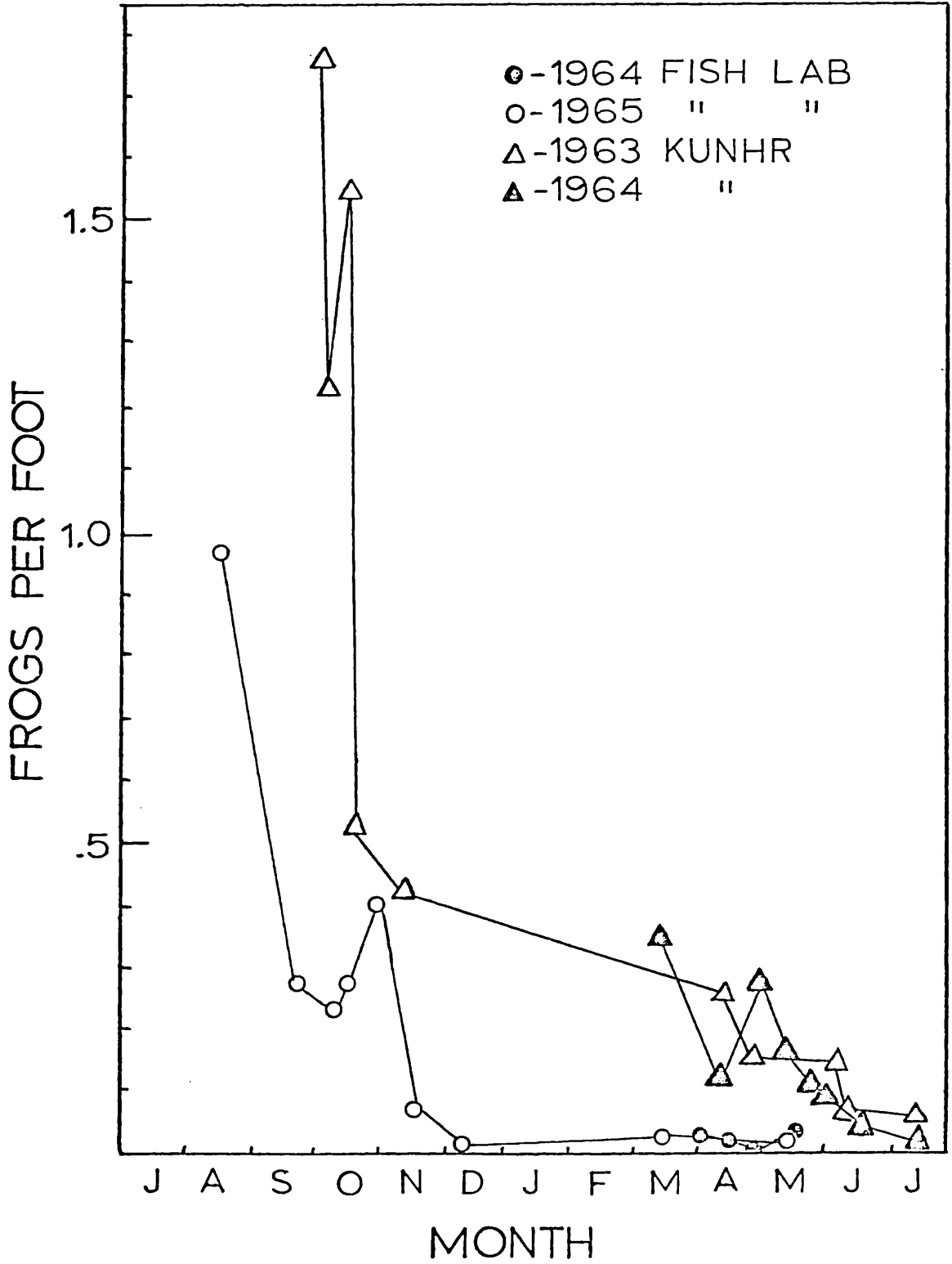
of the unmarked frogs in the ponds may have migrated to the reservoir. A few samples were taken from the ponds and estimates based upon density at the ponds were made from these.

Comparison of the population estimates at both localities indicates that the Reservation population is considerably larger than the Fish Lab population. The Reservation pond is slightly larger than the Fish Lab reservoir; and density, estimated as frogs per foot of shore line, is also greater (Fig. 7). This suggests that the habitat at the Reservation is more favorable than at the Fish Lab. Perhaps in the forest habitat at the Reservation, frogs can move farther from the water's edge in search of food and cover while remaining well protected from the sun and from predators; and the several hydroseral stages present there create ecological diversity with greater density of potential food items. In contrast, the completely open situation at the Fish Lab affords less protection from predators or from desiccation if frogs wander away from water. There is more bare ground and probably less availability of total food items or heavier predation than at the Reservation. The effect of bass (in the reservoir) and catfish (in the ponds) on the frog population is not known. Predation on tadpoles and frogs may explain, in part, the lower density at the Fish Lab.

Reproductive Potential

Estimates of the number of frogs in each breeding population may serve as an additional guide for determining density of the following year's population. Values obtained for the sex ratio (42.4 per cent overall average for females [see Table 5]) and number of eggs laid

Fig. 7.—Estimates of density in frogs per foot of shore line at the University of Kansas Natural History Reservation pond and the University of Kansas Fish Laboratory reservoir.



per female (200 to 275) were used in calculating the reproductive potential (Table 8). At the Fish Lab the estimate for 1966 is

TABLE 8.—Estimated reproductive potential for Acris crepitans in two populations in northeastern Kansas. See text for explanation.

	Year	Approx. no. in pop. in May	Approx. no. of females	Estimated no. eggs laid (200-275 per female)	
KUNHR Pond	1964	90	38	7,600 - 10,450	
	1965	318	135	27,000 - 37,025	
	Stream	1966	100	42	8,400 - 11,550
Fish Lab Ponds	1965	68	29	5,800 - 7,975	
	Reservoir	1965	47	20	4,000 - 5,500
	1966	24	10	2,000 - 2,750	

probably much lower than it should be. Further sampling might have indicated presence of a larger population. The number of frogs found in the ponds seemed to be about the same as in 1965. The population estimates in Table 8 are based upon the MLP in early May and are probably conservative. Estimates of eggs laid per female also may be conservative. However, if most spawning occurs late in May or June, there would be fewer females; and these estimates might approximate the reproductive potential for the two populations. Mortality probably amounts to more than 50 per cent between the time of spawning and early September, unless the populations are much larger than collecting indicates.

Polymorphism and Its Significance

A notable aspect of the population ecology of Acris is polymorphism with respect to color of the vertebral stripe. In some individuals, a middorsal area is green, rust-colored, some shade of brown, or gray; but in most frogs this middorsal area is indistinguishable from the background color, which is some shade of brown, gray, olive, or nearly black. Dark, irregular-shaped patches are present on the back, and there are bronze-colored tubercles and a dark interocular triangle. Small spots or larger blotches of green may be present. The background color and green spots seem to be controlled by chromatophores and may change considerably under different conditions. Frogs on a dark substrate are generally darker than the same individuals on a light substrate. Bayless (in litt.) stated that the color of Acris (especially A. crepitans) in southeastern Louisiana depends on sex and breeding activity of the individual.

The green vertebral stripe is almost always noticeable from a distance, being fairly wide and running almost the entire length of the body and including a rostral spot. In some frogs the stripe is short and narrow and may be absent on the head. The brown or rusty stripe, however, is highly variable and sometimes divided into two small brown spots. At times it is barely distinguishable from the ground color, especially if it is light brown and narrow. A gray stripe is rarely present; other individuals have what appears to be a faint grayish-brown area (not a stripe) slightly lighter than the ground color. On a few individuals, both green and brown are present. On most individuals the stripe is absent.

The genetic basis of the vertebral stripe has been studied by

Pyburn (1961a; 1961b), but it still is not fully understood. Following the precedent set by Pyburn, but using the term "brown" instead of "red", I shall refer to only three classes of vertebral stripe: green, brown, and gray. A frog bearing any trace of a rusty or brown stripe or spots was included in the brown category; frogs were included in the gray category if the stripe area was gray or was not different from other areas of ground color.

Examination of preserved specimens in which color of the vertebral stripe was recorded upon preservation revealed that brown stripes were usually visible, although some became greenish; green stripes became gray or disappeared altogether. Some of the pigments apparently dissolve in formalin or alcohol within a few days.

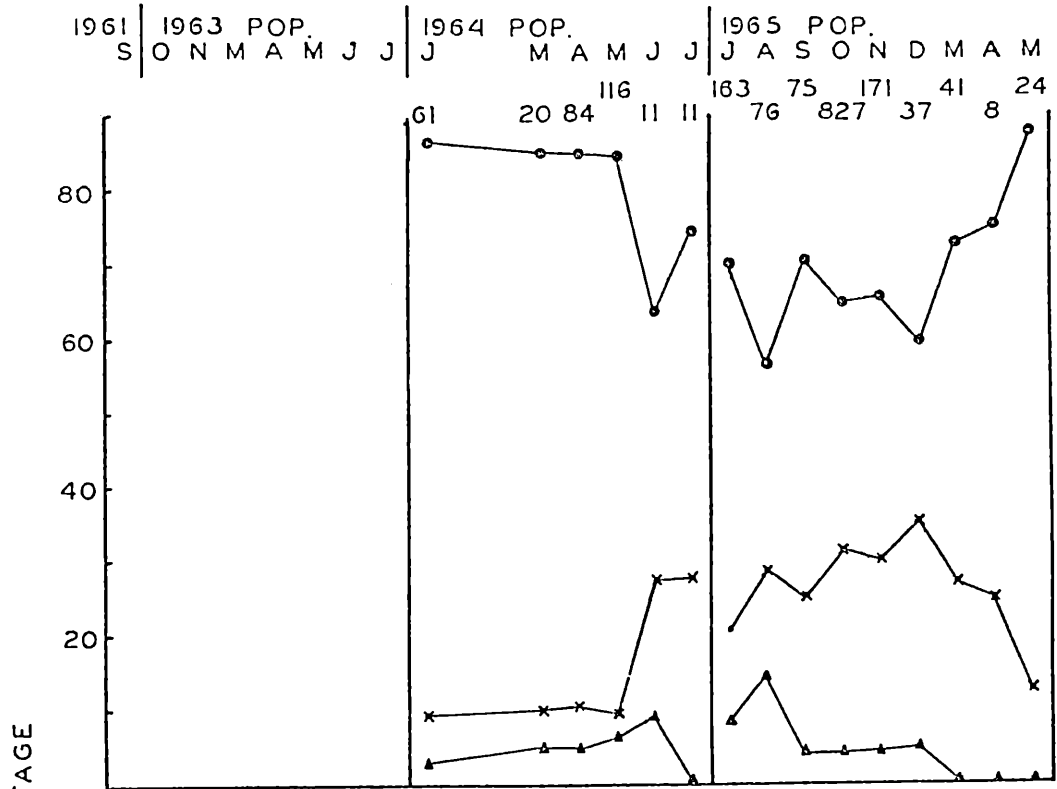
Frequencies of these colors in each population were recorded at each sampling and were combined into monthly totals and the percentage of each color calculated (Fig. 8). Populations differ from one another in the percentages of frogs having vertebral stripes of each color. Also, there is variation within each population at different times of the year. However, there appear to be few definite trends from season to season or year to year, within or between populations. Some of the fluctuations in percentages shown in Figure 8 probably result from small size of the samples.

Data for the different years were combined to determine whether there was any monthly trend in the two populations (Fig. 9). Using these combined totals, the proportion of each color morph was calculated (Table 9).

Comparison of the data in Figures 8 and 9 and Table 9 shows that gray was far more common than the other colors, and green was

Fig. 8.—Frequency of the three color morphs (gray, brown, and green, from top to bottom, respectively) in the populations of Acris crepitans at the University of Kansas Fish Laboratory and the University of Kansas Natural History Reservation. Months are indicated by letters at the top of the figure. The 1964 populations begin with July. Numerals refer to number of frogs in each sample.

FISH LAB



KUNHR

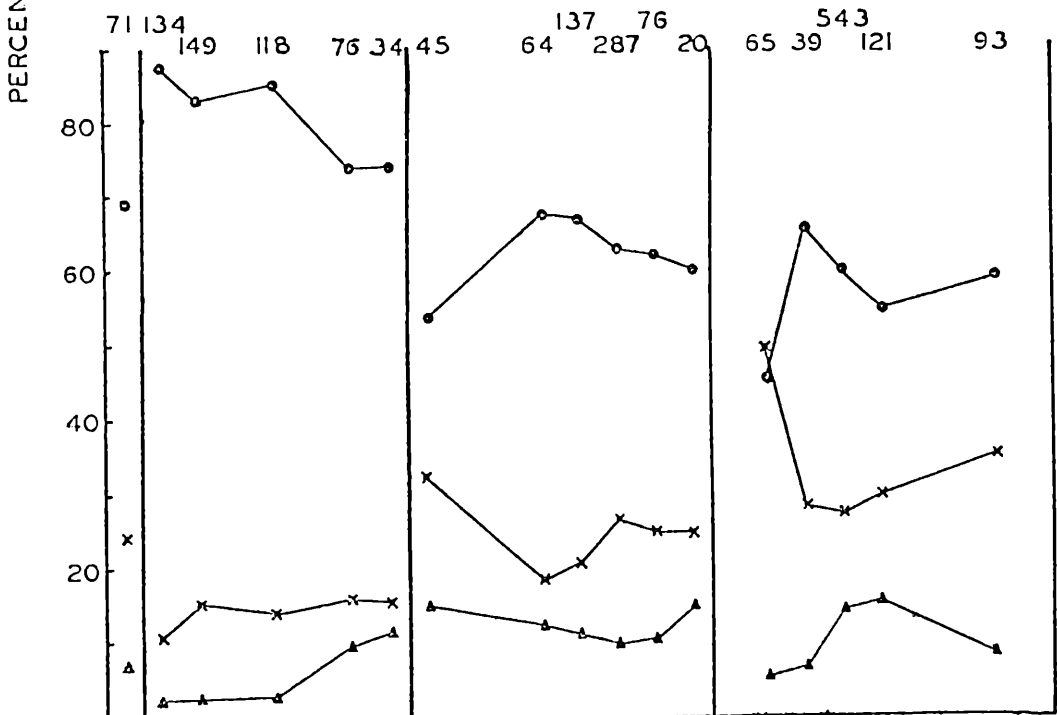


Fig. 9.—Frequency of color morphs from data in Figure 8 combined into monthly samples. Broken lines indicate average values for each color morph.

