THE ECOLOGY AND LIFE HISTORY OF THE MINK FROG, *RANA SEPTENTRIONALIS* BAIRD

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INTRODUCTION

Rana septentrionalis was originally described by Baird (1854). Garnier (1883) gave the species the common name of mink frog, since adults emit a musky mink-like odor when captured. The ecology of the mink frog is comparatively unknown, probably due to its northern distribution. It is the purpose of this paper to report on several aspects of the ecology and life history of *R. septentrionalis* in the region of Lake Itasca, the type-locality of the species. Specifically, growth and development of the species will be described. The breeding season will be delimited and breeding choruses will be discussed. Many physical and biotic elements of the mink frog's ecological niche will be examined, and differences among the niches of the mink frog and other northern anurans will be distinguished. Finally, the state distributional pattern of the mink frog in Minnesota will be outlined.

THE ECOLOGY AND LIFE HISTORY OF THE MINK FROG, *RANA SEPTENTRIONALIS* BAIRD

Several aspects of the ecology and life history of *Rana septentrionalis* were investigated in the vicinity of Itasca State Park, Minnesota.

R. septentrionalis had a one-year larval period, although a few individuals may have spent two years in the tadpole stage. Tadpoles showed a marked reduction in growth during the winter months. Metamorphosis took place during July and August. Transforming individuals had an average snout-vent length of 37.2 mm. Some frogs attained body lengths of 60 mm. by the end of August of the first full summer following transformation. Although 72 mm. was the maximum length of both sexes, there were higher frequencies of females in the larger size classes. This size dimorphism may have been due to higher death rates in males or faster growth rates in females.

In 150 (98%) of 153 frogs 48 mm. or longer, the ratio of snout-vent length to tympanum diameter was below ten in males and ten or above in females. This ratio was employed as the primary means of sex recognition in the field. Frogs of both sexes smaller than 48 mm. usually had ratios above ten and were classified as subadults.

Males became sexually mature during their first full summer following transformation when about 45 to 50 mm. in length. Females became sexually mature during either their first or second summer when about 54 to 59 mm. in length. Calling males were heard from late May through early August. Breeding took place at night from late June through early August. Calling males in a breeding habitat shifted their locations during the summer calling period.

Frogs were found moving across land at night during or immediately following periods of precipitation. Under such environmental conditions the frogs could minimize water loss and maximize water uptake in order to maintain safe body water levels. At all other times mink frogs inhabited both lentic waters and lotic waters without rapid currents. Breeding and hibernating frogs occurred only in permanent waters. Non-breeding frogs occupied both permanent and temporary habitats during the ice-free season. During July and August, the majority of frogs in West Twin Lake rested with only their eyes and snout above the water surface. The distribution pattern of the West Twin Lake population was influenced by the distribution of water surface substrata on which the frogs rested.

R. septentrionalis fed primarily on algae through stage XX, fasted during stage XXI, and commenced on an adult diet during stage XXII (stages based on Taylor and Kollros, 1946). All 74 adult stomachs examined contained animal material. Accidentally ingested plant material occurred in 90.5% of the stomachs. Diet differences among populations were due to differences in habitat and seasonal food availability.

"Red Leg" and the tapeworm Ophiotaenia olor occurred in the aquatic frogs. R. septentrionalis food habits suggested that O. olor utilizes a single intermediate host during its life-cycle. R. septentrionalis had many aquatic and non-aquatic predators. Generally, mink frogs leaped onto shore to escape underwater predators, and dove into submerged vegetation or bottom mud to evade above-surface disturbances.

Body temperatures of 27 partly-submerged frogs ranged from 16.2° C. to 27.1° C. Solar radiation served to raise body temperatures above ambient water and air temperatures.

Mink frogs were found in 15 Minnesota counties for the first time, bringing the number of Minnesota county records to a total of 24. The geographical range of R. septentrionalis in Minnesota overlapped with the Minnesota distributions of R. sylvatica, R. pipiens, and R. clamitans. Aspects of the ecological niche of R. septentrionalis were reviewed and discussed in relation to the ecological niches of the three ranids sympatric with the mink frog.

James C. Underhill

DESCRIPTION OF MAJOR STUDY AREAS

All field work was done from June 1966 through August 1968 in the vicinity of Itasca State Park, Minnesota. This area, hereafter referred to as the Itasca region, includes southern Clearwater County, northeastern Becker County, and west-central Hubbard County. Although observations and collections were made at a number of sites in the Itasca region, the greater part of the field work was done at six permanent aquatic habitats in Itasca State Park. The dominant aquatic plants in these habitats were named according to Gleason and Cronquist (1963).

West Twin Lake is a circular, 2.5-acre lake located in T 143 N, R 35 W, Section 30 in Hubbard County. The dominant aquatic plants in the lake are _Najas flexilis_, _Anacharis canadensis_, _Potamogeton zosteriformis_, _P. natans_, _Utricularia vulgaris_, and _Sparganium chlorocarpum_. Filamentous green algae are also abundant near the shore. The lake is surrounded by a sedge mat made primarily of _Carex lasiocarpa_. The sedge mat has given rise to many sedge islands that float about the lake surface during periods of high water and are stranded in shallower depths during periods of low water.

East Twin Lake is an eight-acre lake located 150 feet southeast of West Twin Lake in T 143 N, R 35 W, Section 30. The dominant aquatics are identical to those of West Twin Lake.

Bog D Lake is a 0.8-acre lake located 1000 feet northeast of West Twin Lake in T 143 N, R 35 W, Section 30. A portion of the lake was shown by Conway (1949) in her Figure 2. Najas flexilis, Ceratophyllum demersum, Potamogeton zosteriformis, and Lemna minor are the common aquatic plants.

Deming Lake is a 12.5-acre lake located 1150 feet south of West Twin Lake in T 143 N, R 35 W, Section 30 in Hubbard County and in T 143 N, R 36 W, Section 25 in Clearwater County. Common aquatics in Deming Lake include Chara, Najas flexilis, Brasenia Schreberi, Nuphar variegatum, Potamogeton amplifolius, and Sparganium fluctuans.

French Creek Bay is a shallow bay located along the west shore of the north arm of Lake Itasca in T 143 N, R 36 W, Section 2, in Clearwater County. The bay supports a rich growth of aquatics including Ceratophyllum demersum, Potamogeton zosteriformis, Nuphar variegatum, Nymphaea tuberosa, Lemna trisulca, L. minor, and Spirodela polyrhiza.

The two Wilderness Drive Ditches are located along the north and south sides of Wilderness Drive where the road crosses a tamarack (Larix laricina) and black spruce (Picea mariana) bog. The north ditch is is T 144 N, R 36 W, Section 34, and the south ditch is in T 143 N, R 36 W, Section 3, in Clearwater County. Both ditches have lengths of 100 feet, maximum widths of ten feet, and maximum depths of six feet. The most abundant plant species in the ditches are Potamogeton foliosus, Lemna trisulca, L. minor, Utricularia vulgaris, Typha latifolia, and Potentilla palustris.

GENERAL METHODS

All tadpoles and frogs in aquatic habitats were approached by means of canoe, rubber life raft, or hip boots. Observations and censuses of frogs were greatly facilitated by a pair of eight-power binoculars. Frogs were captured by the use of a dip net or by hand. A captured frog was held in the palm of the left hand and measured from the tip of the snout to the anterior lip of the cloaca. The left tympanum was measured from the anterior to the posterior edge. Snout-vent length was measured to the nearest millimeter, and tympanum diameter was measured to tenths of a millimeter. All measurements were made by means of steel vernier calipers.

Frogs captured in West Twin Lake were numbered for individual recognition by clipping toes in the manner described by Martof (1953a). If a captured frog had been marked previously, its number was recorded. Every marked frog was released at its point of capture.

Individual shoreline study sections were established at West Twin Lake by placing 56 consecutively-numbered stakes at 24-foot intervals around the entire lakeshore. The resultant 24-foot study sections were considered as having a width of ten feet, the usual distance from the shoreline to the open-water limit of floating vegetation. The location of every frog observed or captured in West Twin Lake was determined with reference to the nearest stake.

Specific methods and materials peculiar to each topic of this paper will be described as the topics are individually considered.

TADPOLE GROWTH

Rana septentrionalis eggs are deposited in permanent aquatic habitats from late June through early August. Previous investigators have indicated that *R. septentrionalis* tadpoles transform into frogs approximately one year from their date of hatching (Garnier, 1883; Wright, 1932; Vladykov, 1941). No previous studies have been made of the growth of the mink frog during its one-year larval period. Consequently, the growth pattern of tadpoles in Itasca State Park was investigated from May 1967 through May 1968.

The tadpoles used in the study were taken from three breeding sites: Deming Lake, East Twin Lake, and the Wilderness Drive Ditches. Tadpoles were collected along the shorelines of these areas by means of long-handled dip nets and minnow traps. The animals were killed immediately in ten percent formalin. From two to fourteen months later, the preserved tadpoles were measured, weighed, and staged. Body length was measured to tenths of a millimeter by means of steel vernier calipers. Body length was measured from the tip of the snout to the tip of the tail. When the snout-tail length of a metamorphosing tadpole was less than the snout-vent length, the latter measurement was recorded and taken as the transformation size of the individual. All tadpoles were blotted dry on paper toweling and weighed to 0.01 gram. The animals were staged according to tables given in Gosner (1960).

Recently-hatched tadpoles were sought beginning 18 July

1967. Bi-weekly samples of ten individuals each were taken from the North Wilderness Drive Ditch beginning 30 July, when the first newly-hatched tadpoles were found. Bi-weekly samples of 20 tadpoles each were taken from East Twin Lake beginning with the first successful collection on 29 August. Adequate late summer and fall samples of tadpoles hatched in 1967 could not be found in Deming Lake.

The final 1967 collection from the North Ditch was taken on 15 October. The ditch froze over soon thereafter. Tadpoles from the 1967 breeding season were never again found in the Ditches. On 22 February 1968 a hole was chopped through 18 inches of ice covering the North Ditch and three minnow traps were placed in the water. Minnow traps had successfully caught many tadpoles during the 1967 summer. However, the traps in the ice-covered ditch caught only mud minnows, _Umbra limi_. Tadpoles had also disappeared from the Wilderness Drive Ditches one year before. Three minnow traps set in the South Ditch from 25 to 27 January 1967 caught only fish, although a large population of recently-hatched tadpoles had been observed in the South Ditch during August 1966. No maturing tadpoles were seen in the Ditches in 1967 or 1968. The Wilderness Drive Ditches were the smallest and shallowest habitats in which _R. septentrionalis_ tadpoles were observed. The relatively confined tadpoles may have been exterminated during the 1966-1967 and 1967-1968 winters by anaerobic conditions, food shortages, predators, parasites, or diseases.

Tadpoles in larger and deeper aquatic habitats survived the winter months. The final 1967 collection from East Twin Lake was taken on 15 October. Samples were taken from the same tadpole population on 29 April, 12 May, and 30 May 1968. No winter collections were attempted at East Twin Lake.

The lengths, weights, and stages of the 1967-1968 tadpoles are given in Table 1, and the mean lengths and weights are plotted in Figure 1. The majority of tadpoles from East Twin Lake either hatched sooner or grew faster than the tadpoles from the North Wilderness Drive Ditch during July, August, and September 1967. By 15 October, however, the ditch tadpoles were approximately the same mean length, weight, and stage as the lake tadpoles.

Vladykov (1941) stated that tadpoles from Laurentides Park in Quebec reached a total length of about 45 mm. by the end of August. Most tadpoles in Itasca State Park did not reach this length before mid-October, although the largest animals may have measured 45 mm. in early September.

Tadpoles hatched in 1967 in East Twin Lake were first collected in 1968 on 29 April. These animals averaged 3.4 mm. longer and 0.20 gm. heavier than tadpoles collected on 15 October 1967. The tadpoles taken on 15 October averaged 4.2 mm. longer and 0.22 gm. heavier than tadpoles collected on 13 September. Thus, growth during a 197-day period including the winter season was less than growth had been during a 32-day period of the previous fall. A reduction in growth during the winter months has

TABLE 1. LENGTHS, WEIGHTS, STAGES, AND SAMPLE SIZES (N) OF *RANA SEPTENTRIONALIS* TADPOLES COLLECTED 25 MAY 1967 -- 30 MAY 1968 IN ITASCA STATE PARK, MINNESOTA. STAGES BASED ON TABLES GIVEN IN GOSNER (1960).

Date	Mean Length (Mm.)	Range In Length	Mean Weight (Gm.)	Range In Weight	Mean Stage	Range In Stage	N	Mean. Length (Mm.)	Range In Length	Mean Weight (Gm.)	Range In Weight	Mean Stage	Range In Stage	N
1967	EAST TWIN LAKE							DEMING LAKE						
25 May	51.5	23.6- 62.5	2.36	0.39- 4.11	29.7	25-34	20	61.0	48.5- 81.1	4.22	2.17- 8.81	31.3	29-36	20
11 June	62.8	48.0- 72.5	4.65	1.80- 7.47	34.4	29-37	20							0
25 June	65.3	53.4- 81.4	5.63	2.95- 9.38	34.3	30-40	20	77.8	55.0-100.1	10.62	5.09-15.95	35.9	31-41	20
9 July	70.8	46.6- 87.1	6.66	3.42-11.46	38.3	30-45	20	79.2	48.4- 90.7	8.56	6.62-11.12	41.5	38-45	20
24 July	41.5	35.4- 69.7	5.90	3.66- 9.34	44.9	44-45	20	51.7	37.1- 87.3	7.29	5.73-10.29	44.6	41-45	20
5 Aug.	44.7	35.9- 85.6	6.61	5.89- 8.36	44.8	43-45	20	48.1	32.8- 81.8	5.33	3.79- 8.01	44.7	44-45	20
15 Aug.	43.0	35.9- 76.8	6.26	4.03- 8.96	44.9	44-45	20							0
29 Aug.	37.0	34.1- 41.7	5.61	4.21- 7.96	45.0	45-45	20							0
1967	EAST TWIN LAKE							WILDERNESS DRIVE DITCHES						
30 July							0	9.7	9.3- 10.0	0.02	0.01- 0.02	25.0	25-25	10
14 Aug.							0	15.3	11.6- 17.6	0.09	0.06- 0.12	25.5	25-26	10
29 Aug.	34.8	25.9- 43.2	0.84	0.39- 1.38	27.9	26-29	20	23.6	20.0- 26.8	0.33	0.18- 0.41	26.7	26-27	10
13 Sept.	41.2	31.7- 49.3	1.31	0.69- 2.06	28.6	26-31	20	29.7	27.5- 33.0	0.68	0.56- 0.84	27.6	27-28	10
27 Sept.	42.7	21.8- 53.9	1.40	0.23- 2.31	28.6	26-31	20	35.5	31.9- 42.4	1.10	0.80- 1.53	28.1	27-29	10
15 Oct.	45.4	36.5- 56.4	1.53	0.85- 2.78	28.6	27-32	20	41.4	39.1- 43.6	1.55	1.36- 1.75	28.6	28-29	10
1968														
29 April	48.8	31.5- 60.7	1.73	0.51- 2.77	29.0	27-31	20							0
12 May	53.7	41.9- 64.3	2.46	1.23- 4.41	30.3	27-34	20							0
30 May	58.8	46.3- 69.5	3.14	1.72- 4.93	31.8	29-35	20							0

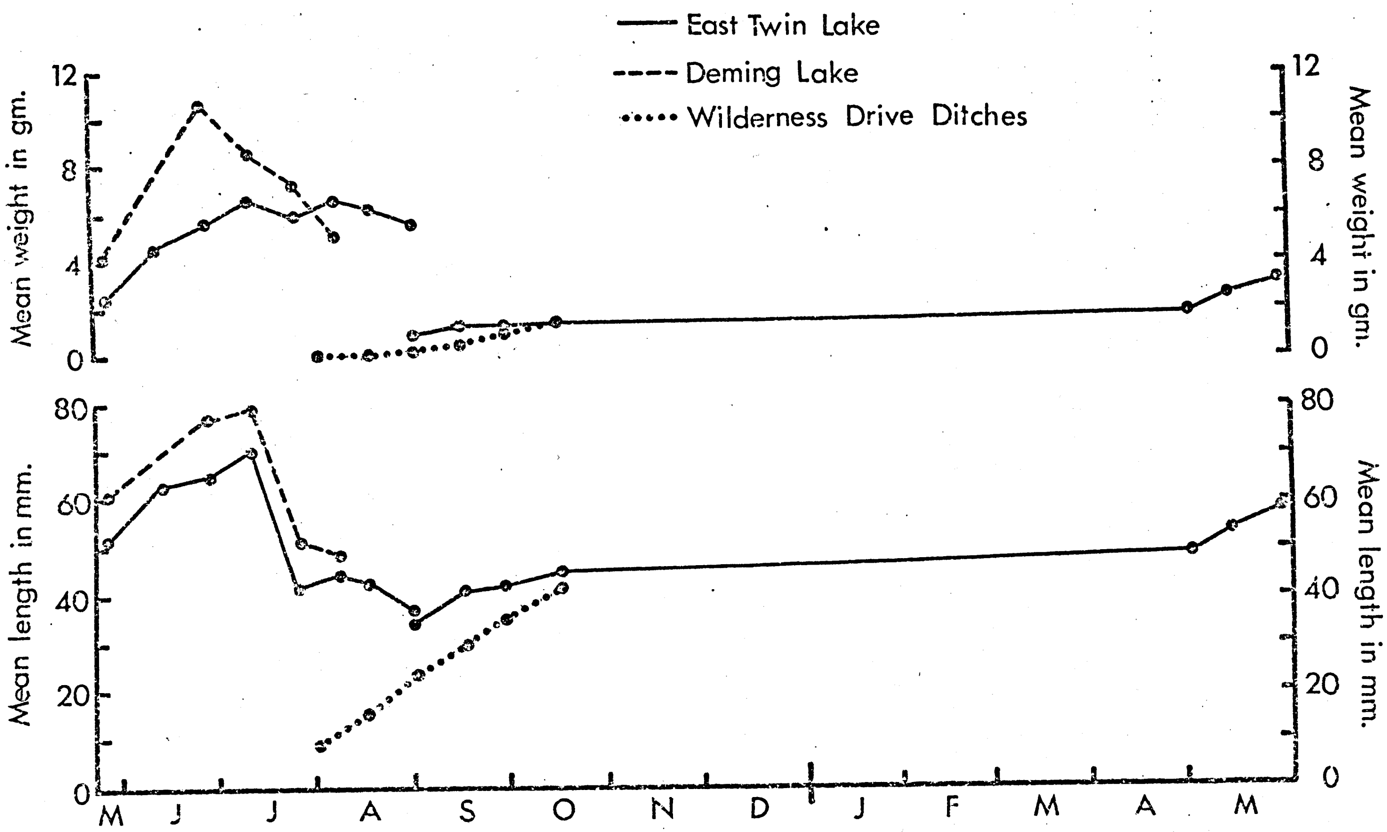


Figure 1. Growth patterns of Rana septentrionalis tadpoles collected 25 May 1967 -- 30 May 1968 in Itasca State Park, Minnesota. Individual data points for East Twin Lake and Deming Lake represent mean measurements of 20 tadpoles. Individual data points for the Wilderness Drive Ditches represent mean measurements of 10 tadpoles.

been previously noted in other species of overwintering tadpoles (Goin et al., 1968) and in salamander larvae (Anderson, 1967).

The growth rate of East Twin Lake tadpoles increased markedly in May 1968 (Figure 1). The final sample of tadpoles hatched in 1967 was collected on 30 May 1968. The premetamorphic growth pattern of R. septentrionalis during the summer months already had been derived from samples of tadpoles hatched in 1966.

Tadpoles hatched in 1966 were first taken on 25 May 1967 from East Twin Lake and Deming Lake. Altogether, eight samples of 20 tadpoles each were collected from East Twin Lake during the period 25 May -- 29 August 1967. Only five samples of 20 tadpoles each were taken from Deming Lake, since on three sampling dates no tadpoles were caught even after thirty minutes of diligent searching. As was reported above, no tadpoles hatched in 1966 were found during 1967 in the Wilderness Drive Ditches.

Tadpoles continued to grow in both length and weight through June 1967 (Table 1 and Figure 1). It is not known why the tadpoles from Deming Lake had higher mean lengths and weights than did the animals from East Twin Lake. The largest tadpole found during the study was taken on 25 June from Deming Lake. The stage 41 larva had a length of 100.1 mm. and a weight of 15.95 gm. The largest tadpole recorded by Wright (1929) had a total length of 99 mm.

Following stage 41 the forelimbs appear and the gape of the mouth begins to widen (Gosner, 1960). Like Rana pipiens (Taylor and Kollros, 1946) and R. sylvatica (Herreid and Kinney, 1967), R. septentrionalis declined in length after stage 41 due to resorption of the tail. R. septentrionalis also declined in weight after stage 41.

Wright (1932) and Wright and Wright (1949) stated that the mink frog transforms at 29 to 40 mm., average 37 mm., during the period 24 June to 30 August. The transformation length of 54 stage 45 tadpoles from East Twin Lake and Deming Lake ranged from 32.8 to 41.9 mm., average 37.2 mm. Newly-metamorphosed (stage 46) mink frogs were found in 1967 from 24 July to 15 August at Deming Lake, and from 5 July to 15 August at East Twin Lake.

Some tadpoles hatched in 1966 did not transform in July and August 1967. Tadpoles exceeding 72 mm. were caught during September in East Twin and Deming Lakes. In December 1967, Alan Baker found a large R. septentrionalis tadpole frozen in an ice block cut from Deming Lake. It has been suggested that some tadpoles of Rana pipiens (Kilby, 1945), R. sylvatica (Hildebrand, 1949), and R. virgatipes (Standaert, 1967) may overwinter and transform one year later than usual. It seems that a few R. septentrionalis individuals might also spend an additional year in the tadpole stage.

POSTMETAMORPHIC GROWTH

The postmetamorphic growth of *R. septentrionalis* was investigated through examination of size-frequency data and by remeasurements of marked animals. The mark-recapture method is most meaningful when the marked animals are of a known age, i.e. metamorphosing frogs at age 0. If animals of an unknown age are marked, measured, and later remeasured, age-specific growth may not be determined as accurately. A special effort was made to mark metamorphosing frogs at the beginning of the present study. From 4 July through 16 August 1966, 128 transforming mink frogs were marked at West Twin Lake along with 20 older frogs. None of these frogs were recaptured during 1967 or 1968. Other investigators have likewise experienced difficulty in recapturing animals marked at metamorphosis (Pearson, 1955; Fitch, 1956; Jameson, 1956). Apparently, very large numbers of metamorphosing frogs must be marked in order to assure some recapture success.

From 24 May through 14 October 1967, 131 individuals of unknown age were marked at West Twin Lake. Thirty-three of these frogs were recaptured during the same year (Figure 2). Only one of the animals was recovered the following year. The determination of yearly growth increments by means of the mark-recapture method was most unsuccessful.

Postmetamorphic growth may also be investigated by means of size-frequency distributions. This method usually involves the examination of size-frequency histograms of large numbers of

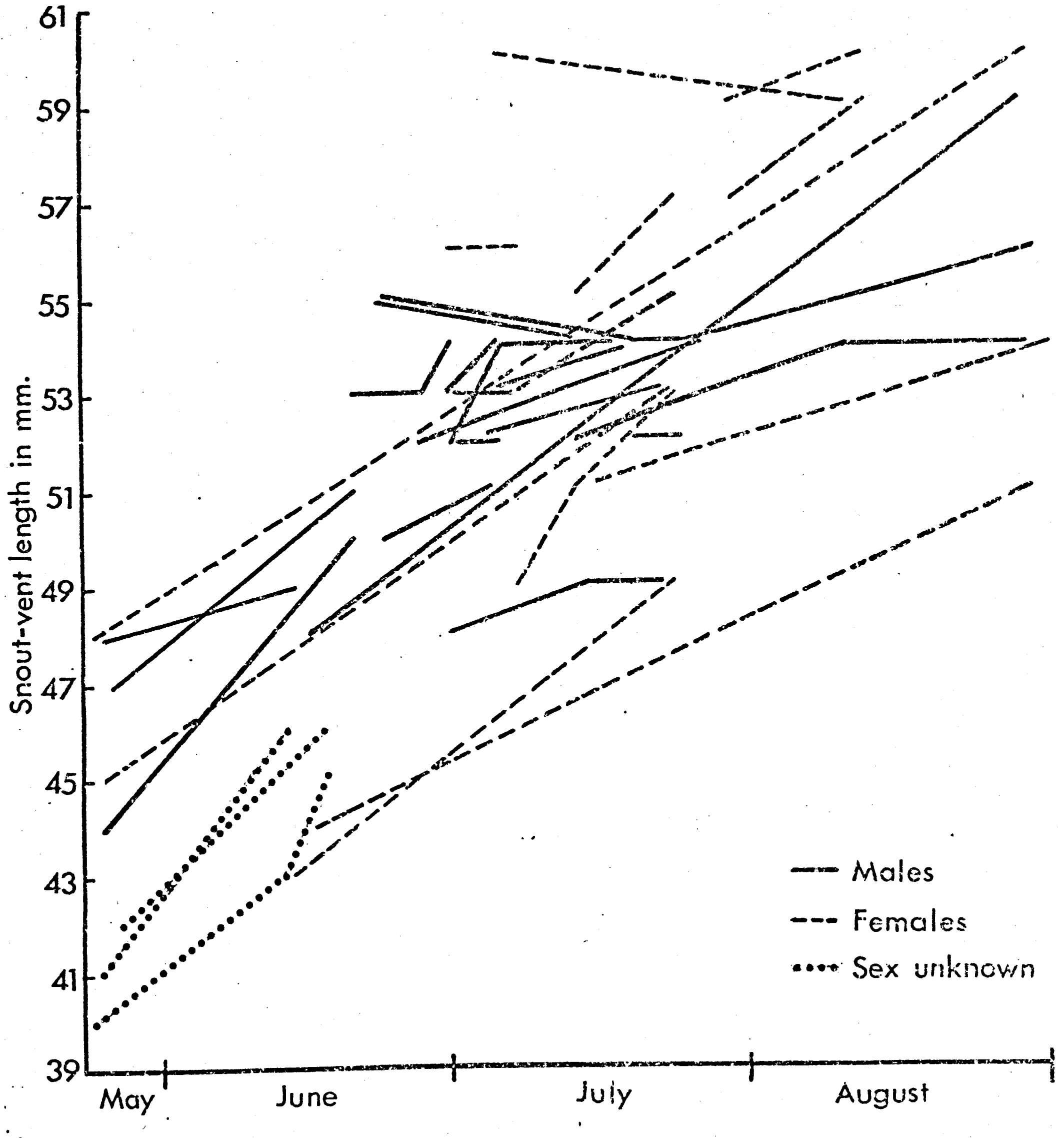


Figure 2. Growth rates of marked mink frogs taken 25 May -- 1 September 1967 in West Twin Lake, Itasca State Park, Minnesota.

frogs collected during successive months. Growth patterns may be deduced from the histograms by first resolving the animals into age-groups and then noting the modal size differences between the successive monthly samples.