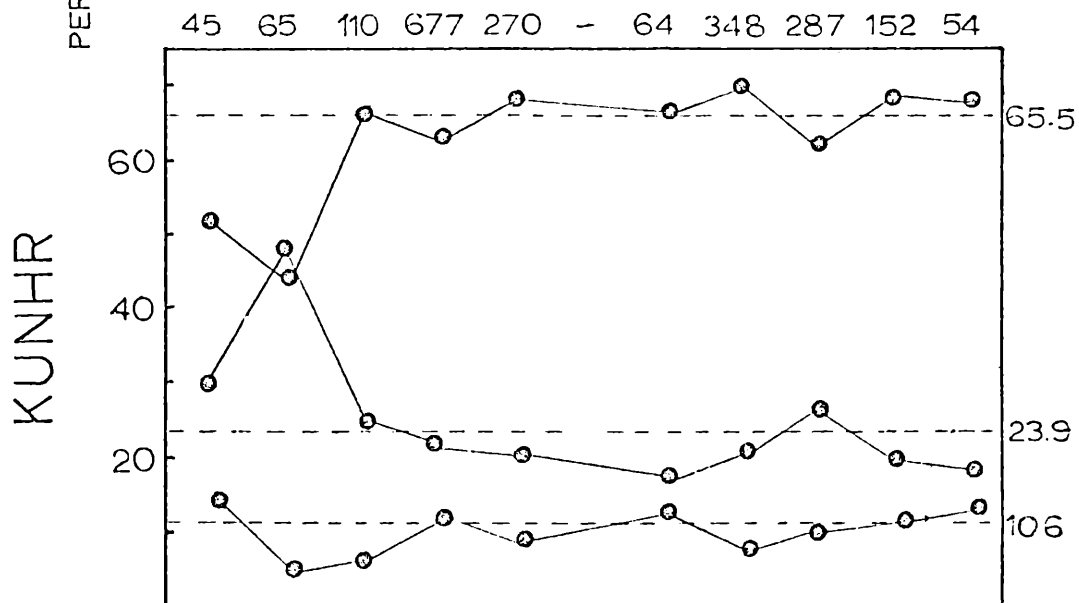
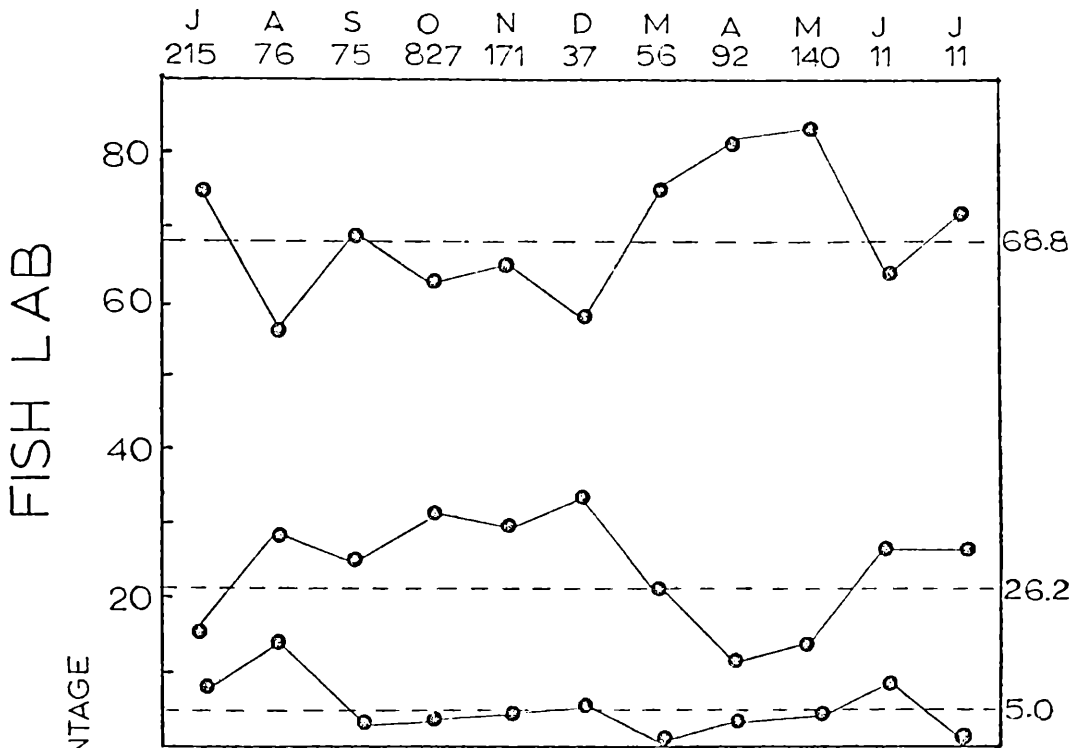


TABLE 9.—Comparison of percentage of frogs having different colored vertebral stripes in populations from northeastern Kansas. The average is followed by the extremes in parentheses, then the number in the sample.

	Fish Lab (open)	Reservation (wooded)	Combined samples from other populations (open) (wooded)	
Green	5.0 (0 -15.0) 86	10.6 (6.2-15.6) 219	5.8 (0 -12.1) 7	11.4 (6.7-15.0) 4
Brown	26.2 (9.5-35.2) 450	23.9 (18.5-49.2) 495	24.8 (11.9-45.5) 29	14.3 (13.3-15.0) 5
Gray	68.8 (56.5-84.2) 1154	65.5 (44.6-70.2) 1358	69.4 (42.5-83.3) 81	74.3 (70.0-80.0) 26

the least common. In one sample brown was more abundant than gray. There was some correlation of frequency of colors with habitat; in open situations the proportion of green usually was considerably lower than in wooded areas, whereas the proportions of gray and brown were more stable.

The fact that green-striped frogs may at times change color and appear gray introduces a source of error into estimates of frequencies of green and gray. Experimental evidence indicates that drying of the skin may be responsible for a color change from green to gray (Pyburn, 1961a:243). Contrary to my findings, Pyburn (op. cit.:244) found that the proportion of green-striped frogs that appeared green was highest at the peak of the breeding season.

Correlation has been found between color of the substrate and frequencies of the three colors of vertebral stripes. Pyburn (1961a:254-259) noted that on bare soils there were very few red (brown) and green morphs. Green morphs increased considerably towards the east in Texas, where rainfall and vegetation along the water's edge increased. Some seasonal variation was related to fluctuations of water level. As water level rose toward the vegetation zone, the proportion of brown- and green-striped frogs increased. Gray-striped frogs showed a proportional increase as the water level fell below the vegetation zone. These temporal and geographical fluctuations were probably caused by selective predation (which would favor cryptic coloration) in relation to changes in plant cover.

In my own studies this same trend is evident. Water in the reservoir at the Fish Lab was highest from June, 1965, until April, 1966, when partial draining occurred. The Reservation pond was nearly

dry in 1963 but filled in early spring of 1964 and remained full or nearly so throughout the remainder of this study. During times when water levels were lowest, gray-striped frogs reached their maximum percentages; and brown- and green-striped frogs made up correspondingly low percentages. Brown- or green-striped individuals were more easily seen by me at these times than were frogs in the gray category. Predators, especially those having color vision, likewise would have detected the brown- and green-striped frogs more easily; hence, these individuals probably were at a selective disadvantage on bare soil.

Green spots or blotches have been noted on frogs of all three color morphs. These spots may be present at one time and absent the next. It is not known whether all cricket frogs have the ability to develop green spots, but certainly a large percentage of them do. The spots may serve to protect brown and gray morphs to the same extent that green morphs are protected on certain backgrounds.

Pyburn (1961a; 1961b) concluded that presence of a green stripe is determined by a single dominant gene and that the recessive homozygote is gray-striped. Brown was dominant to gray and recessive to green. Considerable variation in color and degree of pigment development within the brown class may indicate multiple gene control of this color. In Pyburn's (1961a:246) crosses between red (brown)-striped frogs, he found evidence of a 3 brown: 1 gray ratio, assuming that the parents were heterozygous. However, in four of his experiments only brown offspring were produced, indicating that possibly one or both the parents were homozygous for the brown stripe, a possibility that he failed to mention.

If it is assumed that inheritance of color of the vertebral stripe in Acris is regulated by one pair of factors composed of three alleles (such as those that determine blood type in humans) in which the order of dominance is (G)green > (B)brown > (g)gray, then all of Pyburn's experimental results can be explained readily except for those from the two crosses of green x green (1961b:165) in which all three colors were produced. In order for brown-striped frogs to occur in the F₁, at least one of the parents in each cross had to be heterozygous for green and brown (G/B) and the other could be either G/B or G/g. In either instance the F₁ ratio would be 3 green: 1 brown. If some of the genetically green frogs were gray at metamorphosis, less than a 3 green: 1 non-green ratio would result. In both crosses far too few brown individuals were produced to support this contention. An alternative hypothesis suggested by Pyburn (1961a:248), that two pairs of factors are present of which a gene for green is epistatic to a gene for brown and both are dominant to their alleles (gray), appears more likely. A cross of G/g B/b x G/g B/b would yield a ratio of 12 green: 3 brown: 1 gray; and a cross of G/g B/b x G/g b/b would yield 6 green: 1 brown: 1 gray, both of which possibly could account for Pyburn's results (28 green: 1 brown: 3 gray; and 20 green: 4 brown: 4 gray).

Judging from the foregoing data, selection has been in favor of a recessive gene (or genes) rather than a dominant one. However, this is not an unusual occurrence, for Mayr (1965:153-154) states that the most frequent phenotype in a polymorphic population is often the recessive. It appears that each phenotype has a selective advantage under certain conditions, thus accounting for the wide

degree of geographical variation in color of the vertebral stripe in Acris. The generalizations by Mayr (1965:331) that "... gene frequencies change usually clinally and the morph clines generally run parallel to climatic gradients..." and "... at the periphery or in isolated parts of the species range some genes are generally lost while others may reach 'fixation'..." appears to correspond well with the situation in Acris (see Pyburn, 1961a:254-259).

Selection for protective coloration has been mentioned previously. Experiments by Nevo (in litt.) in central Texas indicate that the morph genes are selected for their physiological effect and that the order of physiological dominance is the reverse of the order for morphological dominance. If such is the case, then the rapid spread of a morphologically recessive gene can easily be accounted for. Nevo's experiments indicate that there is a transition in the ability to tolerate water loss, from a low toleration in green-striped frogs, to medium in brown-striped frogs, to high in gray-striped frogs. The extreme variation in color and pattern of brown morphs may indicate different physiological traits in each phenotype of brown. However, further experiments must be made with standardized conditions and known genotypes before the evidence is conclusive.

Another possible explanation for the greater success of the recessive gray gene(s) may be that egg production or viability is correlated with color of the vertebral stripe. For instance, in laboratory experiments with banded snails (Cepaea), de Ruiter (1958) found that five-banded snails laid almost twice as many eggs annually as unbanded or single-banded snails. I have not yet counted the number of eggs laid by females with different colored stripes, but

data of this nature were obtained from Pyburn (1961a). However, eggs were forced out of the frogs and size was not given; thus the number of eggs obtained does not necessarily reflect the number that would be produced naturally, and correlation between size and number of eggs produced was not obtained. The average number of eggs per female (followed by number of frogs in parentheses) observed by Pyburn was: green -- 75 (3); brown -- 124 (14); and gray -- 121 (36). These figures are significantly different ($P = 0.0008$) from the expected 1:1 ratio, but they may not be biologically significant owing to the conditions under which they were obtained. Viability (average number of metamorphosed offspring) was not significantly different in the three groups; but, again, the results obtained in the laboratory may differ from those obtained under natural conditions.

Possibly polymorphism in Acris has an ecological basis. Numerous authors have suggested that each gene arrangement in a polymorphic species is adapted to a different subniche within the general habitat of the species. Hence the greatest amount of polymorphism is found in the most favorable areas of the species range (Mayr, 1965:245).

The observed fluctuations in ratios of the different color morphs indicate frequent reversals of selective pressures owing to changes in environmental conditions. These seasonal changes contribute to the preservation of genetic variation because they prevent or delay total elimination of certain alleles from populations of Acris. In fact, the presence of different genotypes in the population may add to the adaptive value of each. In monomorphic populations of Acris, selective factors act equally on all individuals, whereas in polymorphic populations each color morph has an advantage at different

times and genetic plasticity is maintained.

Neill (1950:153) stated that A. crepitans was usually gray, whereas A. gryllus usually had a bright green, yellow, chestnut or deep red vertebral stripe. He also mentioned that crepitans has a more squat, toad-like build and is an upland form, while gryllus is a slender, lowland form. Since recessive genes have been selected for in all known populations of Acris crepitans and since these genes are correlated with soil colors and possibly water loss, differential egg production, and viability, it appears that this species may have evolved toward the gray phase and toward greater independence from an aquatic habitat. Extension of geographical range has most likely been from moist, eastern regions of the United States toward dry, western regions.

Judging from present conditions, it is my hypothesis that the two species originated by the splitting of a centrally located, ancestral type in mesic habitats in which color of the vertebral stripe was predominantly green. Selection for the recessive gray condition in crepitans was correlated with the relatively scanty vegetation, lighter-colored soils, and drier conditions that prevail in inland areas. An additional adaptation to a drier habitat was an increase in size with a corresponding decrease in surface-to-volume ratio. Nevo (in litt.) stated that increase in size from east to west is clinal. Correlated with increasing size is a slight change in voice. Meanwhile populations in the area that is now the southeastern states became adapted to more mesic conditions. Changing conditions later allowed a reinvasion of the central area after speciation had been attained.

Acris crepitans was divided into two subspecies (crepitans and blanchardi) by Harper (1947:39-40). It is my contention that since all characters seem to change in a clinal fashion there is no biological justification for the division of A. crepitans into two subspecies. The divergence in characteristics between A. c. crepitans and A. c. blanchardi as mentioned by Harper simply does not exist. Many of the variations in A. crepitans may have arisen in the area of sympatry with A. gryllus as a means of lessening competition between the two species. Although A. crepitans is an upland form and A. gryllus is a lowland form, in a portion of the area of sympatry these roles are reversed. It appears rather paradoxical that an upland species should become a lowland form where it is sympatric with a typical lowland form. However, if we consider the area of sympatry to include the lowest, warmest, and most mesic area in which crepitans occurs (in addition to western Louisiana and the Texas Gulf Coast) and the highest, coolest, and most xeric area in which gryllus occurs, then it is understandable that each species may have been partially adapted to these conditions before competition may have caused natural selection to favor more mesic conditions for crepitans and more xeric conditions for gryllus. The ecological adaptations of the two species are actually quite complex. In Mississippi, crepitans is restricted to the Delta and along the Gulf Coast with the exception of possible isolated populations in other areas of the state. Gryllus also occurs along the Gulf Coast and in the upland areas of the state (Boyd, 1963:201-202). Competitive exclusion, rather than ecological displacement, appears to be operating over most of the state. Considerable overlap occurs in Georgia, but

crepitans remains as an upland species (Neill, 1950:152).

PREDATION AND PARASITISM

Causes of mortality in any population of animals are often difficult to ascertain. In a species such as Acris crepitans, where tadpoles are difficult to find, the causes of mortality of perhaps more than half the population often remain obscure. Savage (1962:65) stated that the larvae of dragon flies often feed on tadpoles, and he quoted incidents of predation on tadpoles by frogs and leeches. Very few instances of predation were observed in my study. A large aquatic spider, Dolomedes sexpunctatus, attacked and killed a young Acris. On a few occasions at the Fish Lab reservoir, fish (Micropterus salmoides) were observed feeding on Acris that had jumped into water to escape capture when disturbed by my activities. Although catfish were numerous in the Fish Lab ponds, predation by them on Acris was not observed. In another instance a bullfrog (Rana catesbeiana) ate four Acris that I tossed into the water. The relatively large size at metamorphosis in Acris probably serves to reduce or completely eliminate cannibalism which is common in some other frogs such as bullfrogs.

Turtles, such as Chelydra serpentina and Pseudemys scripta, often were seen at the Fish Lab and probably feed upon tadpoles and adult Acris. In the area around Lawrence, snakes, such as Natrix erythrogaster, N. grahami, N. rhombifera, N. sipedon, Thamnophis sirtalis, T. radix, T. proximus, and Diadophis punctatus are found; and some of them prey upon Acris. Natrix sipedon and Thamnophis sirtalis appear to be more common and probably prey upon Acris more

than the others. On one occasion a Diadophis had swallowed one hind leg of a juvenile Acris that I observed attempting to hop out of a crack in the ground. The snake was deep in the crack and was pulled out when I picked up the frog.

Birds are potential predators of both tadpoles and frogs. Kildeer, Bronzed Grackles, and Red-winged Blackbirds were common at the Fish Lab and often were seen foraging along the water's edge. Tracks of large water birds, such as Great Blue Herons, sometimes were found around the Reservoir. Fitch (1958:171) observed Great Blue Herons and Green Herons feeding on cricket frogs at the Reservation. Numerous other species of aquatic birds that may prey upon Acris have been seen at the Reservation.

The raccoon (Procyon lotor) appears to be the most common mammalian carnivore at the Reservation pond, and Fitch (op. cit.: 164-165) reported heavy predation by raccoons upon leopard frogs, cricket frogs, chorus frogs, bullfrogs, and American toads. O'possums (Didelphis marsupialis) commonly prowl along the edge of the pond at night and may prey upon Acris.

Although some parasites were found in the populations of Acris near Lawrence, no attempt was made to locate and identify all endoparasites. Metacercariae of flukes were found in the abdominal cavity of several frogs. Dr. Edgar A. Schlueter of the Department of Biology at North Texas State University stated that these looked like strigeid or neoreniferid flukes. If the large infestations of metacercariae in this population are those of strigeid flukes, water birds may be major predators. However, no strigeids have heretofore been reported from Acris, and I suspect that the metacercariae may

be those of Zeugorchis megacystis, a fluke that inhabits the digestive and respiratory tracts of Thamnophis sirtalis, described in 1960 (Stewart, 1960:879). Nematodes were found in the stomach of a few individuals.

The most noticeable parasites of Acris (and Rana pipiens) are larval chiggers: Hannemania eltoni, H. multifemorata, Trombicula alfreddugesi, and T. lipovskyana (Loomis, 1956:1368). According to Loomis (op. cit.:1381), H. eltoni are the most numerous on Acris. No attempt was made to identify the larvae. Hannemania appear as red spots under the skin and usually are found near the anus or on the ventral side. However, they may be located on almost every part of the body except the top of the head. Trombicula occur mainly on the dorsal side. Whenever the larvae drop off, brownish-gray scars remain on the skin for several weeks. At no time are samples of Acris entirely free of chiggers; a few frogs will always be found having from one to several chiggers or scars.

Most young larvae of chiggers were found in summer, at which time they appeared as extremely small red spots on their hosts. They grew rapidly and metamorphosed into adults in autumn then dropped off. Numerous scars also were found in spring, indicating that these species have a highly variable larval and reproductive period, as shown by Loomis' study. Infestation was lowest at the Reservation; only 12 per cent of the total sample from that locality were parasitized. At the Fish Lab, 49 per cent and 23 per cent of the 1964 and 1965 populations were infected, respectively, thus indicating a possible habitat preference for these chiggers in open areas as opposed to woodland areas.

Table 10 shows the distribution, by frequency, of chiggers on Acris for the combined samples for all years of the study. As shown by the Poisson distribution, infestation by chiggers is not random; most frogs tend to have either no parasites or several. The number of frogs having from one to three chiggers was significantly less ($P < 0.001$) than expected, while the number of frogs having no chiggers or more than five chiggers was significantly higher than expected. However, these results were not surprising, for the pattern of distribution by frequency of the parasites upon their hosts is similar to that found by Williams (1964:193-254) for a number of different parasites. Whether the differences from the expected in degree of infestation are due to variation in susceptibility to chiggers or to non-random distribution of host and/or parasite is not known.

MOVEMENTS

Of 2244 of the frogs marked in this study, 1547 (68.9 per cent) were not recaptured, and the remaining 697 were recaptured from one to five times. More detailed records of these frogs are shown in Table 11. Because of the low number of frogs captured four or more times, it was impossible to establish any "preferred" activity ranges of individual frogs, as shown by Pyburn (1958:333). However, preferences for certain areas around the ponds are indicated to some extent by patterns of distribution along their shores.

Cricket frogs are normally restricted to moist soil near the edge of the body of water where they live. Distances moved can be measured around ponds since cricket frogs seldom venture more than

TABLE 10.—Distribution by frequency of chiggers (*Trombiculidae*) on *Acris crepitans* from northeastern Kansas ($\bar{Y} = 0.875$).

Number of chiggers (Y)	Number of frogs (observed)	Poisson (expected)	Deviation from expected (n.s. = not significant)
0	1586	830	+
1	187	727	-
2	78	318	-
3	47	93	-
4	28	20.3	+ n.s.
5	23	3.56	+
6	15	0.52	+
7	5	0.065	+
8	14	0.0071	+
9	5	0.001	+
10	9	<0.001	+
11	2		
12	5		
13	3		
14	1		
15	5		
16	2		
17	4		
18	3		
21	1		
22	1		
28	1		
30	2		
38	1		
45	1		
53	1		
<u>57</u>	<u>1</u>		
1992	1741		

TABLE 11.—Number of captures of 2244 cricket frogs in the 1964 and 1965 populations at the University of Kansas Fish Lab and Natural History Reservation. Elapsed time in months is given in parentheses below the heading for each year-class.

Number of captures per frog	Fish Lab				KUNHR				Total	Per cent
	1964 (7)	Per cent	1965 (10)	Per cent	1964 (11)	Per cent	1965 (7)	Per cent		
1	157	82.6	511	61.0	455	68.5	424	76.6	1547	68.9
2	25	13.2	244	29.2	162	24.4	92	16.7	523	23.4
3	4	2.1	58	6.9	43	6.5	28	5.1	133	5.9
4	2	1.0	20	2.4	4	0.6	8	1.4	34	1.5
5	2	1.0	3	0.4	0		1	0.2	6	0.3
6	0		1	0.1	0		0		1	0.04
Total	190		837		664		553		2244	

a few feet into water. The direction taken in most instances cannot be determined, but movement was assumed to be the shortest distance around the ponds between two successive captures.

During rains and immediately following them or at other times when the ground was damp, frogs tended to disperse in all directions from the ponds and streams. They often were found at considerable distances from water after rains. On one occasion several Acris and one Rana catesbeiana were found in a small roadside puddle beside a boulder more than a quarter mile west-northwest of the Reservation pond, which was the closest permanent body of water. Pyburn (1958:336) stated that precipitation causes dispersal and facilitates rapid occupation of new breeding sites as they become available. Dispersal

due to rain and subsequent return to water probably account for some of the movements around ponds reported herein. Dispersal also accounts for increased mortality rates from desiccation in those frogs that do not return to permanent water. Movements as discussed hereafter refer only to movements within the study areas, rather than dispersal.

Movements were studied in a variety of ways to show their relationship to distance, time, habitat, rainfall, and sexual differences. Regardless of the method of comparison, most recorded distances moved indicate that these frogs tend to remain in fairly small areas; about 45 to 50 per cent of the frogs recaptured were within 25 feet of the previous place of capture (Table 12). The number of frogs moving greater distances steadily decreased. Since group markings only were used on most samples in autumn, the time interval between captures could not be determined for the 1963 year class at the Reservation. In the 1964 year class of the Reservation population, 63 per cent of those recaptured remained in the area (see Fig. 1) of the pond where they were originally captured, 21 per cent moved to an adjacent area, and 16 per cent moved to more distant areas. Each area was 100 feet in length. Movements of more than 300 feet in this population usually involved frogs moving from the stream to the pond. These movements occurred during the breeding season and may have been a response to calling. In the 1965 year class of the Fish Lab population (Table 13), 61.2 per cent of those recaptured remained in the area of the pond where they were originally captured, 24.0 per cent moved to an adjacent area, and 14.8 per cent moved to more distant areas. Although these figures are nearly the same as those of the Reservation population, most areas at the Fish Lab

TABLE 12.—Distances moved between captures by cricket frogs in the 1963, 1964, and 1965 year classes (A, B, and C respectively) at the University of Kansas Natural History Reservation.

A. KUNHR Population, 1963 year class.

Distance moved in feet	Number of frogs	Per cent
0-25	53	45.3
26-75	29	24.8
76-125	14	11.9
126-175	7	6.0
176-225	9	7.7
226-275	3	2.6
276-325	2	1.7

B. KUNHR Population, 1964 year class.

Distance moved in feet	Elapsed time in weeks											Total no. of frogs	Per cent	
	2	3	4	5-6	7-8	9-10	11-16	26	30	35	39			
0-12	17	22	11	8	6								64	40.6
13-37	8	3	12	6	1	3							33	20.9
38-63	2	5	2		2								11	7.0
64-89	2	2	8		4	2							18	11.4
90-115					1								1	0.6
116-141													0	0
142-167	1	1			1								3	1.9
168-193	1		1	1	2		1						6	3.8
194-219	1	1											2	1.3
220-245	1	2			2	1	1						7	4.4
246-271	1												1	0.6
272-297		2	1	1	1								5	3.2
298-323										1			1	0.6
324-349													0	0
350-375					1								1	0.6
376-400								1	1				2	1.3
450									1				1	0.6
500									1				1	0.6
550									1				1	0.6
700									1		1		2	1.3

C. KUNHR Population (stream only), 1965 year class.

Distance moved in feet	Elapsed time in weeks				Total no. of frogs	Per cent
	1	2	3	4		
0-25	48	22	10	1	81	51.0
50	16	2	3		21	13.2
75	8	6	3		17	10.7
100	6	4		1	11	6.9
125	1	4	1		6	3.8
150	4	2	1		7	4.4
175	2	2	1		5	3.1
200	1			1	2	1.3
225	1	1	1		3	1.9
250		1			1	0.6
275		1			1	0.6
300		1			1	0.6
350-375		1			1	0.6
400			1		1	0.6
500-525		1			1	0.6

TABLE 13.—Movements of cricket frogs in the University of Kansas Fish Laboratory Population, 1965 year class. Only the last place of capture is recorded for frogs captured several times.