The histograms in Figure 3 were constructed on the basis of capture records of mink frogs taken in the Itasca region during the summer months of the years 1966, 1967, and 1968. Short-term recapture records of the same frog were not included. The male and female frequencies in each histogram were divided by a base line. Because they usually could not be sexed externally, the frequencies of frogs smaller than 48 mm. in snout-vent length were divided equally above and below the base line.

The size-frequency method is most effective when definite size groups are apparent on the histograms, thereby facilitating the recognition of modal size differences between adjacent age classes. Unfortunately, in R. septentrionalis and other species with long transformation seasons a size group is usually spread out (Underhill, 1960; Schroeder, 1966). Newly-metamorphosed (0-year) mink frogs appeared in the Itasca region from the beginning of July until the end of August. Consequently, the 0-year class was distinct in July but was much less distinct in August, due to the growth of the earliest-metamorphosed frogs. To this initial size variation within an age class was added further size variation due to the differing growth rates of individuals of the same age.

In May of the first full season following transformation

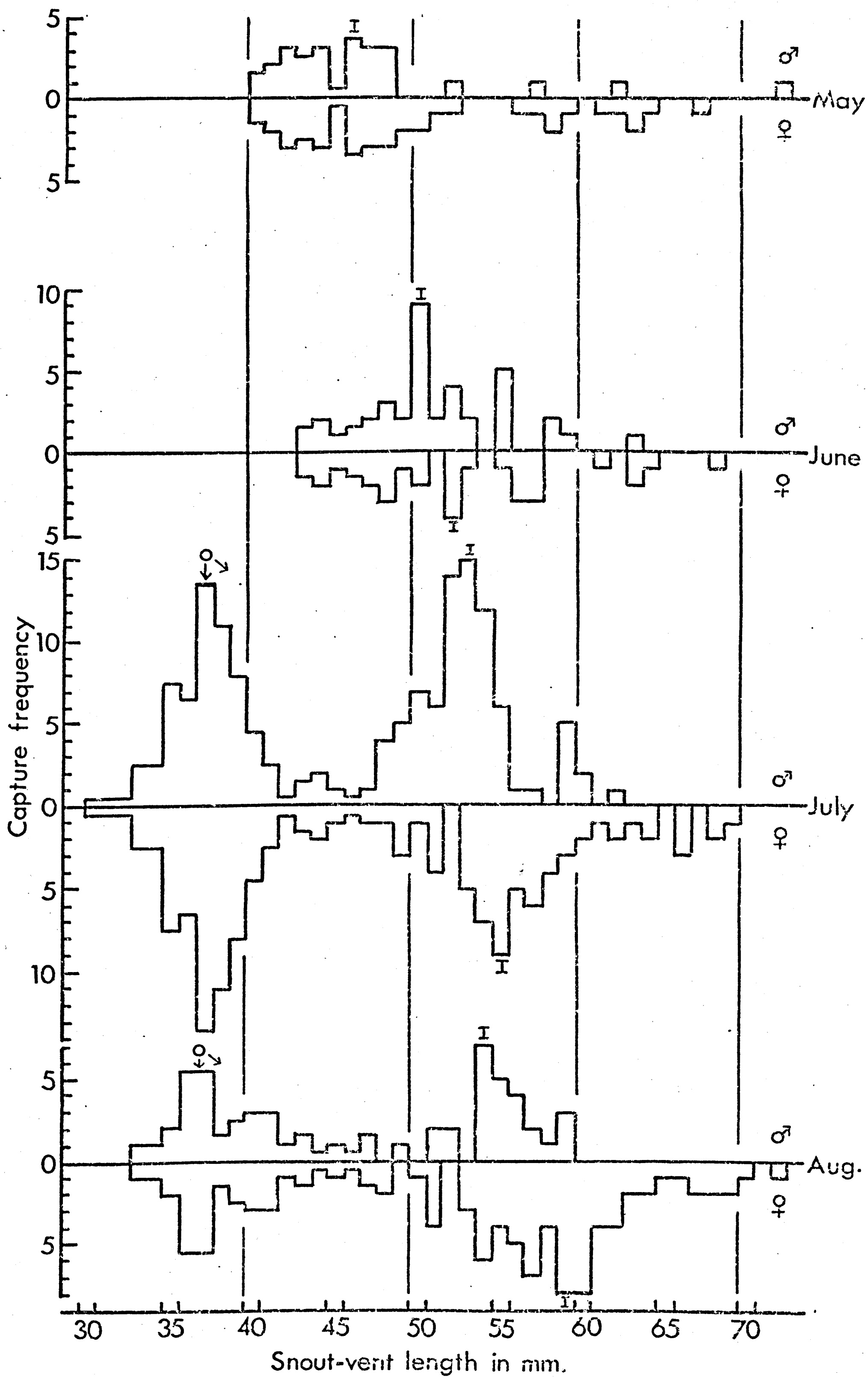


Figure 3. Size-frequency histograms of mink frogs taken 1966 -- 1968 in Itasca State Park and vicinity, Minnesota. The frequencies of frogs smaller than 48 mm. are divided equally above and below the male-female line. Age groups 0 and I are indicated.

(I-year), mink frogs ranged upwards from 40 mm. Some of these I-year animals apparently reached 60 mm. or more by September (Figures 2 and 3). The lengths of larger members of the I-year class certainly overlapped the lengths of smaller members of older age classes, thereby obscuring any size-clusters of older frogs in Figure 3.

During the summer months there always were higher frequencies of females in the larger size categories. One possible explanation of such size differences is the differential mortality between the sexes. If the females outlive the males, the females will be the larger members in a frog population (Turner, 1960). There is some evidence for such differential mortality in mink frog populations. Note in Figure 3 that the number of males decreased markedly from July to August, while the number of females increased slightly. Perhaps the males were subjected to greater predation at the deep-water breeding sites during July than were the females which appeared at the breeding sites for only a short time.

A second possible explanation for the higher frequencies of females in the larger size categories is differential growth of the sexes (Ryan, 1953; Bellis, 1961a). Note in Figure 3 that there is a more rapid rightward movement of the female I-year mode, indicating a more rapid growth of females in relation to males. In Figure 2, however, a more rapid growth of females is not evident.

Although mink frog females were generally larger than males, the largest female and the largest male had identical 72 mm. body lengths. According to Turner (1960), the maximum size of an anuran may be taken as the approximate limit of growth. A metamorphosing mink frog with a mean transformation size of 37.2 mm. is already more than one-half its maximal 72 mm. adult size. In no other United States ranid is the transformation size as large relative to the maximal size of the species (Wright and Wright, 1949; Turner, 1960).

SEXUAL MATURITY

R. septentrionalis rapidly attained sexual maturity, perhaps due to its large transformation size. But before considering the time of sexual maturation it is necessary to outline the method used to distinguish the sexes externally.

Tympanum Dimorphism

R. septentrionalis is one of seven United States ranid species with tympanum dimorphism (Wright and Wright, 1949). The tympana of mature males are much larger than those of mature females and immatures. Unlike many secondary sexual characteristics, the enlarged tympana of the males do not undergo seasonal changes. Tympanum dimorphism has been used year-around as the primary means of sex recognition in three species: *Rana catesbeiana* (George, 1940; Schroeder, 1966), *R. clamitans* (Martof, 1956a), and *R. virgatipes* (Standaert, 1967).

Martof (1956a) formulated a "rule of thumb" for the field recognition of sex in *R. clamitans*: the ratio of the snout-vent length to the tympanum diameter is generally below ten for mature males and ten or above for mature females and immatures. Martof referred to the above ratio as the sex index of the species. To ascertain if the sex index method might also be used for *R. septentrionalis*, 220 mink frogs caught in the Itasca region in 1967 were measured for length and tympanum diameter, and then sexed internally.

Figure 4 shows the relationship of snout-vent length to tympanum diameter in the 220 mink frogs. There was a straight

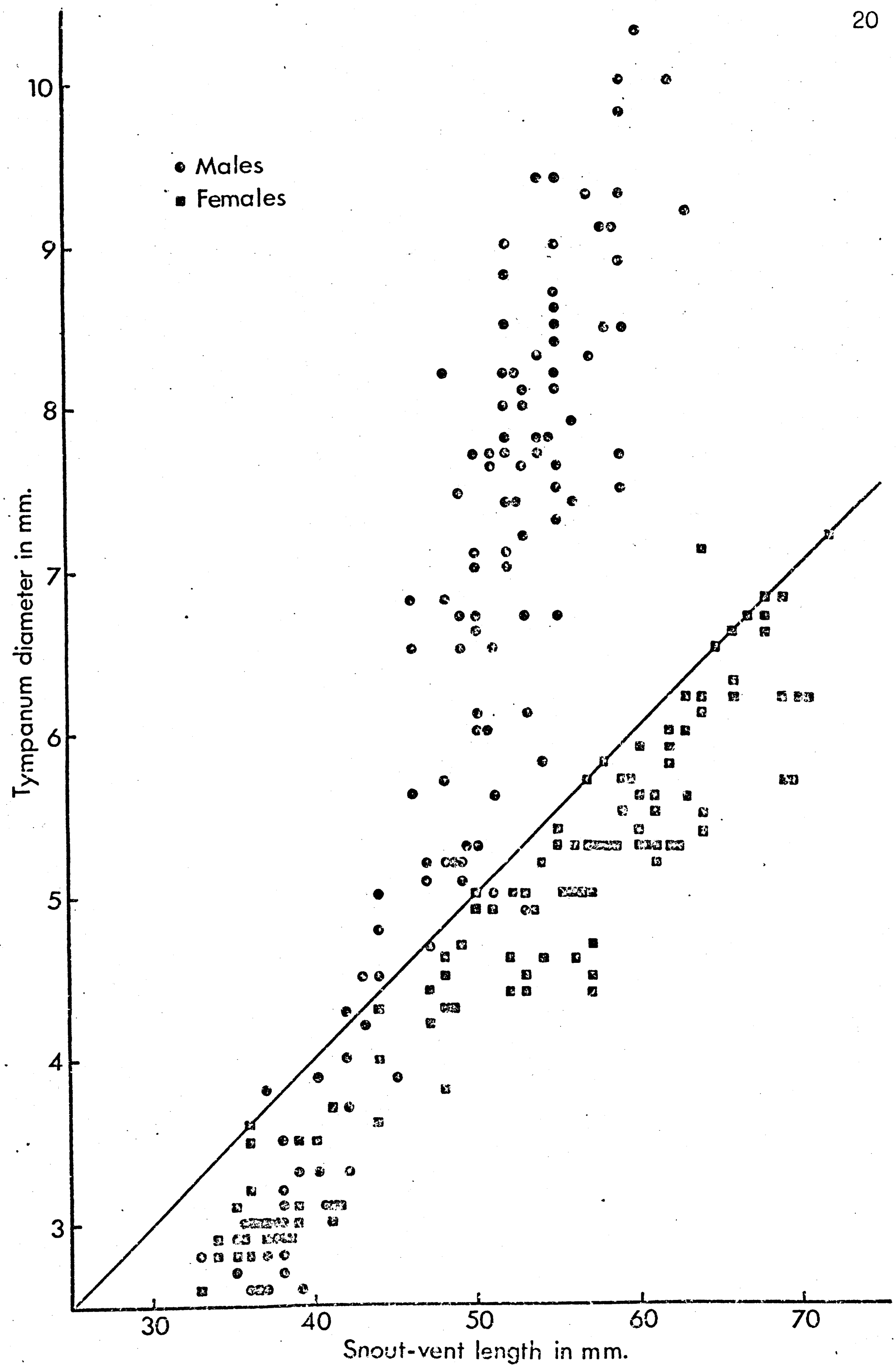


Figure 4. Relationship of snout-vent length to tympanum diameter in mink frogs collected during 1967 in Itasca State Park and vicinity, Minnesota. Solid line indicates where snout-vent length is exactly ten times greater than tympanum diameter.

line relationship between body length and tympanum diameter of both sexes up to 43 mm. snout-vent length. Frogs shorter than 43 mm. generally had sex indices equalling or exceeding ten. In females, the body grew at the same rate as the tympanum at higher snout-vent lengths, thereby maintaining the sex index at or above ten. In most males from 43 mm. to 53 mm. in length, the snout-vent length increased slower proportionately than did tympanum diameter, thereby allowing the sex index to fall below ten. The sex index remained below ten in males larger than 53 mm. as body growth again appeared nearly proportional to tympanum growth.

By determining the ratio of snout-vent length to tympanum diameter, 150 (98.0%) of 153 frogs 48 mm. or longer could be correctly sexed externally (Figure 4). Some males below 48 mm. also could be identified by the sex index method. Females below 48 mm., however, could not be positively recognized from subadult males. Consequently, a mink frog caught and released in the field was classified as: (1) a male if it had a sex index below ten, (2) a female if it had a sex index of at least ten and a snout-vent length of at least 48 mm., or (3) a subadult if it had a sex index of at least ten and a snout-vent length less than 48 mm.

Sexual Maturity In Males

Schroeder (1966) found that the enlarged tympana of male *Rana catesbeiana* individuals are good indicators of sexual maturation. Standaert (1967) identified sexually mature *R. virgatipes* males by means of body-tympanum proportions. Martof (1956b) concluded that *R. clamitans* males become sexually mature and capable of reproduction with the differential enlargement of their tympana.

Based on the appearance of tympanum dimorphism, most male mink frogs become sexually mature when about 45 to 50 mm. in snout-vent length (Figure 4). Males in the Itasca region usually attained this size in less than one year from their metamorphosis (Figure 3). Therefore, most male mink frogs bred during their first full summer following transformation.