Area first captured	Length of shore line (feet)	Area recaptured						Total no. of frogs	Per cent
		1	2	3	4	5	Ponds and swamp		
1	310	82	2	0	6	5	4	99	26.7
2	220	12	20	3	0	3	0	38	10.2
3	202	12	0	8	5	4	0	29	7.8
4	265	19	1	6	59	43	3	131	35.3
5	165	11	0	0	2	58	3	74	20.0
Total number of frogs		136	23	17	72	113	10	371	
Per cent		36.7	6.2	4.6	19.4	30.4	2.7		

were over 200 feet in length, indicating that movements in this population tend to be of greater magnitude. In the latter example, movement to areas other than adjacent ones was believed to be toward more favorable habitat, rather than distance per se. This assumption was made after comparing the percentages of frogs first marked in a particular area with the percentages recaptured in that area. Areas 1 and 5 show a considerable increase in number of frogs, whereas areas 2, 3, and 4 show substantial decreases.

Although most frogs tended to remain in a relatively small area, movements of considerable magnitude sometimes occurred. As time elapsed, the distance moved by most frogs gradually increased, as evidenced by Table 12B and 12C and Fig. 10A. In some instances, however, little or no correlation was found between distance traveled in a single move and elapsed time between captures (Fig. 10B). In fact, many of the longest movements occurred over extremely short periods of time. Pyburn (1958:331) made similar observations in his study of cricket frogs in Texas.

Comparison of distance moved with amount of rainfall between captures is illustrated by two examples in Table 14. Although greater distances usually were moved after rain, the majority of frogs were recaptured within 25 feet of the site of previous capture in almost every instance. The fact that most frogs were recaptured near the previous site of capture indicates that most of those that disperse either move so far as to avoid subsequent recapture or do not survive to return to water. Many may return to the same home area and appear to have remained stationary. Therefore, rainfall alone cannot account for long movements. Relative humidity, temperature, and cloudy

Fig. 10.—(A) Movements of frogs at ponds, University of Kansas Fish Laboratory, 1964 year class. x = males; o = females; arrows indicate successive moves by individual frogs; numerals indicate number of frogs represented by two of the symbols. (B) Movements of frogs at the reservoir, University of Kansas Fish Laboratory, 1965 year class. Since these were immature frogs, sex could not be determined.

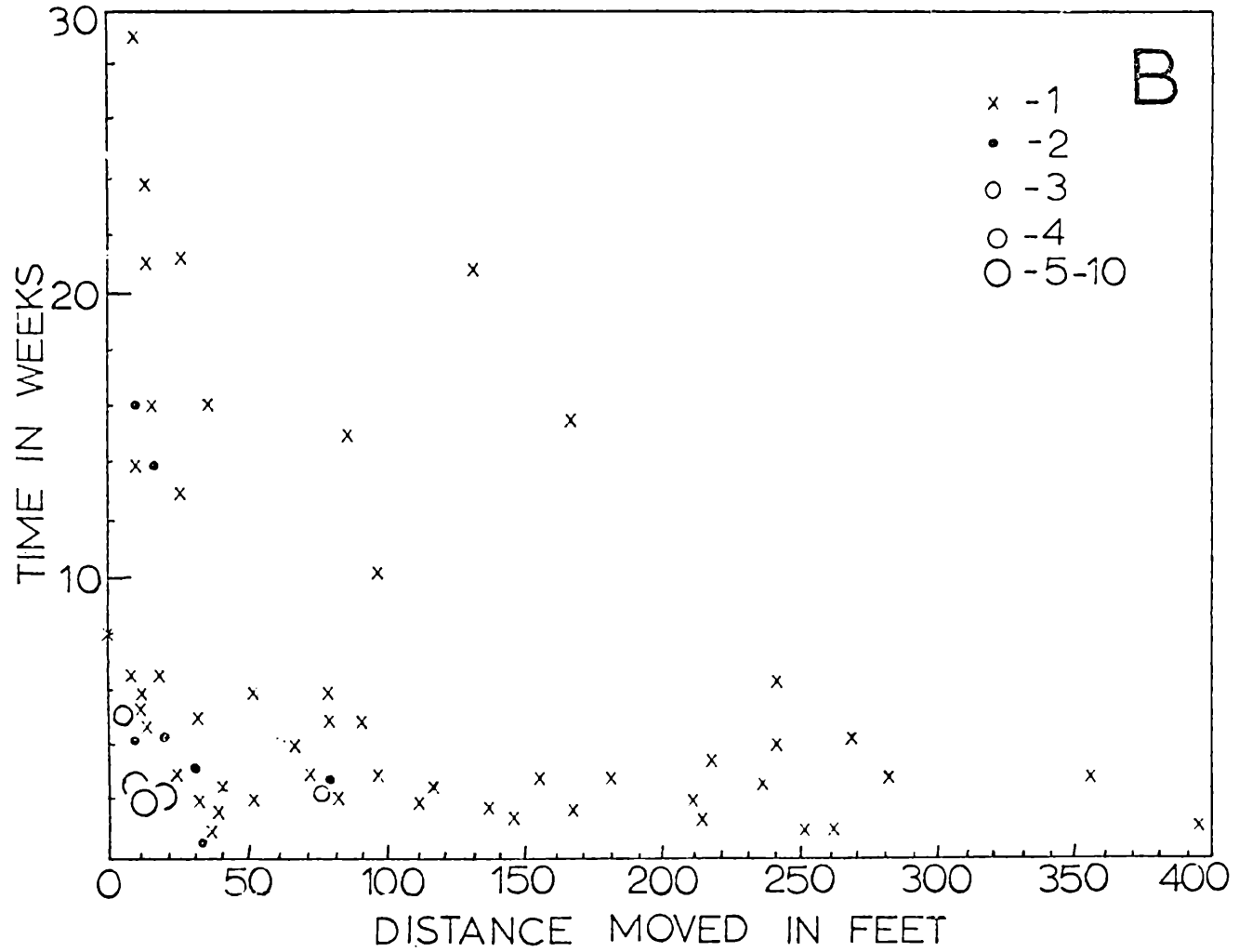


TABLE 14.—Comparison of distance moved with amount of precipitation in the 1965 year class of the University of Kansas Natural History Reservation and Fish Lab populations. Movements between autumn and spring were excluded.

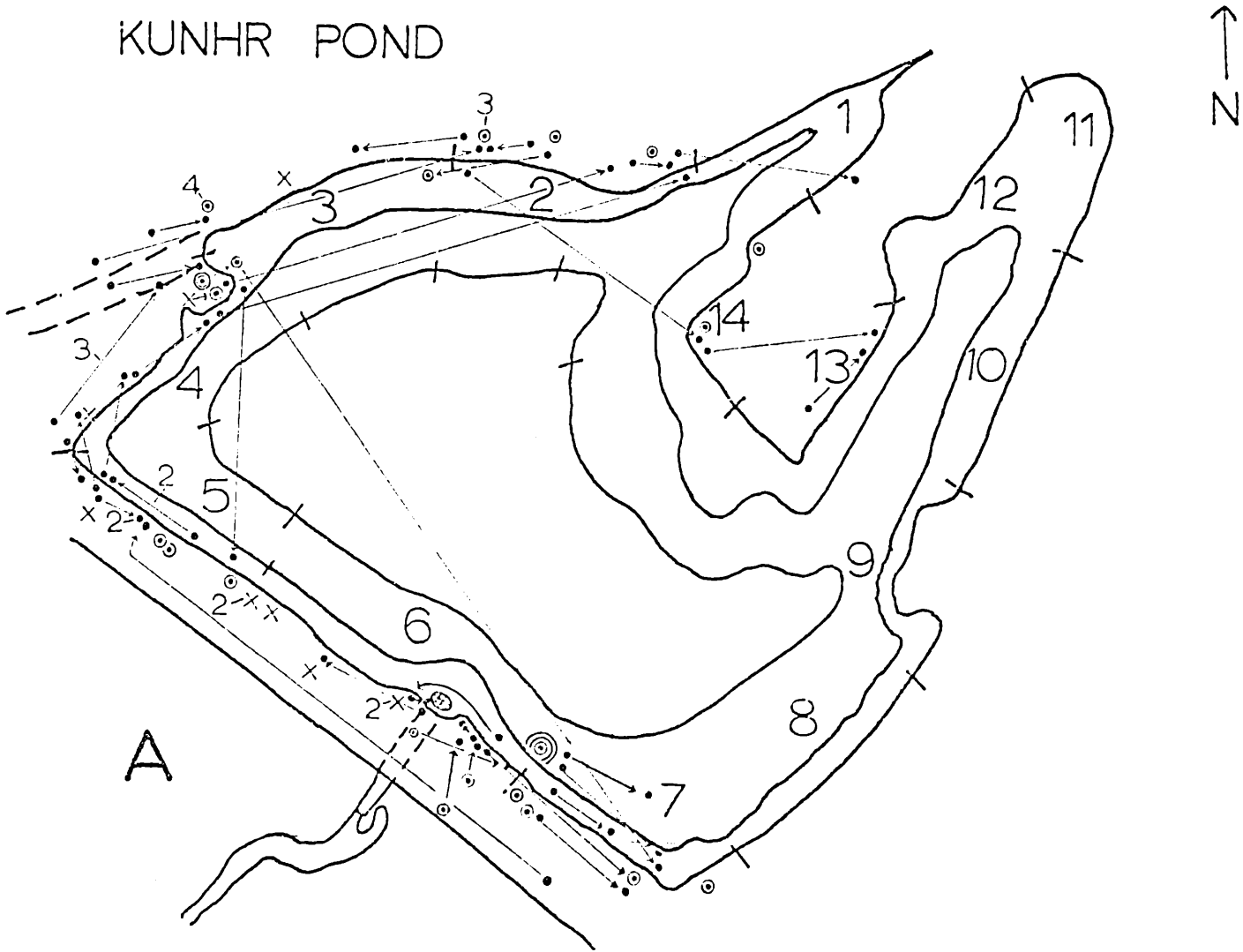
Inches of rainfall	KUNHR		Fish Lab	
	Distance in feet Average (Range)	No. in sample	Distance in feet Average (Range)	No. in sample
0.00	72 (0-215)	61	38 (37-52)	4
0.02			107 (0-425)	4
0.05	54 (0-160)	20		
0.08			40	1
0.13			51 (0-235)	21
0.15			5	1
0.40			6 (2-10)	2
0.42			40 (1-120)	3
0.52	55 (2-244)	20	139 (3-395)	11
0.55			5	1
0.57	74 (0-400)	46	20	1
3.22			54 (0-108)	2

conditions following precipitation are equally important and must be included before correlation can be shown between distance moved and amount of precipitation.

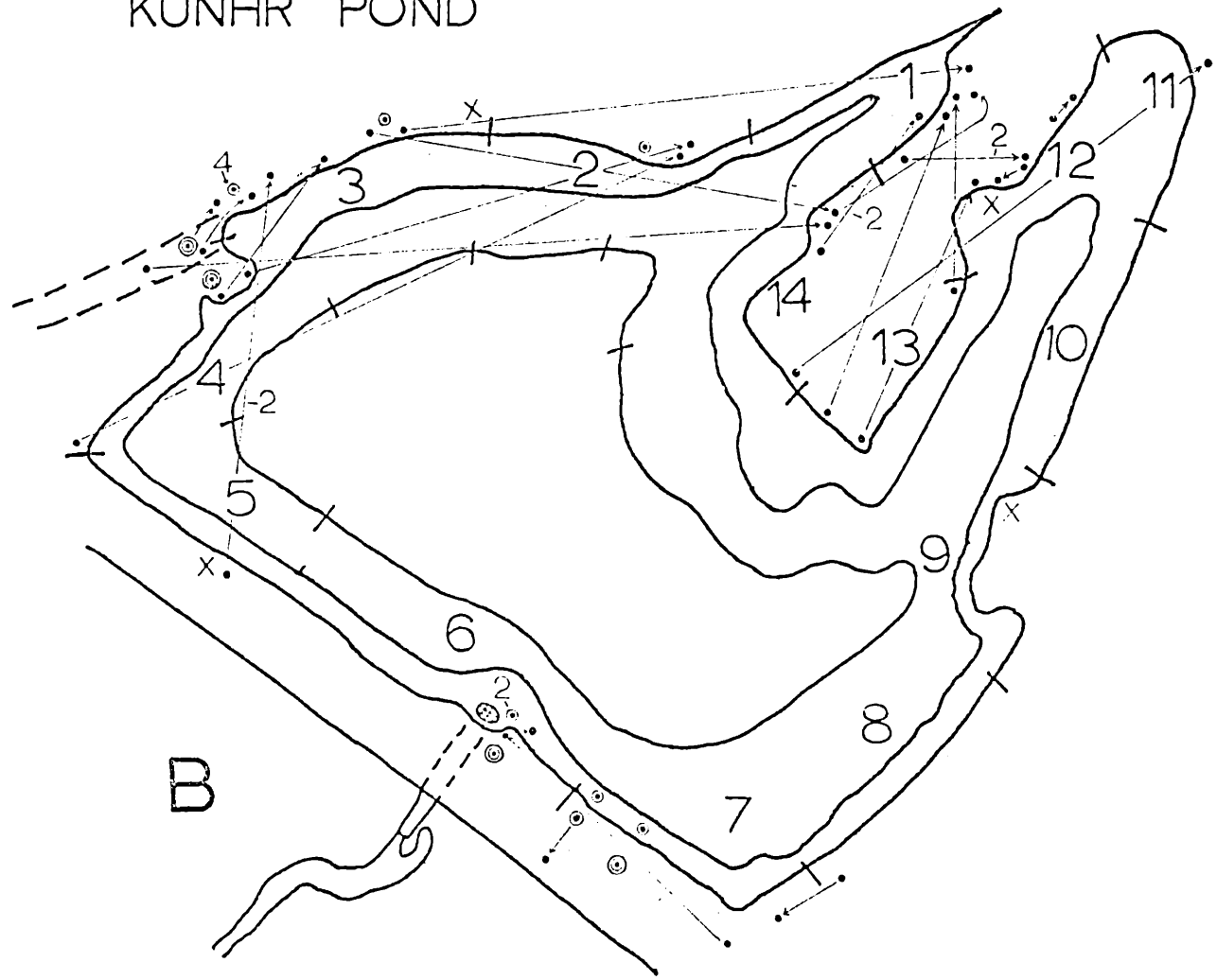
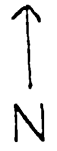
Patterns of movements around the Reservation pond and the various ponds at the Fish Lab are illustrated by Figures 11, 12, and 13. Patterns of distribution around the Reservation pond (Fig. 11) indicate not only where I spent the most time capturing frogs but also areas that seemed to be preferred by frogs themselves. Few frogs were ever found in areas 1 and 8 to 12; these appeared much like the remaining margin of the pond but were shaded most of the time.

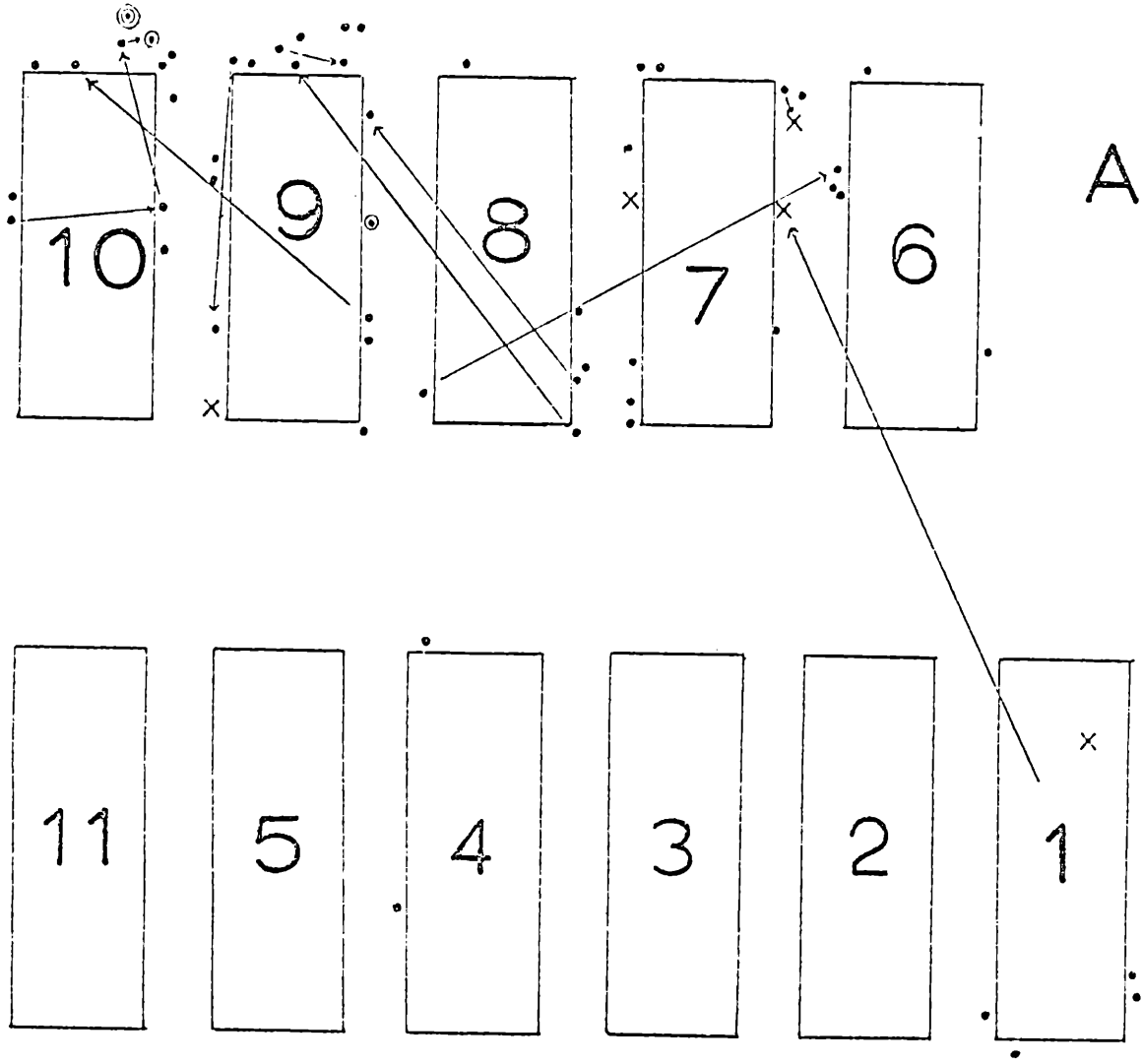
Fig. 11.—Movements of frogs in the University of Kansas Natural History Reservation population 1964 year class. Each dot represents one frog unless otherwise indicated by small numerals. Concentric circles around dots indicate number of times that an individual was captured in the same place. Individuals that moved from the stream are indicated by an "x". Arrows indicate movements. (A) Males; (B) Females.

KUNHR POND



KUNHR POND





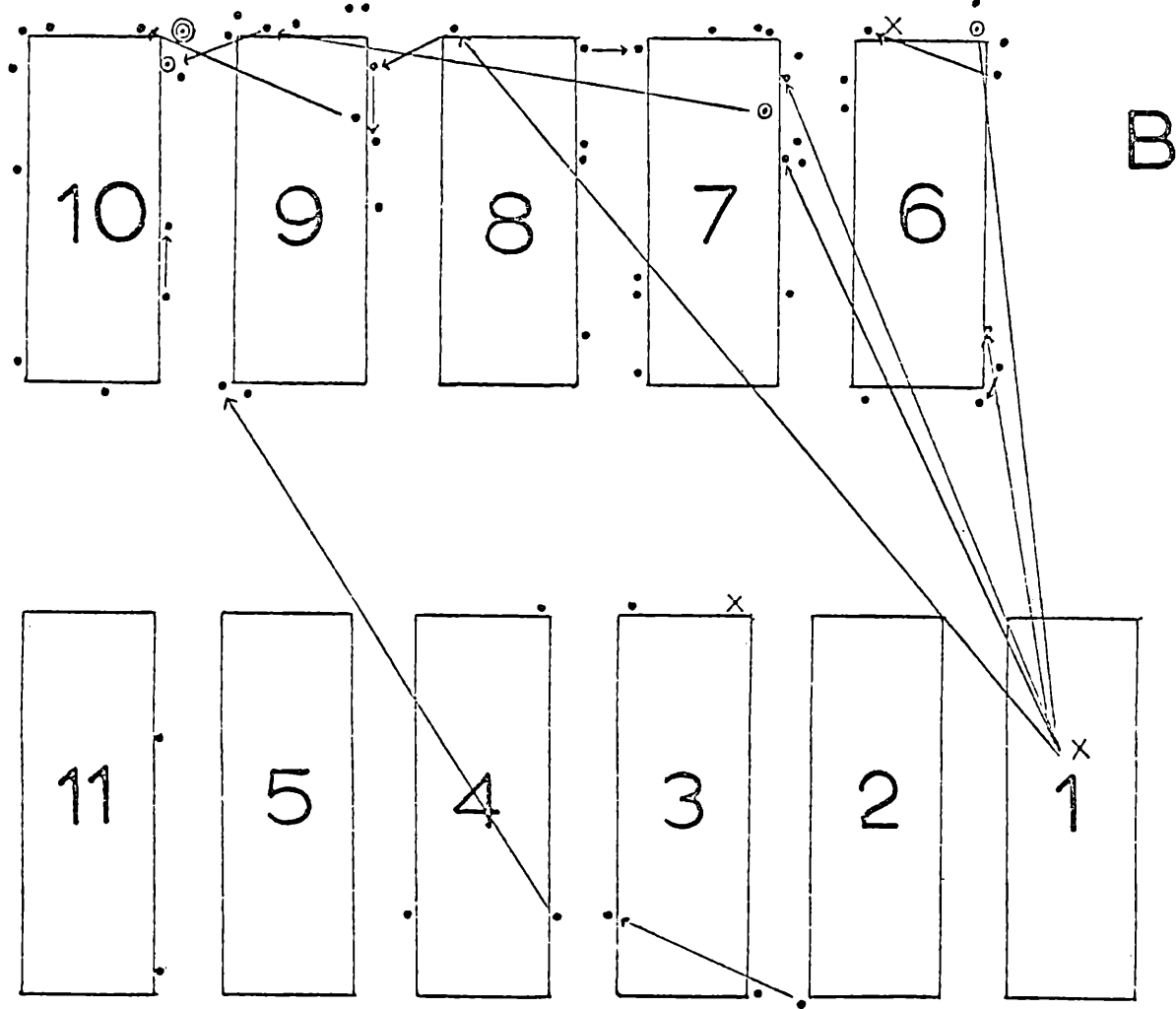
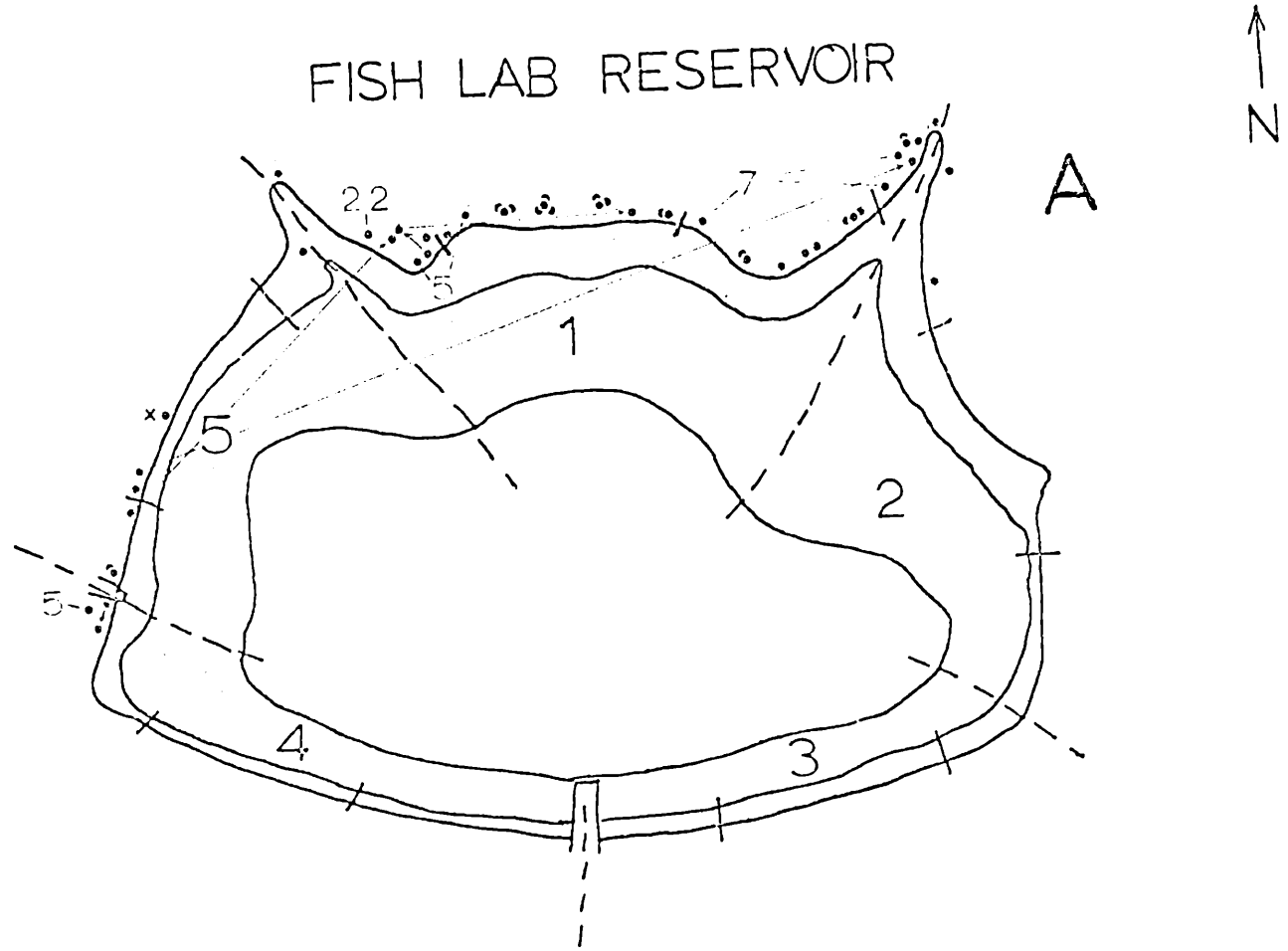
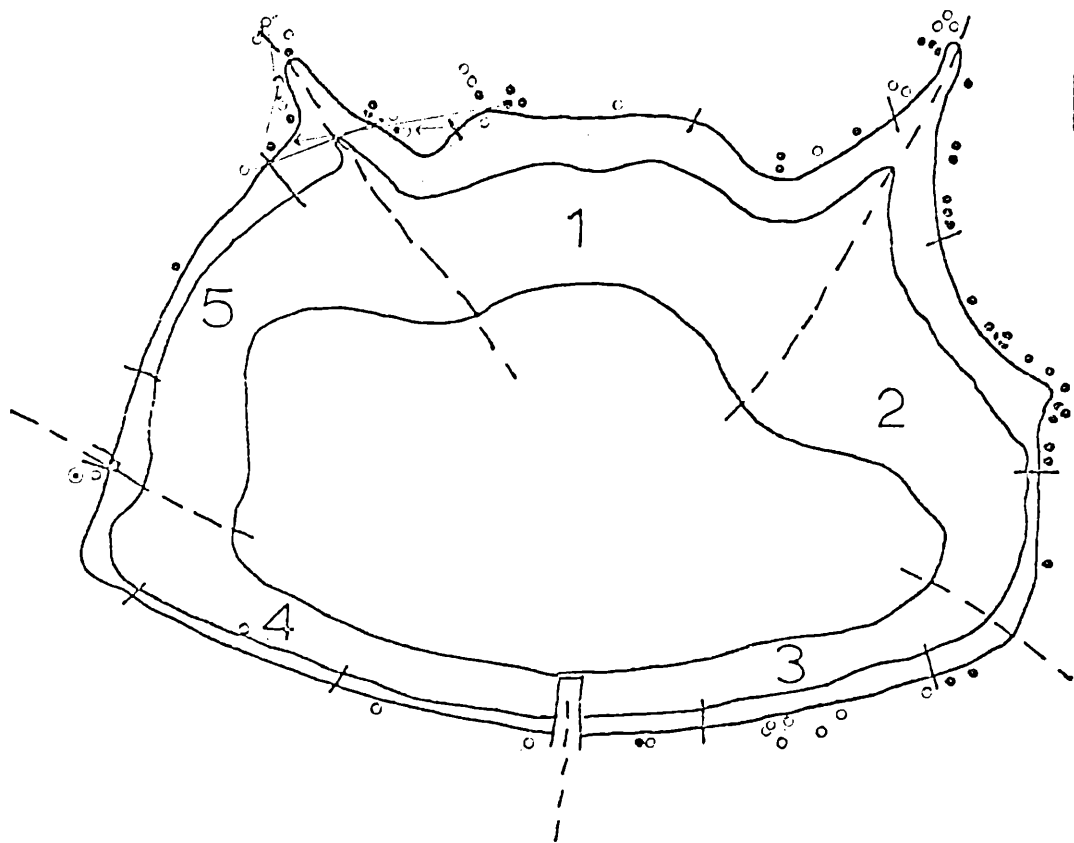