Sexual Maturity In Females

In species with enlarged male tympana, the females usually are not capable of reproduction at the point when tympanum dimorphism becomes apparent. Martof (1956a) suggested that *Rana clamitans* females in Michigan did not breed as soon as the males since more time was required for the development of the female gametes. Females also bred later than males in Missouri populations of *R. catesbeiana* (Willis *et al.*, 1956; Schroeder, 1966). Since external features such as tympanum enlargement do not indicate sexual maturity in females, internal features must be examined. For example, the sizes and colors of ovarian eggs are often used to determine the breeding readiness of females (Anderson, 1954; Willis *et al.*, 1956; Bellis, 1957).

Several hundred ovarian eggs were removed from each of 85 preserved females taken in the Itasca region in 1967. Ten or more of the most mature eggs from each female were measured to tenths of a millimeter by means of steel vernier calipers.

The eggs in the female mink frogs appeared to pass through three distinct stages. The first of these stages was characterized by unpigmented or light brown eggs up to 0.5 mm. in diameter. These eggs were present in all females. Eggs in the first stage were the only ones present in animals up to 50 mm. in length (Figure 5).

Eggs belonging to the second stage were gray to black, and often showed polarity. These eggs ranged in diameter from 0.4 to 1.0 mm. They were found in ovaries of most females over 50 mm. in length.

Eggs belonging to the third and final stage were distinctly polarized. The vegetal hemispheres were white, and the animal hemispheres were black. These eggs ranged in size from 0.9 to 1.5 mm. The mature eggs were found only in frogs over 53 mm. in length.

In addition to developing eggs, degenerating eggs were also noted in ovaries of many females over 53 mm. in lingth.. These eggs probably had failed to ovulate or had been caught in the ovarian tissues after ovulation (Anderson, 1954). Some unshed eggs were as large as Stage 3 eggs, while others were visible only as small spots of dark pigment in the ovarian wall. Degenerating eggs suggested previous breeding, although they were not found in all frogs which had certainly bred previously (<u>e.g.</u> a 69 mm. female contained no unshed eggs).

Developing eggs in Stages 1 and 2 as well as a few unshed

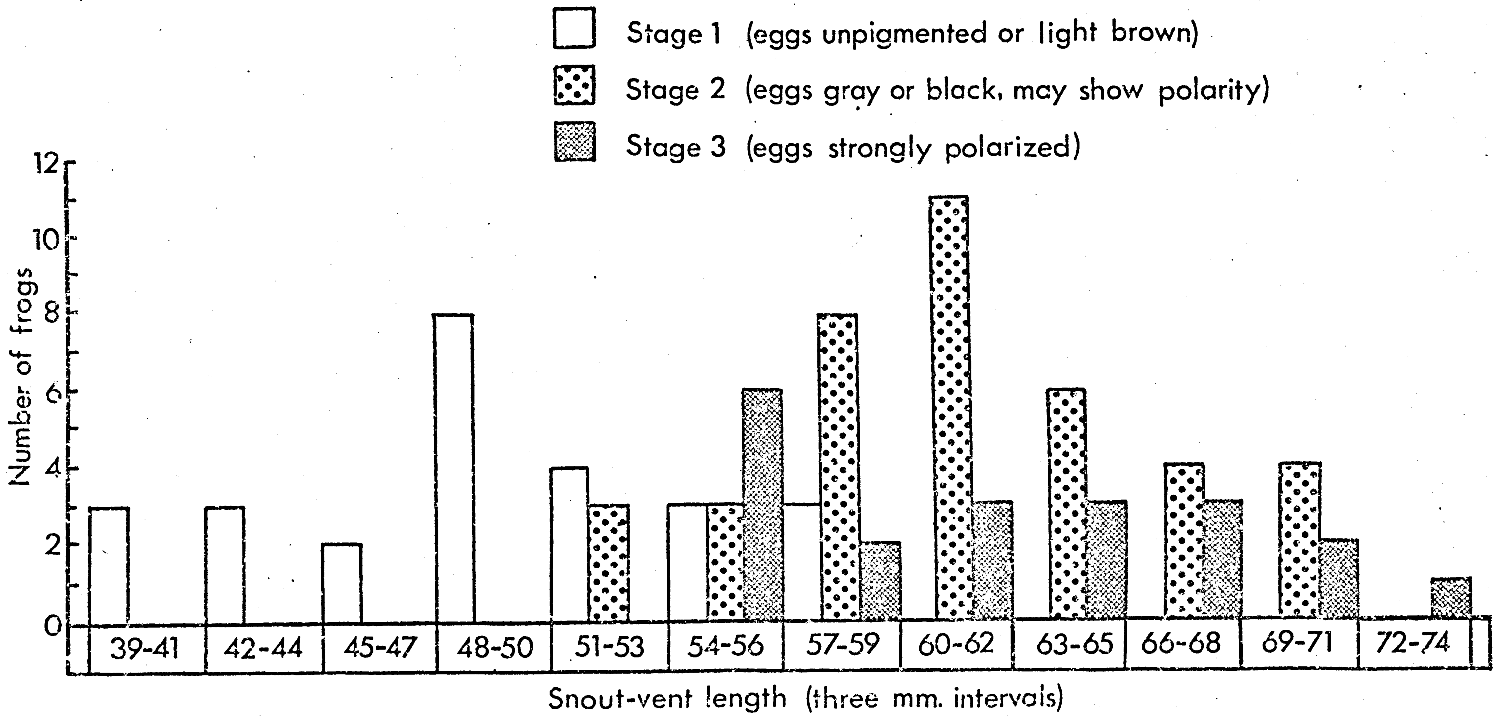


Figure 5. Ovarian egg stages in 85 female mink frogs collected during 1967 in Itasca State Park and vicinity, Minnesota.

eggs remained in the ovaries of females that had recently bred. The developing eggs were destined for use in subsequent breeding seasons.

Based on the presence of Stage 3 eggs or degenerating eggs, female mink frogs become sexually mature when about 54 to 59 mm. in length (Figure 5). Females in the Itasca region often attained this size approximately one year after their metamorphosis (Figure 3). Some females apparently bred during July and August of the first full summer following transformation. Late-metamorphosing and slow-growing females, however, probably did not breed until their second full summer.

BREEDING CHORUSES

R. septentrionalis choruses have been heard as early as the first week in June in eastern Quebec (Bleakney, 1958) and as late as 16 August in northern Maine (Pope, 1915). The earliest calling males recorded in Itasca State Park were heard at 2 P.M. on 30 May 1968. The seven frogs which comprised the chorus were located in a beaver-flooded meadow in shallow 16° C. water. *Rana pipiens*, *Hyla crucifer*, *H. versicolor*, *Pseudacris triseriata*, and *Bufo americanus* males were also calling in the same area and elsewhere throughout the park. Mink frogs were heard in the one beaver pool only.

Lee (1967) suggested that early calling in frogs is due to local microclimate conditions. The first mink frog males heard in 1966, 1967, and 1968 were all located in shallow, relatively warm waters. In addition, these frogs were heard only during the mid-afternoon, the warmest part of the day. The relationship of warmer temperatures to the onset of calling in amphibians is well known (Brattstrom, 1963). Perhaps early-calling mink frogs illustrate the triggering effect of temperature on the breeding cycle of *R. septentrionalis*.

During June, there was a steady increase in the number of calling males at mink frog breeding sites. The developing chorus at West Twin Lake was studied in detail during the period from 14 June through 5 July 1967. The chorus was censused semiweekly during the early-morning hours before sunrise. The positions of the calling males were determined by means of 56 consecutively-numbered stakes set at 24-foot intervals in the shoreline around the circular lake.

The size of the West Twin Lake breeding congress grew steadily during the last half of June (Table 2). The chorus consisted of 23 frogs by 1 July. During the study period some breeding males undoubtedly were taken by predators, like the great blue heron, *Ardea herodias*, who regularly fed at West Twin Lake (Hedeen, 1967).

The male frogs called at night while floating at the surface of West Twin Lake near the sedge mat shoreline. Calling frogs occurred much further from shore in breeding habitats where, unlike West Twin Lake, floating and emergent vegetation grew far offshore. Croaking males were observed on Lake Itasca in emergent beds of wild rice, *Zizania aquatica*, located over 100 feet offshore.

The compass position of the calling males around the circumference of West Twin Lake changed during June and early July 1967 (Table 2). Beginning with two frogs on 14 June, the number of males along the north shoreline increased to a high of 16 on 24 June. This number decreased to ten on 28 June, and then to zero on 1 July. Between 24 June and 1 July, the males had moved eastward. The number of males along the northeast shoreline increased from three on 24 June to eight on 28 June, and then to 19 on 1 July. Further movement took place by 5 July.

Mark-recapture records of two mature males reflected the easterly movement of the West Twin Lake breeding chorus during

TABLE 2. POSITION AND NUMBER OF CALLING MALE MINK FROGS DURING THE PERIOD 14 JUNE -- 5 JULY 1967 IN WEST TWIN LAKE, ITASCA STATE PARK, MINNESOTA

Stake Numbers	Shoreline Section	June 14	June 17	June 21	June 24	June 28	July 1	July 5
1- 8	NE	3	2	3	3	8	19	11
8-15	N	2	11	14	16	10	0	2
15-22	NW	0	1	0	0	1	2	1
22-29	W	3	0	0	0	0	0	0
29-36	SW	0	0	1	1	1	0	0
36-43	S	0	0	0	0	1	1	4
43-50	SE	1	0	1	1	0	0	2
50- 1	E	0	0	0	2	1	1	0
		9	14	19	23	22	23	20

the latter part of June. A calling male caught along the north shoreline at 10:55 A.M. on 24 June was recaptured 150 feet east along the northeast shoreline at 9:45 A.M. on 28 June. A breeding male taken along the north shoreline at 5:35 P.M. on 21 June was recaptured 235 feet east along the northeast shoreline at 8:50 A.M. on 28 June. The calling males were obviously not restricted to spatially-fixed areas. Similar shifts in the location of breeding males have been noted in a chorus of *Rana clamitans*, another species which possesses a prolonged breeding season (Martof, 1953a).

During diurnal periods the male mink frogs either took up feeding positions in the vicinity of floating vegetation or retreated into more protected areas such as water-filled openings in the sedge mat. During daytime censuses of West Twin Lake in 1967, the number of males decreased markedly toward the end of July. A chorus was last heard at West Twin Lake on the evening of 30 July. The last chorus heard during 1967 in the Itasca region was calling on 9 August at French Creek Bay. In 1966, the last chorus was heard on 5 August, also at French Creek Bay.

After the disappearance of choruses in early August, calling males were still heard at various times of the day and night. For example, during a three-minute period soon after sunset on 30 August 1967, two mink frogs were heard calling along with nine *Rana pipiens*, one *Hyla crucifer*, and one *Pseudacris triseriata* at the Wilderness Drive Ditches. None of the latter three species form breeding choruses after June in Minnesota

(Breckenridge, 1944), although their calls are heard infrequently during the weeks preceding hibernation. The mink frogs heard briefly in late August and September were likewise calling outside of their normal late May to early August calling period.

BREEDING SEASON

The breeding season is usually considered to be that period in which the female frogs are laying eggs. The breeding season is often equated with the calling period. However, the only sure correlation between the breeding season and the calling period is that the latter period includes the former (Cagle, 1956).

The breeding season may be accurately delimited through the observation of egg deposition or of freshly-laid eggs (Jameson, 1955). Egg masses of R. septentrionalis have been observed in late June and July in Ontario (Garnier, 1883; Wright, 1932), and in July in Quebec (Vladykov, 1941) and New York (Wright, 1932; Moore, 1952).

One egg mass was collected at West Twin Lake in Itasca State Park on 20 July 1966. The cylindrical mass was three centimeters in diameter and encircled a Sparganium leaf from the water surface to a depth of ten centimeters. Of the 509 eggs in the mass, 485 hatched in the laboratory on 24 July. No other egg masses were seen in aquatic habitats of the Itasca region during the years 1966, 1967, and 1968. Egg masses were deposited in the laboratory by recently-captured females on 17 July 1967 and 4 August 1968. Although both females had been continuously clasped by males prior to oviposition, the eggs proved infertile.

Nine adult females collected in the Itasca region from 25 June through 30 June 1967 all contained mature eggs. Ovulating females were found in breeding areas on 28 June, 1 July, and 28 July. Seven of ten adult females collected in July had deposited their eggs, while the remaining three frogs were distended with mature ova. Eight adult females collected from 1 August through 5 August held only small, developing eggs to be laid the next year.

On the basis of egg masses and reproductive conditions of females from various eastern localities, Wright (1932) and Wright and Wright (1949) concluded that R. septentrionalis breeds from 24 June to 30 July, with the peak of ovulation occurring in July. Similar data gathered from the Itasca region indicated a late June through early August breeding season for R. septentrionalis near the western edge of its geographical range.

HABITAT NICHE

The term "ecological niche" is usually defined as the sum of all the features of the ecosystem acting on a species (Hutchinson, 1944; Dice, 1952; Udvardy, 1959). The many factors included in such a broad definition make exact measurement of a niche difficult. Consequently, most authors delimit an animal's niche by what they consider to be the essential environmental elements utilized by the animal. For example, Inger and Greenberg (1966) defined the niches of three Asian *Rana* species by their trophic relations and microclimate and habitat preferences. In like manner, other authors speak of food niches, microclimate niches, and habitat niches.

The habitat niche is the most important subdivision of an amphibian's overall ecological niche since the structural boundaries which delimit various habitats also mark changes in microclimate conditions and food types. Few adequate measurements of habitat niches of vertebrates have been reported, largely due to the difficulty of describing habitats (Elton, 1949; Breckenridge, 1956). In an attempt to solve this problem of habitat description, Elton and Miller (1954) proposed a system by which habitats can be distinguished on the basis of easily recognized discontinuities in the landscape. Since the habitat niche of the mink frog will be described by using the habitat classification scheme proposed by Elton and Miller, their system must be outlined in detail.

Elton and Miller's method of habitat recording is based on four main categories: (A) Habitat Systems, which are divided horizontally into (B) Formation-types, and perpendicularly into (C) Vertical Layers, with (D) Qualifiers being used to indicate important subdivisions of the other three categories. Excluding the sea, Elton (1966) lists seven habitat systems: Terrestrial, Aquatic, Transition (aquatic-terrestrial), Subterranean, High Air, Domestic (semi-sterile habitats of man), and General (mostly small centers of decaying organic matter scattered through the other major habitats). Each of these habitat systems is further divided into subsidiary parts. For example, the Terrestrial System is divided laterally into four formation-types: Open Ground, Field, Scrub, and Woodland. The Terrestrial System is also stratified into vertical layers: (1) Subsoil, (2) Topsoil, (3) Ground Zone, (4) Field Layer, (5) Low Canopy or Shrub Layer, (6) High Canopy or Tree Layer, and (7) Air Above. Finally, qualifiers are added to take care of a few further special distinctions, e.g. Deciduous, Conifer, and Mixed (deciduous and conifer).

The aquatic-terrestrial Transition System lies between the often ill-defined boundary of the Terrestrial System and the sharply-delineated edge of the Aquatic System. Special features of the transition zone include periodic flooding, waterlogged soil, and the invasion of animals (mostly emergent insects) from the adjoining water body. Because the unique characteristics of the Transition System are due to the bordering water body, the transition habitats are identified by the aquatic formation-types they adjoin, rather than by neighboring terrestrial habitats.

In the Aquatic System all formation-types are based on water body size and speed of flow. By using five sizes graded from puddles to large lakes, and five speeds rated from still water to the current of waterfalls, a theoretical maximum of 25 formation-types is obtained. The larger of these formation-types may in turn be stratified into eight vertical layers: Bottom (Light and Dark), Water Mass (Light and Dark), Submerged Vegetation, Water Surface, Emergent Vegetation (i.e. the part above the surface), and the Air Above. Qualifiers in the Aquatic System include Temporary and Permanent.

Aquatic System

The habitat of the mink frog was first described by Garnier (1883) as "spring creeks and rivers," as opposed to "lakes and ponds" and "fields and woods." In their general handbooks, Dickerson (1906) and Melancon (1950) also characterized the mink frog as a fluvial species, probably following Garnier. Ruthven (1909), on the other hand, found mink frogs around the shores of Isle Royale's inland lakes, and so disagreed with Garnier's habitat description. Likewise, Hoopes (1938) found mink frogs in the deeper ponds and lakes of northern Maine, but never in the numerous streams of the region. Dickinson (1965) recorded the frog as "a pond or lake form" in Wisconsin.

In contrast to the above descriptions of *R. septentrionalis* habitat as being exclusively lotic or exclusively lentic, Logier (1937), Oliver and Bailey (1939), and Breckenridge (1944) reported the mink frog from both types of aquatic environments in Ontario, New Hampshire, and Minnesota, respectively. Recently, Cook (1967) portrayed the frog's habitat in eastern Canada as both lakes and rivers. Cook also stated that the mink frog is restricted to fairly large, permanent bodies of water throughout its range.

That mink frogs may also occupy temporary aquatic habitats was first noted by Gaige (1915) when she found animals in flood-plain pools along the Manistique River in Michigan. Mink frogs have also been reported from such temporary habitats as ditches (A.H. Norton in Pope, 1915), shallow pools (Wright, 1932), and puddles (Moore and Moore, 1939). All of these investigators observed frogs in more permanent aquatic situations as well.

This brief review of the literature clearly shows that a great deal of uncertainty exists in regard to the aquatic habitat of the mink frog. Does the animal prefer standing or flowing water? Is it almost solely a resident of permanent aquatic systems, or may it often inhabit temporary water bodies as well? In order to answer these questions, a thorough search was made in 1966 of all aquatic formation-types in the Itasca region. Many of the mink frog populations found in the course of this habitat investigation were subsequently used to study other aspects of the amphibian's ecology.

Fourteen aquatic formation-types were found in the Itasca region. As Table 3 shows, mink frogs occurred in eleven of the formation-types. Observations in other regions of Minnesota

TABLE 3. AQUATIC FORMATION-TYPES PRESENT IN ITASCA STATE PARK AND VICINITY, MINNESOTA

	A. Very Small	B. Small	C. Medium	D. Large	E. Very Large
1. Still	Sedge mat pools*	Small ponds* (<20 sq. yd.)	Ponds* (<1 acre)	Lakes* (<100 acres)	Lakes*
2. Slow	Trickles*	Ditches*	River backwaters*		
3. Medium	Trickles*	Small streams*	Rivers*		
4. Fast	Springs	Small streams			
5. Vertical		Small weirs			

*Formation-types inhabited by mink frogs.

indicated that mink frogs would occupy additional formation-types in the Itasca region if they existed there. For example, the author collected specimens 100 miles southeast of Itasca State Park in Mille Lacs County from the Rum River, a large river with a medium current. Mink frogs were also collected 180 miles east in Lake County from the Baptism River, a large river with a slow current.

Current is a primary limiting factor in the mink frog's freshwater environment. That current influences the local distribution of the frog is made obvious by observing the animal's usual resting position along medium and fast lotic formation-types. In these habitats the mink frog sits in areas of least current, or leaves the water altogether to take up a position in the Transition System bordering the creek or stream. Although it is sometimes found along medium and fast current formation-types, the mink frog appears to prefer lentic waters and lotic waters with little current.

Terrestrial System

Many of the aquatic habitats in which mink frogs were collected proved to be temporary, *e.g.* sedge mat pools and small ponds (Table 3). Most of the temporary habitats were never connected to permanent habitats by watercourses, and so the resident mink frogs must have travelled overland in order to reach the temporary sites. Yet, there are only two known records of mink frogs moving through the Terrestrial System. A frog was found in a mousetrap set eight feet from the nearest water in the

Temagami region of Ontario (Coventry, 1931). A female was collected in 1964 along an Itasca State Park road not close to water (Lang, unpublished manuscript).

In order to find mink frogs moving overland, amphibians were censused at night along Itasca State Park roads running through all four Terrestrial System formation-types. Mink frogs were also counted as they were caught in fence traps erected north of Itasca State Park by Michael Ewert.

No mink frogs were encountered on land in 1966, although all other common local species of frogs were found in large numbers. In 1967 and 1968, however, a total of 31 mink frogs were found in the Terrestrial System: 26 on roads, one on bare soil beneath an oak leaf, and four in fence traps. These frogs were taken from all four terrestrial formation-types.

Mink frogs appeared to move overland only during periods of nocturnal precipitation. The four trapped frogs were found on days following rainy nights. Of the 27 terrestrial individuals collected in the park, five were caught at night during rains, eighteen were captured at night immediately following periods of precipitation, and four were taken on mornings following rainy nights. Of the latter frogs, three were dead juveniles which had apparently succumbed to dehydration. The fourth diurnal individual was found under an oak leaf. This frog had assumed a very flat body position between the leaf and the moist soil beneath, and had only its head projecting from under the leaf. The animal was partly dehydrated and proved sluggish in its movements when picked up, but regained its normal plumpness and level of activity after it was placed in water.

The dehydrated appearance of diurnal terrestrial individuals and the limiting of nocturnal overland movements to periods of rainfall set *R. septentrionalis* in marked contrast to the region's other common anurans: *Rana pipiens*, *R. sylvatica*, *Hyla versicolor*, *H. crucifer*, *Pseudacris triseriata*, and *Bufo americanus*. Active individuals of the latter six species were found in the Terrestrial System at all times of the day and night under all sorts of climatic conditions. Interestingly, these observations are in accord with recent physiological studies on the water economies of Minnesota anurans. Schmid (1965), by expressing desiccation tolerance as the percent of water lost before death occurs, found that the mean tolerance to desiccation of the mink frog (35.1%) is significantly less than the mean tolerances of the other six above-mentioned species (47.2% to 58.0%). Absolute rates of evaporative water loss are approximately the same in all seven anurans, and so the mink frog must be hardest pressed to sustain its body moisture above lethal levels while moving across dry land. It will be shown below that although the mink frog is not physiologically well-adapted to terrestrial life, it is behaviorally well-adapted to brief movements through the Terrestrial System.

Frogs may maintain safe levels of body water by maximizing water uptake and minimizing water loss. Water uptake in terrestrial frogs is accomplished not by drinking but by absorption of moisture through the skin (Adolph, 1932). Such a method of water uptake permits Rana pipiens to remain independent of standing water for over thrity days (Dole, 1967), and enables the Australian frog Heleioporous eyrei to lead an entirely terrestrial life following metamorphosis (Packer, 1963). Stille (1952) found that Bufo woodhousei fowleri of the Indiana Dunes absorbed moisture from wet sand. He noted that the animals assumed a characteristic posture prior to imbibing the substrate water, a posture that Stille termed the "water absorption response." In this posture the tarsus and foot were placed distal to the knee, thereby allowing maximum contact between the amphibian's groin and the moist substrate. Stille (1958) elicited the water absorption response in the laboratory in eight other anurans, including all of the species present in Itasca State Park with the exception of the mink frog.

The water absorption response has since been noted in mink frogs. Mink frogs exposed to evaporation in room atmosphere assumed the water absorption posture when provided with a moist substrate (e.g. a wet cloth). Under natural conditions, the aforementioned leaf-covered frog was found on moist soil in the characteristic water absorption posture. Yet this animal was partly dehydrated. The bodily appearance of this terrestrial mink frog contrasted sharply with the fully-hydrated shapes of Rana pipiens and Bufo americanus individuals seen in the same area under drier conditions. These field observations are consistent with interspecific physiological differences. Of the three species, the mink frog has both the smallest concentration of dissolved materials in its plasma and the least permeable skin with respect to water (Schmid, 1965; Schmid and Barden, 1965). By referring to Fick's law of diffusion, Schmid (1965) showed that the rate of passive water influx is a function of the effective osmolarity of the blood plasma and the permeability of the skin, other factors remaining constant. Thus, the mink frog's comparatively low values of plasma concentration and skin permeability are probably reflected in a low water uptake rate through the skin. Likewise, passive water influx from the external environment is probably more rapid in R. pipiens and B. americanus than in R. septentrionalis, thereby allowing the former two species to maintain adequate body moisture more easily. R. pipiens and B. americanus may also make greater use of bladder water than R. septentrionalis by means of their larger bladder capacities and the increased permeability of their bladders to urea (Schmid, 1968; 1969). Of the three species, the mink frog is poorest adapted physiologically to the uptake of water in a terrestrial habitat.

If physiological characteristics of the mink frog are poorly adapted to increase water absorption, maybe they are well-adapted to reduce water loss. On the contrary, Adolph (1932) showed that the integument of frogs in no way limits evaporative water loss. Schmid (1965) found that absolute rates of water loss under constant atmospheric conditions are approximately the same for all of the anurans of the Itasca region, varying only as a function of size. Like the other species, the mink frog is unable to control evaporative water loss through physiological adaptations.

Although evaporative water loss cannot be reduced by physiological characteristics, it can be minimized through behavioral adaptations. The primary determinant of evaporation rates is the amount of moisture in the air, with water loss in frogs being inversely related to relative humidity (Hall and Root, 1930; Adolph, 1932). Increased terrestrial activity of diurnal Rana sylvatica and nocturnal R. clamitans individuals during daily periods of high humidity has been related to the low evaporation rates of body water during these times (Bellis, 1962; Martof, 1953b). Activity peaks in both of these species take place during cloudy, rainy weather when the humidity increases. Similarly, the restriction of terrestrial movements of mink frogs to times of precipitation may be due to reduced evaporative water loss during these periods.

Possibly a better reason for rainfall-induced terrestrial activity is that a frog can maximize water uptake during or immediately after precipitation. Terrestrial Rana pipiens individuals utilize rainwater by obtaining moisture directly from their wetted skin and indirectly from temporary puddles and wet surfaces (Dole, 1967). The maximizing of water uptake during rainfall may account in part for the increased terrestrial movements of Rana clamitans during rainy weather (Martof, 1953b). Absorption of rainwater is also thought to explain the hyperactivity of Rana sylvatica during or just after periods of rainfall

(Bellis, 1962). In like manner, the mink frog probably moves overland during periods of precipitation in order to make full use of its relatively poor capability for water absorption. By intercepting rain droplets, by brushing against wet vegetation and by moving through temporary rain puddles, the integument of a terrestrial mink frog is kept thoroughly wet.

The limiting of the mink frog's terrestrial movements to nocturnal periods is consistent with the restriction of such movements to periods of rainfall. The 18 active mink frogs found on land during nocturnal periods following rains showed that the frogs continue to move overland even after precipitation ceases. Rainfall-induced high relative humidities reduce body water losses and also maintain dew and temporary rain puddles, important sources for water uptake. The four dehydrated (three dead) animals found on sunny mornings following nocturnal rains directed attention to the diurnal hostility of dry land. The evaporative power of solar radiation soon dries the frogs' sources of environmental water, and dehydrates the frogs as well. Survival chances are small for mink frogs caught in the Terrestrial System under clearing diurnal weather conditions.

In summary, mink frogs may be found moving through the Terrestrial System at night during or immediately following periods of precipitation. Only during these times may the frogs sufficiently minimize water loss and maximize water uptake in order to maintain safe body water levels. At all other times mink frogs are confined to the Aquatic System.