Fig. 13.—Locations of recapture and movements of frogs at the University of Kansas Fish Laboratory, 1965 year class. Symbols same as for Figure 11. An individual that moved to the ponds is indicated by an "x". Sex was not determined on these frogs since they were immature. (A) Frogs first captured in Area 1; (B) ● = frogs first captured in Area 2; ○ = frogs first captured in Area 3; (C and D) Area 4; (E) Area 5.

FISH LAB RESERVOIR

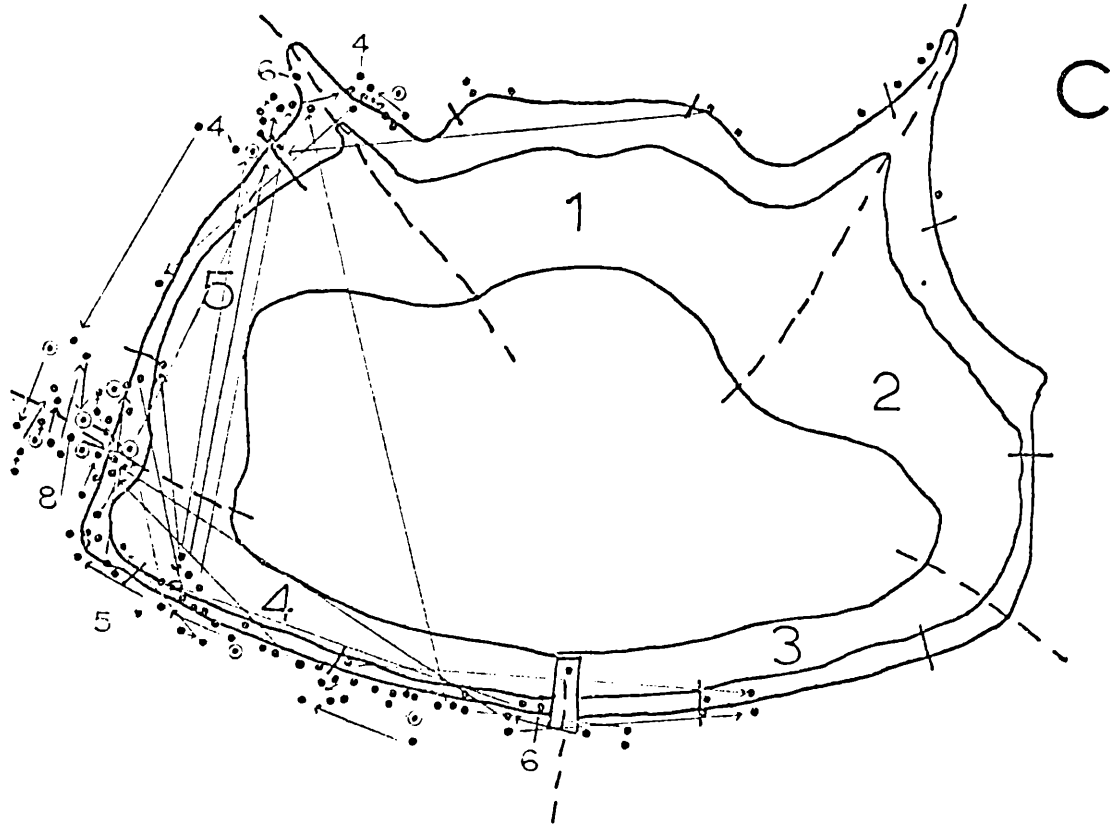


FISH LAB RESERVOIR

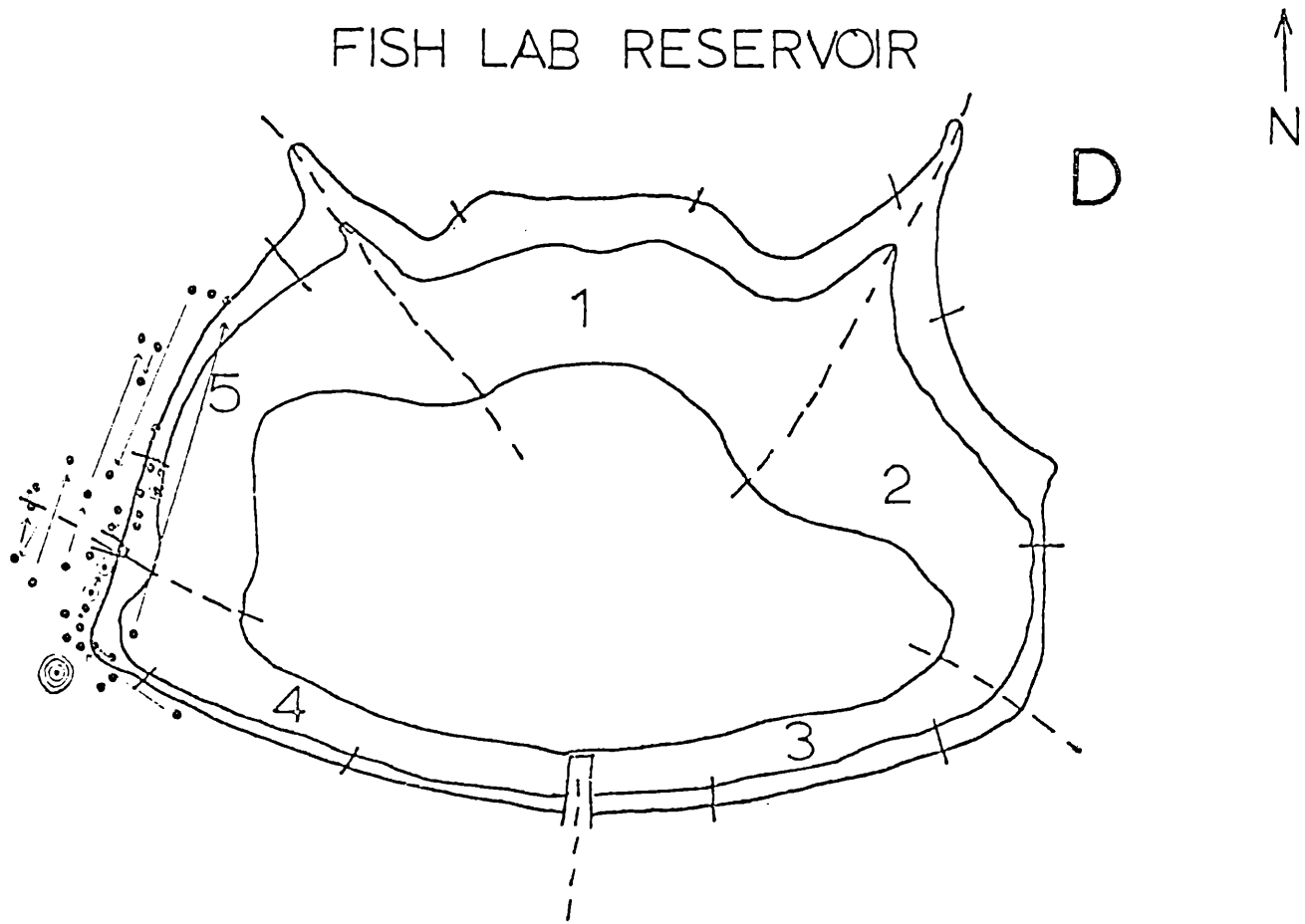


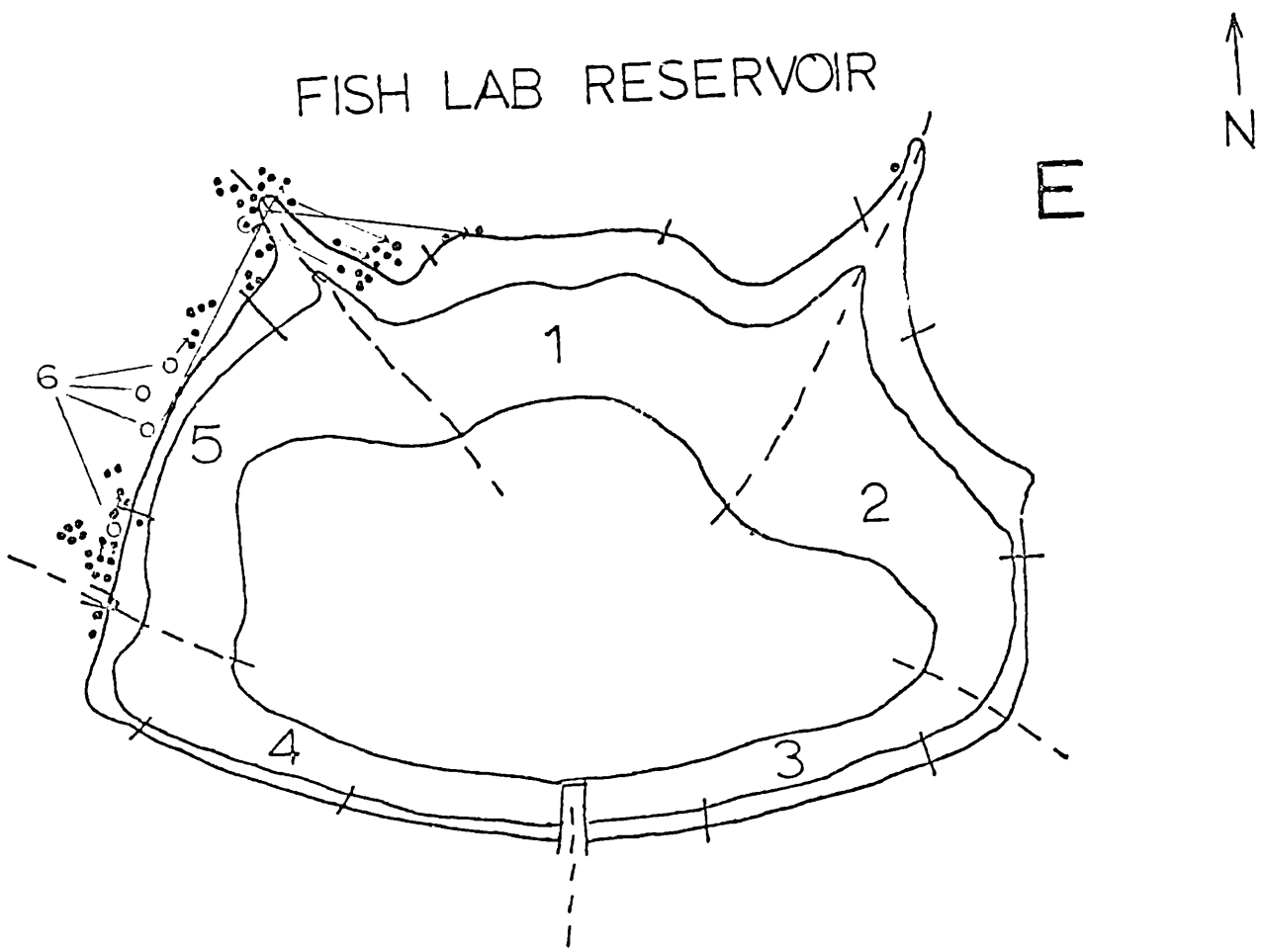
B

FISH LAB RESERVOIR



FISH LAB RESERVOIR





Distribution and movements of the Fish Lab population, 1964 year class (Fig. 12), reflect variations in habitat and preferences for certain areas. The greater distances of movements here over those at the Reservation probably result from division of the habitat into several separate ponds with intervening areas. The portions of each pond usually occupied by several frogs were those having a muddy beach-like area near water level. Breeding activity was restricted almost entirely to ponds 1, 9, and 10 (and the reservoir), thus explaining the relatively large number of frogs in these areas.