Aquatic System In Detail

A mink frog spends all but a few nights of its lifetime in the Aquatic System. Therefore, the aquatic portion of the habitat niche of *R. septentrionalis* will be described in greater detail. A habitat niche cannot be properly delineated solely on the basis of the sum total of habitats occupied by a species. For example, *R. septentrionalis* occurred in all four terrestrial formation-types, but only in the metamorphosed form, only at the ground level, and only during or immediately following rainfall. Likewise, *R. septentrionalis* occurred in eleven aquatic formation-types in the Itasca region, but not all life stages were represented in all formation-types. And even within a single formation-type, certain life stages were restricted to specific vertical layers of the water body.

Tadpoles did not occur in most temporary water bodies due to the one-year larval period of *R. septentrionalis*. The only temporary water bodies in which tadpoles were found were those connected to permanent water bodies in which breeding took place. Tadpoles did not inhabit rapidly-flowing waters because the adults did not breed in fast current and because the tadpoles were not adapted to stream life. In the aquatic formation-types where tadpoles occurred they were found in Light Bottom and Submerged Vegetation Vertical Layers. Tadpoles were never seen in the limnetic Light Water Mass. It is not known if the tadpoles utilized the profundal Dark Water Mass or the benthic Dark Bottom.

Transforming tadpoles began to appear in the Water Surface Vertical Layer during the first week of July. The bulk of transformation took place in July and August. Newly-metamorphosed frogs either remained and hibernated in the water body in which they transformed, or they emigrated to surrounding water bodies. The course of action taken by a particular frog was probably dependent on stimuli provided by the immediate habitat.

On 31 July 1967, 50 recently-transformed frogs were counted along a 216-foot portion of West Twin Lake's southeast shoreline, and 49 frogs of the same age were recorded along a 20-foot section of the southeast shoreline of Deming Lake. Subsequent counts along the shoreline portion of West Twin Lake totalled 80 on 13 August, 55 on 30 August, and 58 on 25 September. Successive censuses at Deming Lake revealed one recently-transformed frog on 15 August, one on 31 August, and none on 13 September. These results indicated that juvenile frogs at West Twin Lake largely remained in the habitat in which they transformed, while those at Deming Lake emigrated to other water bodies. In fact, overland movements of juvenile frogs from Deming Lake were observed on the evening of 28 July, and during the early morning hours of 31 July and 8 August. No frogs were seen moving out of West Twin Lake during the same nocturnal periods.

The juveniles of both lakes occupied offshore, floating vegetation mats. At Deming Lake the mat was formed by the floating portions of *Sparganium fluctuans* leaves. At West Twin Lake the mat consisted of *Najas flexilis*, *Anacharis canadensis*, Potamogeton zosteriformis, P. natans, Utricularia vulgaris, and masses of filamentous algae. Since the vegetation mats of both lakes remained unvaried into September, changes in the juvenile populations could not be ascribed to changes in water surface substrata.

The most obvious difference between the juvenile populations was their initial densities on 31 July. The high density of 49 juveniles along the 20-foot shoreline section of Deming Lake was in marked contrast to the average density of 4.6 juveniles per 20 feet in West Twin Lake. Perhaps the stimulus of overcrowding accounted for the almost complete emigration from Deming Lake by 15 August, while the lack of this stimulus allowed the juveniles on West Twin Lake to increase to a density of 7.4 frogs per 20 feet on 13 August. However, Bovbjerg (1962; 1965) found that the emigration of newly-metamorphosed Rana pipiens individuals was not in response to population pressure.

Bovbjerg and Bovbjerg (1964) mentioned food shortage as a possible biotic stimulus to Rana pipiens emigration. Certainly, the availability of prey may have been a factor influencing the greater emigration of juvenile mink frogs from Deming Lake. The number of insects along the shore area was noticeably less on oligotrophic Deming Lake than on dystrophic West Twin Lake.

Juvenile mink frogs may emigrate as a negative response to open water. Goin and Goin (1962) suggested the existence of such a behavioral mechanism in immature Rana clamitans. Although both Deming Lake and West Twin Lake were of the same formation-type, the appearance of their respective vegetation mats was different. Pondweeds and algae formed a dense, thick mat over the water near the shore of West Twin Lake, while Sparganium leaves produced only a sparse, thin mat on the surface near the shore of Deming Lake. Although both mats floated approximately three feet above the lake bottom, the compact West Twin Lake mat conveyed the impression of shallow, densely-vegetated water while the Deming Lake mat did not impart this effect. Possibly the emigration of juvenile mink frogs from Deming Lake was triggered by the obvious open water conditions. Conversely, the lack of emigration from West Twin Lake may have been due to the absence of the stimulus provided by open water.

One factor which is known to trigger emigrations of juveniles is precipitation (Blair, 1953). Only during periods of rainfall were juvenile mink frogs found dispersing. Of course, the precipitation factor alone could not account for both the total dispersal of young frogs from Deming Lake and the lack of juvenile emigration from West Twin Lake. Nearly equal amounts of rain must have fallen on both lakes located 1150 feet apart.

During nocturnal rains in 1967 many of the juvenile frogs from Deming Lake were observed moving 80 feet overland to a shallow, half-acre water body. Young mink frogs also moved much longer distances. On 23 August 1966 a juvenile was found in a shallow forest pool located 1300 feet from the nearest water body containing tadpoles.

Juvenile frogs which dispersed overland to shallow waters returned to deeper water bodies in the autumn in preparation for hibernation. On the rainy night of 12 September 1967, four juveniles were observed moving overland from a tamarack bog containing shallow pools to West Twin Lake, a lake in which mink frogs overwintered. Juveniles at a hibernation site remained at the water surface if adequate warmth was provided by the air or by direct solar radiation. With the onset of cool weather the young frogs submerged. On 25 September 1967, 58 juveniles were counted along a 216-foot portion of shoreline at West Twin Lake. The day was clear, the air temperature one inch above the surface was 25 degrees C., and the water temperature one inch below the surface was 19 degrees C. No frogs were seen on overcast 26 September when the air was 5 degrees C. and the water was 14 degrees C. Nor were any frogs observed at the water surface on sunny 27 September when temperatures were identical to those of the previous day. The whereabouts of the young frogs on the cool days was indicated by an inactive juvenile found on 27 September buried in <u>gyttja</u> beneath one foot of water. On 14 October 1967, four juveniles were counted along the 216-foot shoreline area. The sky was partly cloudy, the air was 13 degrees C., and the water was 12 degrees C. Apparently, short intervals of warmer autumn weather brought juveniles to the surface where they remained until temperatures again turned cool. Such pre-hibernation behavior has also been noted in <u>Rana catesbeiana</u> (Willis <u>et al.</u>, 1956). On 11 November 1967 a thin sheet of ice covered West Twin Lake, signalling the onset of five months of ice.

Temperature also influenced the Spring emergence of frogs entering their first full season following transformation. Immature frogs appeared at the water surface of overwintering sites during warm periods and then disappeared again as air temperatures dropped. Like dispersing recently-metamorphosed frogs, some emerging immatures appeared to move away from open water. Whereas thirteen immatures were found along a 216-foot shoreline portion of West Twin Lake on 27 May 1967, only four were counted there on 18 June, and none were seen there on 5 July. An immature was taken in a trap 2300 feet from the nearest water body on the evening of 12 June. On this same night two immatures were found moving overland from a river toward a temporary pond.

Many male frogs in their first full season following transformation did not move away from their deep water hibernation sites but entered nearby breeding choruses instead. Of 34 immatures caught and marked at West Twin Lake during the period 24 -- 28 May 1967, six were recaptured during the period 14 -- 21 June. At the time of their recapture three frogs were still immatures while three had become breeding males. In relation to points of initial capture the immatures were recaptured at distances of two, nine, and ten feet. The mature males were recaptured at distances of 20, 250, and 350 feet. The long movements of the latter two mature males reflect their movement into a breeding congress which was forming along the north shore of the lake. The shorter twenty foot movement of the third mature male was of sufficient distance to place him in the midst of the breeding chorus.

Frogs which became mature males during their first full season following transformation joined males of older age classes in the breeding choruses. Mature males were seen only at breeding sites on permanent bodies of water during the late June to early August breeding period. Immature males were found in shallower habitats during the breeding season.

The breeding congresses disbanded at the end of the breeding period in early August. Post-breeding males either dispersed to other aquatic habitats or remained at the water bodies in which they bred. Those males that moved to shallow habitats in the late summer returned to deeper water in the autumn in order to hibernate.

Some female frogs matured during July and August of their first full summer following transformation. Along with the females of older age classes, the newly-matured females usually occupied shallow non-breeding habitats except when spawning. For example, on 6 July 1967, 22 immatures, ten mature females, and no mature males were seen in a temporary pond. Yet in the nearest breeding habitat one quarter mile west only three immatures and four mature females were found along with 19 mature males.

The marked disproportion of sexes at breeding sites was due to the females' short length of stay in the spawning area. Mature frogs caught and marked at West Twin Lake during the 1967 breeding season included 20 females and 34 males. The recapture frequency of the females was 20 percent, while that of the males was 65 percent. The relatively low recapture frequency of the females indicates a sexual difference in the period of stay at a breeding site. A shorter length of stay by females at a breeding site also has been noted in Rana clamitans (Martof, 1956b), Bufo woodhousei (Underhill, 1960), and B. americanus (Oldham, 1966).

Female frogs moved away from the breeding choruses following egg-laying. Females dispersed to any available aquatic habitat, including the shallower portions of the water body in which they bred. Like males, the females that moved overland to shallow habitats returned to deeper overwintering sites in the autumn. At the hibernation sites the mature males and females showed the same behavior during the autumn and spring as that exhibited by juvenile frogs: disappearing underwater on cool days and reappearing at the water surface on warm days.

Mink frogs occupied many shallow aquatic formation-types which could not be inhabited by tadpoles. Mink frogs also utilized aquatic vertical layers which were inaccessible to tadpoles. The frogs during the summer months usually rested in the Water Surface Vertical Layer on floating substrata. Mink frogs also infrequently rested in the aquatic-terrestrial Transition System around the edge of the water. Food was taken from both the transition and surface zones, as well as from plants in the Emergent Vegetation Vertical Layer. When escaping from either predators or adverse climatic conditions, mink frogs dove into either the Submerged Vegetation or the Light Bottom layers.

Females anchored their non-floating eggs on underwater vegetation. Frogs were never seen in the Light Water Mass. It is not known if the frogs utilized the Dark Water Mass or Dark Bottom.

Water Surface Vertical Layer In Detail

Water surface substrata.--Vertical layers of the Aquatic System may be subdivided in order to define more strictly a habitat niche. For example, mink frogs in the Water Surface Vertical Layer are generally restricted to surface substrata on which they may rest partially or completely out of the water. Some authors subdivide the Water Surface layer by listing water lilies as the primary resting places of mink frogs (Conant, 1958; Barker, 1964). Cochran (1961) remarks that the mink frog "prefers to live among clusters of water lilies, where it can hop from pad to pad." Cook (1967) states that "*R. septentrionalis* seems restricted throughout its range to fairly large, permanent bodies of water which have a dense growth of water lilies."

In the Itasca region the mink frogs in the Water Surface layer were not restricted to lilies. Of 311 frogs observed on West Twin Lake during the period 4 July through 16 August 1966, only three were sitting on *Nymphaea tuberosa*, the only water lily species present in the lake (Table 4). Nearly 75 percent of the aquatic habitats in which mink frogs were observed during the years 1966 -- 1968 did not contain any representatives of the water lily family Nymphaeacae. In all habitats the frogs used the surface substrata which were locally available.

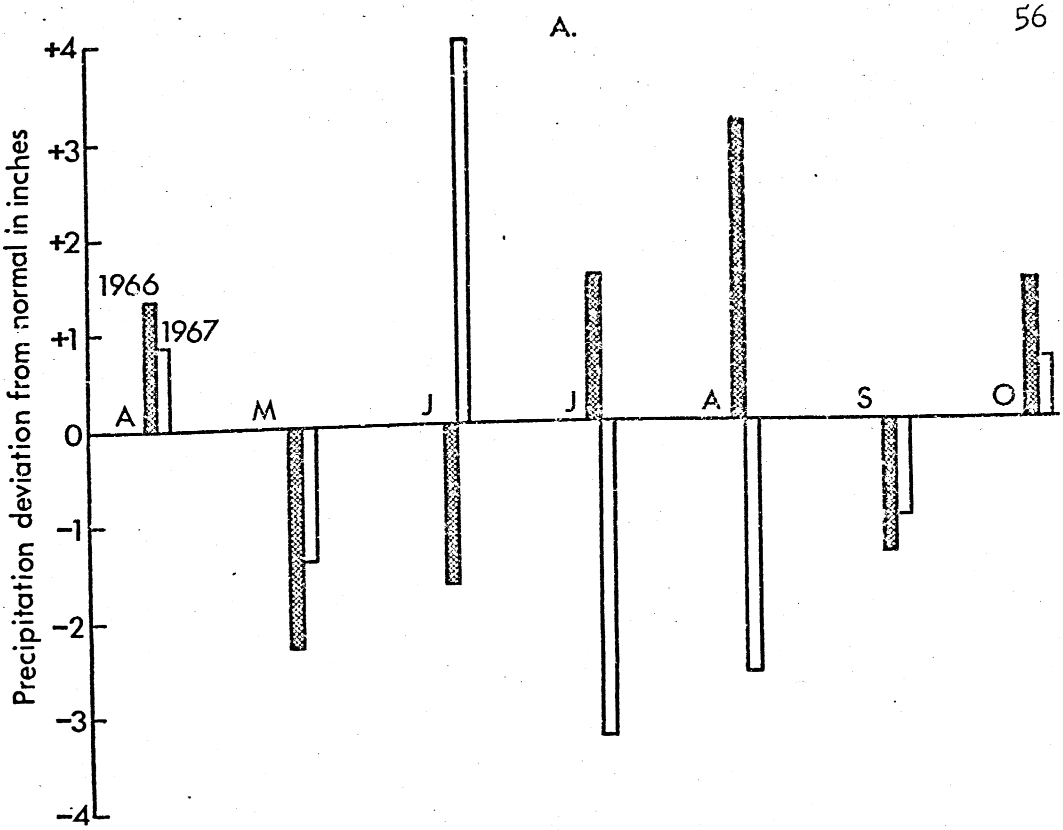
The substrata available to mink frogs changed from one year

TABLE 4. RESTING PLACES OF 311 MINK FROGS SEEN DURING THE PERIOD 4 JULY -- 16 AUGUST 1966 AT THE WATER SURFACE OF WEST TWIN LAKE, ITASCA STATE PARK, MINNESOTA

Substratum	Number of Frogs
Carex spp.	200
Vegetation mat	52
Upside-down sedge island	26
Bryophyta	13
Log	11
Nymphaea tuberosa	3
Iris versicolor	2
Water	2
Typha latifolia	1
Menyanthes trifoliata	1

to the next, even within a single aquatic habitat. During the period 4 July through 16 August 1966, 200 of 311 frogs in West Twin Lake were observed sitting on downed, floating *Carex* leaves (Table 4). Although detailed substratum records were not kept in 1967, general observations during July and the first half of August indicated that more than two-thirds of the West Twin Lake mink frog population occupied vegetation mats. These floating mats consisted of *Najas flexilis*, *Anacharis canadensis*, *Potamogeton zosteriformis*, *P. natans*, *Utricularia vulgaris*, and masses of filamentous algae. The mats blanketed the water surface beginning from near the shoreline and ending two to ten feet away, depending on the slope of the lake bottom. While at least two-thirds of the 1967 frogs occupied vegetation mats, only one-sixth of the 1966 frogs were found on similar mats (Table 4). This difference was ultimately based on the contrasting rainfall patterns of the two summer seasons (Figure 6A). The monthly precipitation data used herein were taken from measurements made at the Lake Itasca Forestry and Biological Station located four miles north of West Twin Lake.

In 1967, rainfall was 4.01 inches above the normal 4.18 inches during June, 3.29 inches below the normal 3.58 inches during July, and 2.64 inches below the normal 3.50 inches during August. The effect of this rainfall pattern on the water level of West Twin Lake was obvious (Figure 6B). A higher water level was recorded on 14 June following 2.85 inches of rain in three days than was recorded on 28 April during spring run-off. With below



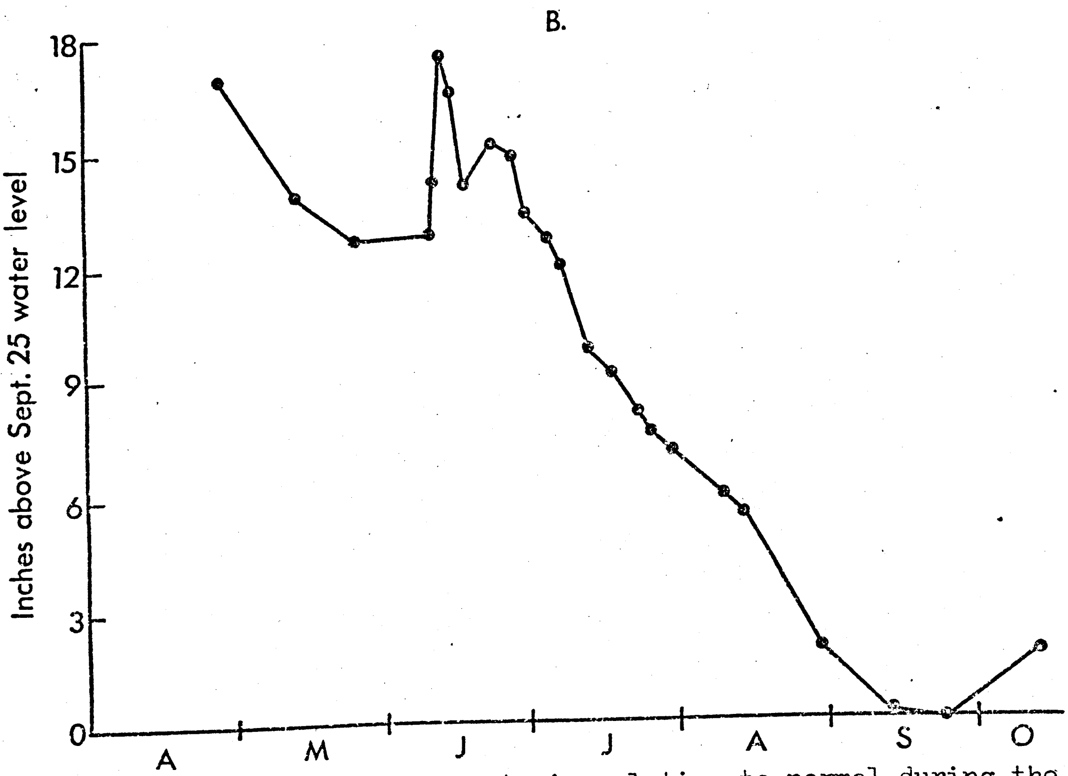


Figure 6. A, precipitation amounts in relation to normal during the months April -- October, 1966 and 1967, at the Lake Itasca Forestry and Biological Station; B, water level readings taken 28 April -- 14 October 1967 at West Twin Lake, Itasca State Park, Minnesota.

normal precipitation in July and August, however, the water level dropped 12.0 inches between 14 June and 14 August. As the water level declined during July and August the uppermost parts of usually submerged plants (*Najas flexilis*, *Anacharis canadensis*, *Potamogeton zosteriformis*) appeared at the water surface. Where many of these plants were exposed by the low water they formed large vegetation mats in which *Utricularia vulgaris* and algae masses grew. It was on these anchored floating mats that the great majority of mink frogs were seen during July and August, 1967.

The rainfall pattern during the summer months of 1966 contrasted sharply with the 1967 pattern (Figure 6A). In 1966, rainfall was 1.66 inches below normal during June, 1.54 inches above normal during July, and 3.10 inches above normal during August. Water level readings were not taken during 1966, but it is believed that the water level of West Twin Lake did not drop during July and August 1966. This belief is based on general observations made in 1966 and on the apparent correlation in 1967 between the West Twin Lake surface level and monthly rainfall totals. With a higher water level during July and August 1966, there was little development of the vegetation mat substratum, which was so common in 1967. The mats which did exist in 1966 were largely composed of floating parts of dead pondweeds mixed with algae masses and were located along protected portions of shoreline. These mats composed only a small amount of the total available floating surface material. Most of the water surface substrata were downed Carex leaves along the shoreline. Consequently, nearly two-thirds of the mink frogs observed during July and August 1966 occupied downed, floating sedge. The contrasting summer rainfall patterns of 1966 and 1967 were ultimately responsible for the different surface materials available to mink frogs at West Twin Lake.

Not only may water surface substrata vary from habitat to habitat and from year to year, but they may also vary from season to season. The mink frogs at West Twin Lake in 1967 were found primarily on downed Carex during May and June, on vegetation mats during July, August and the first half of September, and again on downed sedge during the second half of September and October. The frogs returned to the sedge in September because the vegetation mats disappeared as the aquatic plants died in the autumn. Similarly, mink frogs at a river in 1967 occupied downed Typha and Carex bordering the river during May and June, moved out onto Ceratophyllum demersum mats which choked the river during July, August and the first half of September, and retreated again into the cattails and sedges as the C. demersum died during the autumn.

Distribution across the Water Surface Vertical Layer.--The surface distribution of the West Twin Lake mink frog population was studied during July and August, 1966 and 1967. Most of the circular shoreline of West Twin Lake is a pioneer-mat dominated by Carex lasiocarpa. The floating sedge mat is interrupted only along 120 feet of the eastern shore where it is replaced by road-fill. Along the 1220 feet of pioneer-mat shoreline, downed sedge constitutes a large part of the water surface substrata. Aquatic plants representing additional surface substrata are also regularly distributed in shallow areas around the lake's circumference. Due to the homogeneous distribution of surface substrata, it was thought that the West Twin Lake mink frog population would be uniformly distributed.

The numbers of frogs in the 56 shoreline study sections established around West Twin Lake were recorded during 16 days of the period 5 July through 16 August 1966. No censusing was done on days when either the cloud cover exceeded 50 percent or the wind speed exceeded ten miles per hour. On breezy days only those shoreline sections not effected by waves were checked. Approximately fourteen study sections were censused each day. Each section was censused four times during the 1966 study period. The five sections along the roadfill portion of the shore were censused but are excluded from further consideration due to their disturbed condition.

Soon after the investigation was begun in 1966 it became apparent that the postulated uniform distribution of the West Twin Lake population did not exist. The lack of a uniform distribution became obvious when the 1966 data were treated statistically by means of a Chi-square test for homogeneity. This statistical method was employed by Evans (1942) in testing for the presence of uniform distribution in various rodent populations. In using this test it is assumed that the cumulative record of the number of animals found in each study section will give an aggregate picture of occupation in each section. If the animals are uniformly distributed, then an equal number of individuals should be expected in each study section. Consequently, the expected number to be used in the Chi-square test is determined by dividing the number of study sections into the total number of individuals found during the study period.

In 1966 a total of 242 frogs was counted in 51 shoreline sections. Using 4.7 frogs per section as an expected value, the calculated Chi-square is 136.13 with 50 degrees of freedom. Such a high Chi-square value indicates a probability of less than 0.001 that the West Twin Lake mink frogs were uniformly distributed during the 1966 study period. If the distribution of a local frog population is determined by the distribution of substrata at the water surface, then the above results suggest the existence of some type of an irregularly-distributed substratum, e.g. sedge islands.

Sedge islands originate when portions of the floating pioneer-mat are torn loose from shore, probably through the action of ice (Gates, 1942). These floating islands may continue to grow by means of the same mat-forming method which extends the pioneer-mat out over the water (Buell and Buell, 1941). Sedge islands often attain considerable size. A large West Twin Lake island measured 45 feet long and 15 feet wide. The sedge islands drift before the wind except when they are stranded in shallower depths during periods of low water. Mink frogs used the downed sedge floating on the water around the islands for support.

The frogs also occupied the edges of upside-down islands (Table 4). The latter substratum comes into existence when high winds turn over smaller floating islands, thereby exposing the brown, peaty soil characteristic of a sedge mat.

Winds determine sedge island distribution and so most islands are found bunched together along the shoreline. During July and August 1966, all of the West Twin Lake islands were stranded in five study sections. Although these five sections constituted less than ten percent of the total 51 study sections, they held more than 25 percent of the local mink frog population. The mean numbers of frogs found in the 46 sections without islands and the five sections with islands were 3.9 ± 2.34 and 12.6 ± 3.58, respectively. A high t-value of 7.508 shows that the average number of frogs in the sections containing islands was significantly greater ($P<0.01$) than the number in those sections without islands.

The non-uniform distribution of mink frogs around the circumference of West Twin Lake in 1966 was due primarily to the additional water surface substrata provided by irregularly-distributed sedge islands. Considering only the 46 sections without islands a Chi-square test for homogeneity gives a value of 63.195. If the standard level of probability ($P<0.05$) is used, then the above Chi-square value should be no larger than 61.656 in the case of a homogeneous distribution. Probably other habitat factors in addition to sedge islands were responsible for the non-uniform distribution of mink frogs around West Twin Lake.

One of these factors may have been the vegetation mats which were occupied by one out of every six frogs observed in 1966 (Table 4). Unfortunately, the placement of these mats was not recorded in 1966.

In 1967, the numbers of frogs present in the West Twin Lake study sections were recorded during 16 days of the period 14 July through 1 September. Each of the 51 study sections was censused four times during the study period. Censusing procedure was identical to that employed in 1966.

During July and August 1967, the West Twin Lake sedge islands were stranded in three study sections as well as along the roadfill area. In the 48 sections without islands 1480 frogs were counted. It was obvious that these frogs were not uniformly distributed among the island-absent sections but were instead concentrated in those sections containing vegetation mats. A Chi-square test for homogeneous distribution gives a value of 370.569 with 47 degrees of freedom. Such a very high Chi-square total indicates a probability of much less than 0.001 that the frogs were uniformly distributed among the island-absent sections.

Of the 48 sections without islands, 31 contained vegetation mats while 17 did not have mats. The mean numbers of frogs found in the mat-present and the mat-absent sections were 39.2 ± 11.06 and 15.5 ± 9.98, respectively. A high t-value of 7.269 shows that the average number of frogs in the sections containing mats was significantly greater ($P<0.01$) than the number in those sections without mats. The non-uniform distribution of mink frogs around West Twin Lake during the 1967 study period was largely due to irregularly-distributed vegetation mats.

Some environmental factor(s) in addition to substratum availability also contributed to the non-uniform distribution of West Twin Lake mink frogs during July and August 1967. During the study period it became obvious that more frogs were found along the west shoreline than were found along the east shoreline. In order to determine if this general observation was statistically significant, each study section was designated as being part of either the east or west shoreline according to the section's location east or west of the north-south diameter of the lake. Of the 17 mat-absent sections, eight were part of the east shoreline and nine were included in the west shoreline. Of the 31 mat-present sections, 16 were located in the east shoreline while 15 were included in the west shoreline.