Distribution and movements of the 1965 year class at the Fish Lab (Fig. 13) likewise indicate preferred areas. Since group markings were used in the original marking of these frogs (see Methods), actual distances moved could not be calculated until a frog received an individual mark at recapture and then was captured a third time. Therefore, Figure 13 is subdivided into groups, each of which contains dots representing individuals first marked in a particular area. Dots indicate that a frog has moved from a particular area but not the specific part of that area. Thus, each dot outside the designated area could indicate a movement of a few feet or more than 200 feet.

Sexual differences in movements were compared in the 1964 year classes at the Fish Lab ponds and at the Reservation (Table 15). Movements at the Fish Lab were considerably greater than those at the Reservation, and males moved slightly farther than females. At the Reservation, females moved much farther than males. When movements from the stream to the pond were included in this sample, distances still averaged greater for females than for males, but these

TABLE 15.—Average distance moved by sexually mature male and female cricket frogs in the 1964 year classes at the Fish Lab ponds and Reservation. Movements occurred during the breeding season (spring, 1965). Significance values from χ^2 test follow average distances.

Location	Number of frogs		Average distance moved in feet		P
	(Males)	(Females)	(Males)	(Females)	
Fish Lab	17	18	203	191	0.60
Reservation Pond (only)	65	37	44.6	74.3	<0.01
(including stream)	76	42	114	133	0.23

differences were not significant. Since almost all of the movements recorded for the 1965 year class at the Fish Lab dealt with juveniles, sexual differences (if any) could not be detected. The average distance moved by 59 frogs was 144 feet, which was significantly less than that moved by adults in the 1964 year class. There were not enough recaptures at the Fish Lab reservoir in the 1964 year class to determine whether movements of the adults were significantly different from those of their offspring. There appears to be no clear-cut difference in distances moved associated with differences in age or sex in Acris crepitans; rather, the differences most likely depend upon variations in habitat, weather, and breeding activity. The greater distances moved by frogs at the Fish Lab in comparison with the Reservation are not surprising when variations in habitat are considered. At the Reservation frogs inhabit only one pond and one stream, whereas at the Fish Lab there are eleven rectangular ponds, a reservoir, a stream, and an additional pond surrounded by a swampy

area. Studies on other species indicate that age and/or sexual differences in movements sometimes occur. Turner (1960:267) found no differences in movement associated with age or sex in Rana pretiosa. On the other hand, Fitch (1956a:300) and Anderson (1954) stated that in both Gastrophryne olivacea and G. carolinensis males move farther than females. Additional notes on movements of several species in Kansas, some of which reflect age or sexual differences, were reported by Fitch (1958:88-98). Pearson (1955) reported that the young of Scaphiopus holbrooki moved greater distances than adults and also reported that differences in population density and habitat were related to differences in distances moved.

Additional investigations are needed to determine the significance of the differences in movements reported herein for Acris crepitans.

DISCUSSION

Throughout this report various ecological factors have been compared in populations of cricket frogs from northeastern Kansas, mainly the two populations occurring at the University of Kansas Natural History Reservation and at the University of Kansas Fish Laboratory. Although the central thesis of this report is to elucidate the ecological variation in these populations, many other topics deserve additional discussion.

Acris crepitans is somewhat restricted to riparian situations, but like many other common and widespread species, it occurs in a wide variety of habitats. It may be found in abundance along the banks of lakes, ponds, rivers, streams, and occasionally temporary ponds or rain pools and even relatively dry stretches of intermittent streams.

The bodies of water or streams may be clear or muddy; the bottoms may be solid rock, gravel, sand, clay, or mud; and the banks range from bare to heavily wooded. It was anticipated that populations in such diverse habitats might differ considerably in habits. However, in the populations studied, a remarkable similarity was found in the preferred microhabitat. Most frogs appeared to aggregate on relatively level, bare areas at the water's edge, avoiding steep, vegetation-covered slopes in most instances. Cricket frogs were found in the water away from the shore line only when mats of algae were present. From these seemingly preferred places Acris can readily see the various small animals on which they feed and any large animals which may be predators.

Aggregations probably increase individual security through the protective effect that greater density may have in distracting predators. It is much more difficult for me to capture one individual when several are jumping in different directions than it is when I can concentrate on the movements and location of one frog. The simultaneous movement of several frogs is highly distracting, making it difficult to focus on the location of a non-moving frog long enough to effect capture. I presume that a predator might have the same problem and in fact might be least efficient where density of frogs is greatest. In escaping, a cricket frog usually will hop once and remain motionless; hop two or more times along the shore before stopping; hop into the water and immediately return to shore; or hop into the water, dive to the bottom, and remain there for up to five minutes. The frogs usually will not dive to the bottom unless there is something under which they can hide. Since cricket frogs

rapidly adapt to the color of the substrate, they are extremely difficult to detect when they are motionless. Their ability to remain motionless soon after each jump is of obvious selective value. Also of survival value is the habit of returning to shore after jumping into water. Although their light underside may help conceal them from fish when they are on the surface of water, any movement is probably noticed immediately from below. Acris are probably much more vulnerable to attack from water by fish, other frogs, snakes, shore birds and even mammals than they are on land. The behavior pattern of Acris in water has probably been evolved by selection and by elimination of those individuals that tended to swim out into the water rather than orient toward shore. The studies by Ferguson, Landreth, and Turnipseed (1965) and Ferguson, Landreth, and McKeown (1967) have demonstrated the tendency to orient toward shore in both Acris gryllus and A. crepitans.

With regard to life cycle and population dynamics, a similar pattern is evident in both populations, but many characteristics are unique to each population. In both populations there is an annual breeding season with calling from late April until the end of July and with most breeding concentrated in late spring and early summer. Metamorphosis begins before mid-July and a population peak is soon reached as young frogs continue to be recruited into the population. Thereafter, attrition of the annual crop occurs until there are hardly any frogs left a year later. Due to the rapid recruitment of young into the population and rapid mortality of adults during the latter part of the breeding season, composition of the populations shifts constantly at this time. The shift from populations

consisting entirely of adults to those consisting almost entirely of juveniles takes less than a month. Those frogs that metamorphose early grow rapidly; and, since metamorphosis continues for over two months, the range in size of young frogs in any sample is large. Thus, samples taken in autumn do not show distinct size classes, even though a few adults may be present. This general life pattern, consisting of annual turnover, differs from the pattern in most vertebrate animals that have been studied. Even among anurans, most common species live through more than one breeding season as adults, and a breeding population is made up of animals representing several age classes. However, in populations of Acris crepitans in Kansas (and probably all other areas with a growing season shorter than the one here or equal to it) only one age class is represented in a breeding population, and those members of a population that survive to breed have all been exposed to relatively similar conditions. Rates of evolution in such populations undoubtedly differ from those in populations in which different generations are not genetically isolated from one another. This species is ideal for studies of both life patterns, since young-of-the-year may mature and reproduce before the end of the breeding season in central Texas (Pyburn in Blair, 1961:106), and some adults survive through two breeding seasons in southern Louisiana (Bayless, pers. comm.). It is not surprising to find such wide variation in the life pattern of Acris crepitans, since this species occupies an extensive geographic range. Under most circumstances natural selection can be expected to favor rapid development. Mortality rates are almost always higher in early stages of development, and the sooner an organism matures the better

are its chances of reproducing before it dies. However, the climatic conditions are such in Kansas that sufficient growth and maturation cannot occur (at least in females) before winter. The production of sperm by young males in early autumn is of questionable value since it seems unlikely that any adult females would be gravid at this time. If mating did occur, development of tadpoles could not occur before winter, and chances of survival would be nil. On the other hand, southern populations tend to remain active throughout the year, and the breeding season is protracted. Since frogs are active longer in the south, their exposure to possible predation, desiccation, and disease is increased. Thus, selection would favor rapid development to compensate for these factors.

Rather than considering a two-year life span an adaptation to conditions in the south, perhaps the annual cycle is an adaptation to the harsher climatic conditions in the north. With the relatively short breeding season and the sudden appearance of large numbers of young in northern Kansas, death of the adults would remove one of the main sources of intraspecific competition for food and may allow for more rapid growth of the young through an increased food supply for each individual. Adult Acris have not been studied in captivity to determine longevity, but their rapid disappearance from the population suggests that natural death could play an important role.

The greatest differences between the two populations (Reservation and Fish Lab) were in size of individuals, density of the populations, and proportions of each color morph (color of vertebral stripe) in each sample. Although the size of individuals was about the same at metamorphosis, the growth rate and maximum size of individuals

at the Fish Lab were greater than at the Reservation (see Table 3 and Fig. 4). Examination of several individuals revealed large numbers of metacercariae of a fluke in the abdominal cavity of 97.5 per cent of the sample from the Reservation. The same kind of parasite was found in 47.1 per cent of a sample from the nearby Rockefeller Experimental Tract (RET) and in only 9.1 per cent of a sample from the Fish Lab. The frogs from the Rockefeller Experimental Tract averaged 19.4 mm. in length, approximately the same size as frogs from the Reservation at this time of year (late September and early October) but much smaller than frogs at the Fish Lab. Correlation was found between number of metacercariae and size of frogs (Table 16). Generally, smaller frogs averaged more metacercariae than did larger frogs. However, this does not offer conclusive proof that metacercariae inhibit growth; samples taken at this time of year tend to vary considerably in size because post-metamorphic age varies from less than one month to more than two months. If most cercariae did not appear until September and if they infect tadpoles or juveniles in the process of metamorphosing, they would be more numerous in small frogs. On the other hand, if correlation was lacking, it would not disprove inhibition of growth because the time lapse between infestation and capture of the frogs is not known. Since correlation was found both within and between populations and other causative factors were not readily apparent, the hypothesis of growth inhibition is strengthened. Other possibilities which must be considered follow. Estimates of density measured as number of frogs per foot of shore line (Fig. 7) usually indicated about three to four times as many frogs per foot of shore line at the Reservation. With greater

TABLE 16.—Relationship between number of metacercariae and size of frogs in four samples of Acris crepitans. KUNHR = University of Kansas Natural History Reservation; RET = Rockefeller Experimental Tract; Fish Lab. = University of Kansas Fish Laboratory. Average size of each sample is given in parentheses below the date of collection.

Location and date of collection	Size range of frogs (in mm.)	Number of frogs in sample	Number of metacercariae Total (Range)	Average number of metacercariae per frog
KUNHR Sept. 25, 1965 (15.85)	12.5-14	8	243 (4-107)	30.4
	14.5-16	18	461 (0-80)	25.6
	16.5-18	9	221 (1-73)	24.6
	18.5-20	4	51 (3-26)	12.8
RET Oct. 3, 1965 (19.72)	16.5-18	5	103 (1-49)	20.6
	18.5-20	16	226 (0-79)	14.1
	20.5-22	9	68 (0-25)	7.6
	22.5-24	4	11 (0-11)	2.8
Fish Lab. Sept. 22, 1965 (22.77)	18.5-20	2	0	0
	20.5-22	14	0	0
	22.5-24	7	0	0
	24.5-26	2	0	0
	26.5-28	3	0	0
Fish Lab. Oct. 15, 1965 (23.43)	18.5-20	1	0	0
	20.5-22	7	0	0
	22.5-24	7	1	0.14
	24.5-26	5	29 (in 1 frog)	5.8
	26.5-28	1	0	0
	28.5-30	1	0	0

density, there is less food per individual unless density of food also is proportionately greater. No estimates of invertebrate populations which are utilized as food have been made. Examination of digestive tracts show that most frogs in both populations feed regularly; nearly every individual examined had a full stomach (Table 17). Variations in the importance of different food items may result partially from the small size of the samples. Since food habits were not studied in detail, these differences cannot be used to show trends in feeding. One of the most outstanding differences in the samples was the utilization of Collembola in the Reservation population. Collembola were extremely abundant at the Fish Lab but were not used by any of the frogs in these samples. Perhaps this finding indicates that there is much more competition for food at the Reservation, and a secondary food source must be utilized. Even if food is scarcer at the Reservation pond, the wooded habitat there affords more protection from desiccation and frogs can forage farther from water. However, more energy may be utilized in searching for food, whereas at the Fish Lab, with lower density, there may be more food per individual and less utilization of energy in seeking food. It seems unlikely that differences in food are directly responsible for the differences in size.

Since desiccation is more likely to occur in an open situation, a rapid growth rate and larger size may have been selected for in the Fish Lab population to reduce the surface:volume ratio. Acris in the northern and western extremes of the range are larger than those in the south; the same selective forces may work to a lesser degree with variations in the habitat. Division and partial isolation of

TABLE 17.—Stomach contents of four samples of *Acris crepitans*. Abbreviations are the same as in Table 16. The average number of items per frog was calculated as the total of each item divided by the total number of frogs in each sample and not by the frequency for each item. Thus it represents the average for the sample, not the average of these frogs feeding on a particular category.

Location	KUNHR		RET		Fish Lab.			
	Date	9/25/65	10/3/65		9/22/65	10/15/65		
Number in sample	38		34		28	22		
Per cent of sample containing food	94.8		94.2		89.3	100		
Food item	Average no. of items per frog	Per cent freq. of occurrence	Average no. of items per frog	Per cent freq. of occurrence	Average no. of items per frog	Per cent freq. of occurrence	Average no. of items per frog	Per cent freq. of occurrence
	Coleoptera	0.18	15.8	0.85	58.9	0.32	25	0.68
Collembola	13.16	71.0	0	0	0	0	0	0
Diptera	0.74	47.4	1.00	58.9	0.32	25	0.32	13.6
Hemiptera	0.05	5.3	0.32	23.6	1.11	32.2	0.23	13.6
Homoptera	1.26	44.8	0.18	14.7	0.32	14.3	0.18	18.2
Hymenoptera	0.29	13.2	0.65	41.2	0.67	35.8	0.46	27.3
Lepidoptera	0.32	26.4	0.09	8.8	0.07	7.1	0	0
Orthoptera	0	0	0	0	0.07	3.6	0	0
Unidentified Insect	0.11	10.5	0.26	20.6	0.29	14.3	0.77	45.5
Arachnida	0.11	7.9	0.35	29.4	0.36	35.8	0	0
Crustacea	0.05	5.3	0	0	0.07	7.1	0.05	4.6
Total	16.3 4.43*		3.71		3.57		2.68	

*If 10 Collembola = 1 other item

local populations of cricket frogs in ponds undoubtedly results in more genetic changes than would be found in a large, randomly breeding population inhabiting a stream. Although isolation is not complete between any of the local populations, gene flow may be retarded to some degree. Sufficient evidence is not available to determine the validity of this supposition. Sex ratio also must be considered in measuring samples for comparison of size differences among populations. Since females are larger than males, a sample containing mainly females will average larger than one containing mainly males. Therefore, allowance must be made for differing sex ratios when two or more samples are compared.

Although variation in proportions of each color morph have been discussed previously, other factors which influence the appearance of each color deserve brief mention. The part played by selective predation in determining adaptability of each color morph depends upon the ability of various predators to see (and capture) frogs with a vertebral stripe of one color more readily than another. The ability to see a certain colored stripe depends not only on color vision but also on the shade of the color and how it contrasts with the ground color of the individual and color of the substrate on which the frog is sitting. Both the shade of the vertebral stripe and the ground color may be altered considerably within a few hours by movements of dark pigments of the melanophores. Thus, under certain conditions, the vertebral stripe is less conspicuous than at other times, though still visible. In certain instances the color of the substrate is simulated almost perfectly. These subtle variations in color are likely to have considerable consequences with respect to

selective predation and also render it difficult to quantify variations or experiment with predators.

Although the methods used in censusing and the results (as they apply to the populations under consideration) have been discussed previously, the applicability of these methods to future studies on this and other species has received only brief mention. In any study involving capture-recapture data, several factors will influence population estimates. While loss of toes and limbs, mortality, and emigration will occur in both the marked and unmarked groups of animals, natality (or recruitment) and immigration will occur only in the unmarked group. Hence, many methods tend to have a positive bias and may show an increase in the population while it actually is decreasing. One of the major difficulties in the study of populations is determining which of the aforementioned factors is involved in the disappearance or appearance of animals. While animals added through natality or recruitment usually may be recognized by their small size, mortality and migrations are more difficult to recognize both as to time and rate. Analysis of stomach contents of predators usually necessitates killing the predators, causing an unnatural change in mortality rate. The disappearance of one individual for a period of time may indicate that it has moved to another locality temporarily or that it has become inactive or more elusive.

In Acris or any other animal with an annual population turnover and limited breeding season, population parameters are easier to estimate than in species composed of several in distinct size or age groups. Population estimates can be made in any animal population by using several methods, but estimates in species with annual turnover

also supply information on age-specific mortality rates. If the minimum living population (MLP) can be calculated for any given time, it serves as a reference point from which to judge the estimates made by other methods. However, ideally the MLP should be based on samples taken as soon as the first young appear and continued at short intervals throughout the year, so that a large majority of the population is marked. Also, efforts should be made to capture every active animal in each sample. If individuals of a relatively isolated population of Acris were marked at weekly intervals beginning as soon as the first young emerged, the MLP would probably suffice for determining most population parameters. Each individual should be accurately measured and described; toes or limbs are often lost subsequent to marking, making identification of individuals difficult or impossible. A few individuals in each population had to be eliminated from census computations in my study because their markings were altered by loss of toes or limbs, presumably by predators. From supplementary descriptive notes, I was able to identify such anomalous individuals in a few instances. Such sampling should serve for construction of life tables for many other animals besides amphibians. In species whose high density prevents including an entire local population in a sample at short enough time intervals to minimize the effect of mortality, more rapid methods of marking need to be developed.

Tadpoles have been largely neglected in this study because of the difficulties involved in locating, capturing, and marking them. Developmental rates and mortality rates of tadpoles and their relationship to success of adults are in need of intensive, long-term

study. Mortality rates of larvae and adults of each population are most likely unique to each population and also from year to year within a population. The causes of mortality among populations may be the same (i.e., desiccation, predation, parasitism, winter kills, and natural death), but the specific interactions of each of these vary considerably. These differences may be slight in populations within a restricted area; but, owing to the large range of Acris and its wide variety of habitats, the causes of different mortality rates may determine the difference between survival or extinction in certain areas.

Both the amount and distribution of precipitation vary widely and are extremely critical to populations of Acris. Those living near semipermanent or temporary bodies of water are much more dependent on distribution of precipitation than those living near permanent water. Fluctuations in water level are believed to influence selective predation in favor of certain color morphs. Complete evaporation of temporary pools or streams during the breeding season may completely eliminate some populations.

The types and number of predators as well as times of predation differ from population to population. One pond has been observed near Denton, Texas, where all the adults and almost all the young frogs appear to have been eliminated by predators (mainly shore birds, raccoons, bullfrogs, and ribbon snakes) within a few weeks after metamorphosis began, whereas another nearby population seemed to have but few predators.

Winter kills due to freezing must vary in different parts of the range. In some parts freezing temperatures rarely occur,

whereas in others they occur frequently. Of the various causes of mortality in the populations in northeastern Kansas (excluding tadpoles), it is believed that at least 30 per cent was due to winter kills, since less than 10 per cent of the group marked in the autumn was recaptured in spring and nearly 60 per cent was eliminated before winter. Desiccation probably was highest in the summer and autumn when the frogs were small and had a high surface-to-volume ratio. Rains caused mass dispersals, and the chances of small frogs surviving long enough to return to water were reduced. Peak periods of predation were not determined, but predation probably was heaviest from late spring through early autumn. The adults that lived through the breeding season may have been preyed upon or may have died of natural causes after breeding.

SUMMARY

A population of cricket frogs, Acris crepitans, was studied at the University of Kansas Natural History Reservation from autumn, 1963, to spring, 1966; another population was studied at the University of Kansas Fish Laboratory from spring, 1964, to spring, 1966. Samples also were taken from additional populations near Lawrence, Douglas County, Kansas. The two primary study areas consisted of a pond and stream in woodland and a reservoir and eleven ponds in grassland. Most differences recorded between frogs in the two areas probably resulted from variation in habitat rather than genetic isolation.

Cricket frogs are usually the most abundant anurans near Lawrence. They are active from March to November or December, and active individuals may be found after two or three warm days in winter.

Calling begins in late April, but most spawning occurs from late May to early July. In Kansas females may mate at least twice during the breeding season, which ends in late July. Larval development appears to require from five to ten weeks, and newly metamorphosed frogs are found between mid-July and late September. Some young males are capable of calling soon after metamorphosis, but they do not breed until the following spring. By early October males produce motile sperm, and in the following March or April the vocal pouch forms and darkens. Females reach sexual maturity in late April when the eggs enlarge.

Two periods of rapid growth were observed: from July until late September and from March through July. Size and growth rate of females exceeded those of males at all ages. The Fish Lab population contained frogs that were considerably larger than individuals in the Reservation population. The small size of individuals at the Reservation was attributed to inhibition of growth by heavy infestations of metacercariae of an unidentified species of fluke and to competition for food. Weight varied from about 0.1 gram in newly metamorphosed frogs to between 1.0 and 2.5 grams in adults, depending upon sex and breeding condition. The relationship between tibia length and snout-vent length is curvilinear and reflects allometric growth but does not vary between males and females of the same size. However, since females are larger than males, these values usually differ in any sample; the differences reflect the composition of the sample with respect to size, age, and sex rather than genetic differences between populations.

The sex ratio varied from nearly five females per male in

juveniles to approximately one and one-half males per female in adults. The overall percentage of males was 57.6, indicating higher mortality rates in females if my samples were representative of the populations from which they were taken.

Group markings by toe-clipping were used to conserve time and to allow a large proportion of the population to be marked. This method allowed the dates of 15 sampling periods and the differentiation of 15 areas to be indicated by clipping no more than two of the toes on each hind foot. Individual markings were given by clipping toes on the front feet whenever frogs were recaptured. A method of recording data on capture and recapture of individuals was devised that allowed the minimum living population at any time to be calculated. Several methods of calculating population density indicated a "Type 2" survivorship curve for post-metamorphic frogs. The average life expectancy for post-metamorphic frogs is believed to be about four months, about five per cent survive the winter, and complete population turnover occurs in about sixteen months. Density, estimated as number of frogs per foot of shore line, was greater at the Reservation, suggesting that the wooded habitat there is more favorable than the grassy habitat at the Fish Lab. Perhaps the greater ecological diversity of the habitat at the Reservation allows greater density of potential food items and of frogs.

Estimates of reproductive potential indicate an average annual production of about 10,000 eggs at the Reservation compared with only about 5,000 at the Fish Lab reservoir and 5,000 at the Fish Lab ponds.

Polymorphism with respect to color of the vertebral stripe (green, rusty, brownish, or gray) is striking in Acris. But in most

frogs the middorsal area is indistinguishable from the background color which is some shade of brown, gray, olive, or nearly black. For convenience in handling data, three classes of vertebral stripe coloration were distinguished: green, brown, and gray. Frogs lacking the stripe were classed in the "gray" category. In all populations sampled, gray morphs were predominant (usually accounting for more than 60 per cent of the sample), brown morphs were less common (about 25 per cent), and green morphs were scarce. In open situations the proportion of green morphs was usually near 5 per cent, while in wooded situations it was about 10 per cent. In dry periods when decreasing water level exposed more bare ground, the percentage of green and brown morphs decreased and the percentage of gray morphs increased. This trend was reversed when water levels were high. Correlation has been found between color of the substrate and frequencies of the three color morphs. Green blotches or spots sometimes appear on frogs of all three color morphs and may serve to enhance protective coloration on certain backgrounds. Literature on mode of inheritance of polymorphism in A. crepitans is reviewed, as is literature on comparable color morphs in A. gryllus. Judging from present geographical distribution of these two species, it appears that the two originated by the splitting of a centrally located group. The increase of gray morphs of crepitans toward the northern and western limits of its range indicates that crepitans appears to have evolved toward the gray phase and toward more xeric conditions, whereas gryllus has become adapted to more mesic conditions.

Known and suspected predators in northeastern Kansas are mentioned.

Infestation by trombiculid chigger-mites was studied. The number of chiggers occurring on each frog deviated significantly from the expected number if frogs and chiggers were distributed at random over the areas where infestations occur; most frogs either had no chiggers or several. Effects of these parasites are not known.

Most frogs occupied shore lines having muddy, beach-like areas. Variation in habitat influenced the patterns and magnitude of movements. During dry periods frogs were restricted to moist soil near the edge of the water; movements occurred along this marginal strip rather than by crossing any body of water more than a few feet wide. Dispersal in all directions occurred following rains and in cool, humid weather; at such times movements were likely to be relatively lengthy.

Most cricket frogs remain in a small area, but movements of several hundred feet are not uncommon. Nearly half of the recorded movements were less than 25 feet. Movements at the Fish Lab tended to be greater than those at the Reservation, probably a result of division of the habitat at the Fish Lab into several separate ponds with intervening areas.

While there are many similarities between populations of cricket frogs living in close proximity to one another, there also are many differences. These differences often appear to be the result of non-genetic factors and should be thoroughly investigated before taxonomic and evolutionary implications are made concerning such populations.

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