The mean numbers of frogs found in the east and the west mat-absent sections were 8.6 ± 8.11 and 21.7 ± 7.18, respectively. A t-value of -3.302 shows that the mean number of frogs in the mat-absent sections of the east shoreline was significantly less ($P<0.01$) than the mean number in the mat-absent sections of the west shoreline.

The mean numbers of individuals found in the east and west mat-present sections were 32.5 ± 9.13 and 46.4 ± 8.11, respectively. A t-value of -4.469 shows that the mean number of frogs in the east mat-present sections was significantly less ($P<0.01$) than the mean number in the west mat-present sections.

Considering both mat-absent and mat-present sections, significantly fewer mink frogs were located in east shoreline sections than in comparable west shoreline sections. These results were not due to a non-uniform distribution of surface substrata. In the east and west mat-absent sections there was an equal amount of surface substrata. Likewise, the vegetation mats along the east and west shorelines had the same total areas. The east-west difference in frog numbers in the mat-present sections could not be ascribed to differences in the surface areas of the vegetation mats. Some factor(s) in addition to substratum availability affected the local distribution of West Twin Lake mink frogs.

Shade is one factor which may partially control the distribution of poikilotherms (Schmidt-Nielsen, 1964). At West Twin Lake this agent may be ignored during the summer months. Except when long shadows are cast by surrounding tamaracks at sunrise and sunset, the entire sedge mat shoreline is unshaded during July and August.

Another physical factor known to influence the local distribution of small animals is wind (Vose and Dunlap, 1968). Wind never directly affected the census of West Twin Lake frogs since censusing was done only during days when wind speed was less than ten miles per hour and only in the windward sections (i.e. those shoreline sections situated toward the direction from which the wind was blowing). Study sections on the leeward side were not censused because few, if any, frogs would be found in the wind-disturbed Water Surface layer. The lack of insect prey in the face of wind and waves or the wave-caused instability of water surface substrata perhaps accounted for the paucity of frogs in leeward sections.

Despite the daily census precautions taken against its influence, wind may have been a factor in the unequal east-west distribution of frogs during the period 14 July through 1 September 1967. In July, the resultant wind direction was WNW at International Falls, Minnesota, and WSW at Fargo, North Dakota. In August, the resultant wind direction was SW at International Falls and SSW at Fargo (Environmental Data Service, 1967). West Twin Lake is located 125 miles southwest of International Falls, and Fargo is located 80 miles southwest of West Twin Lake. Therefore, the resultant wind directions at West Twin Lake during July and August probably were W and SW, respectively. Such resultant wind directions would have made the eastern shoreline more often leeward and the western shoreline more often windward during July and August 1967. The total amount of time available for feeding activities by a frog would have been less along the eastern shoreline than along the western shoreline. Consequently, the West Twin Lake mink frogs may have aggregated along the western shoreline where prey were available most often. Such local movements by anurans to areas of maximum food-availability have previously been noted in populations of *Scaphiopus holbrooki* (Pearson, 1955), *Hyla regilla* (Jameson and Myers, 1956), *H. crucifer* (Oplinger, 1967), *Rana clamitans* (Hamilton, 1948), and

R. catesbeiana (Van Bergeijk, 1967).

That wind was at least partially responsible for an unequal east-west frog distribution is a tenuous hypothesis at best. Wolfe (1945) rightly questions the correlation of local biotic phenomena with Weather Bureau data gathered miles away. The effect of wind on a local distribution of mink frogs in the Water Surface Vertical Layer needs to be fully investigated by means of microclimate measurements.

Distribution through the Water Surface Vertical Layer.---A vertical layer may be subdivided vertically as well as horizontally (Elton, 1966). Two distinct sublayers of the Water Surface layer are separated by the surface film. The under and upper sides of the surface film each support certain characteristic organisms (Elton and Miller, 1954).

Mink frogs in the Water Surface layer usually occupied the two surface sublayers at the same time. Some frogs rested with only their eyes and snout in the sublayer above the surface film. Other individuals rested with a greater portion of their body exposed.

During the period 4 July through 16 August 1966, observations were made of the vertical positions of undisturbed mink frogs in the Water Surface layer of West Twin Lake. Of 61 transforming frogs, 42 (69%) had only their eyes and snout above water. This same position was recorded for 42 (70%) of 60 recently-transformed individuals and for 18 (58%) of 31 frogs belonging to older age classes.

During the period 4 July through 16 August 1967, vertical positions of older frogs only were recorded. Many of these animals had been transforming frogs during the previous summer. Of the 92 frogs observed in the Water Surface layer, 53 (58%) had only their eyes and snout above the surface film. In both 1966 and 1967, the majority of frogs in the Water Surface Vertical Layer of West Twin Lake rested with most of their body beneath the surface film.

Comparative Summer Habitat Niches

Martof (1953b) stated that the ecological niches of the four *Rana* of lower Michigan may be clearly distinguished from one another solely on the basis of habitat. The bullfrog (*Rana catesbeiana*) is aquatic, the green frog (*R. clamitans*) is riparian, the leopard frog (*R. pipiens*) is a field dweller, and the wood frog (*R. sylvatica*) is a forest dweller. Due to the distinct habitat niches of these frogs little competition exists.

Jackson (1914) catalogued the land vertebrates of Ridgeway Bog in northern Wisconsin and showed that niches may be delineated on the basis of habitat. Jackson divided Ridgeway Bog into faunal zones corresponding to the successive plant associations of the lake-bog-upland series. In the aquatic association the mink frog was the most characteristic vertebrate while the leopard frog was listed as occurring. In the surrounding sedge association the leopard frog was one of the most plentiful animals while the mink frog was absent. The mink frog was also absent in the moss-heath zone where the leopard frog was rare.

Neither the mink frog nor the leopard forg occurred in the successive tamarack-spruce, cedar-balsam-hemlock, or hillside (pine) associations, while the wood frog appeared in all three of these zones. The wood frog inhabited associations of the Woodland Formation-type, the leopard frog primarily occupied associations of the Field Formation-type, and the mink frog resided exclusively in an Aquatic Formation-type.

Another investigation concerned with the occurrence of anurans in relation to bog associations was carried out from 1949 through 1953 at Bog D in Itasca State Park (Marshall and Buell, 1955). The vegetation zones sampled extensively included the Sedge, Tamarack, Spruce, and Fir-Ash Zones. The pine-dominated upland slopes were ignored because preliminary collecting there revealed only a very few wood frogs. The central Aquatic Zone was never sampled since the margin of the unstable sedge mat was difficult to approach. All collection was done during a day in mid-August between 9:00 and 11:30 A.M. An area of approximately 3000 square feet was sampled within each vegetation zone. All positively identified animals were recorded regardless of whether they were caught or missed.

A total of 857 identified anurans was recorded during the five yearly collecting sessions. The distribution of the amphibians in relation to the four bog vegetation zones studied is diagrammed in Figure 7A. The usually arboreal gray tree frog (<u>Hyla versicolor</u>) was represented in all four plant zones, but only by recently-metamorphosed animals. The spring peeper (<u>H. crucifer</u>)

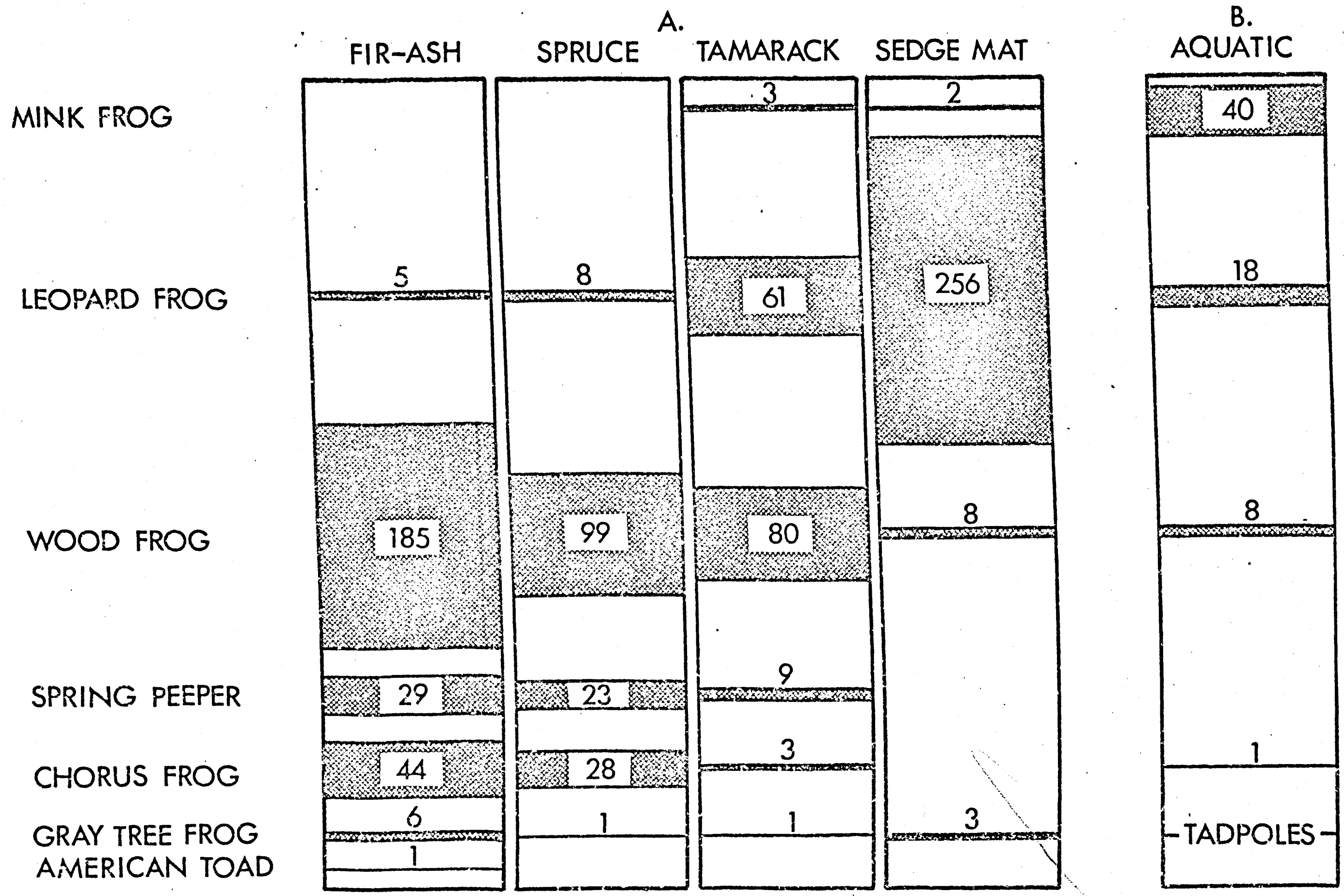


Figure 7. A, occurrence of anurans in four vegetation zones of Bog D for the five years 1949 through 1953, based on yearly sampling areas of approximately 3000 square feet (from Marshall and Buell, 1955); B, occurrence of anurans in the Aquatic Zone of Bog D for the two years 1967 and 1968, based on yearly sampling areas of 7500 square feet.

and the chorus frog (Pseudacris triseriata) were found to increase in numbers as the amount of material in the shrub layer increased. A single American toad (Bufo americanus) was found in the driest of the plant zones. Most of the 372 wood frogs were found in the wooded bog zones. Conversely, most of the 330 leopard frogs were found in the sedge mat zone. The five mink frogs taken during the five-year study were collected in the sedge mat and tamarack zones. Additional mink frogs were observed in the bog lake but could not be counted accurately (Marshall and Buell. 1955).

In order to complete the study of amphibian distribution across the lake-bog series of vegetation zones and to compare the mink frog's habitat niche to the habitat niches of other Itasca State Park anurans, the frogs of the Bog D Aquatic Zone were censused on the mornings of 7 August 1967 and 2 August 1968. During both years an area 300 feet long and 25 feet wide was censused by means of a rubber life raft. The census area was located immediately next to the sedge mat shoreline.

A total of 64 frogs was found in the Aquatic Zone: 40 mink frogs, 18 leopard frogs, five wood frogs and one spring peeper (Figure 7B). Most frogs were found either on downed sedge or on the exposed Ceratophyllum demersum, which covered approximately one-fifth of the census area. In addition to the frogs, several large Hyla versicolor tadpoles were collected in 1967 from below the surface of the bog lake.

The single spring peeper found was a young-of-the-year animal. The five wood frogs collected were also recently-metamorphosed animals. Spring peepers, wood frogs, and gray tree frogs apparently bred in the bog lake or in an inlet to the lake. All size classes were represented among the 18 leopard frogs which were found. Of the 40 mink frogs counted, 17 were either transforming or recently-transformed individuals, while 23 were frogs belonging to older age classes.

Jackson (1914), Martof (1953b), and Marshall and Buell (1955) pictured the preferred habitat of the wood frog as an area dominated by trees and that of the leopard frog as an area dominated by grass-like plants. In relation to these two ranids and to the other four anurans found in Bog D, the mink frog was decidedly the most aquatic species (Figure 7). However, the habitat niche of the leopard frog overlapped with that of the mink frog to quite some extent. Immigrating leopard frogs joined resident mink frogs during July and August in several aquatic habitats in the Itasca region, e.g. French Creek Bay (Figure 8). Movement by leopard frogs into the Aquatic System might be attributed to a number of possible factors: greater food availability on floating vegetation, late summer aridity in the Terrestrial System, a tendency of adult leopard frogs to occupy regions where crowding is least (Dole, 1965). Whatever the reason, the habitat niches of the leopard frog and mink frog overlapped during the latter part of the summer.

In the Itasca region the habitat niche of R. septentrionalis also overlapped with that of R. clamitans. A green frog taken by

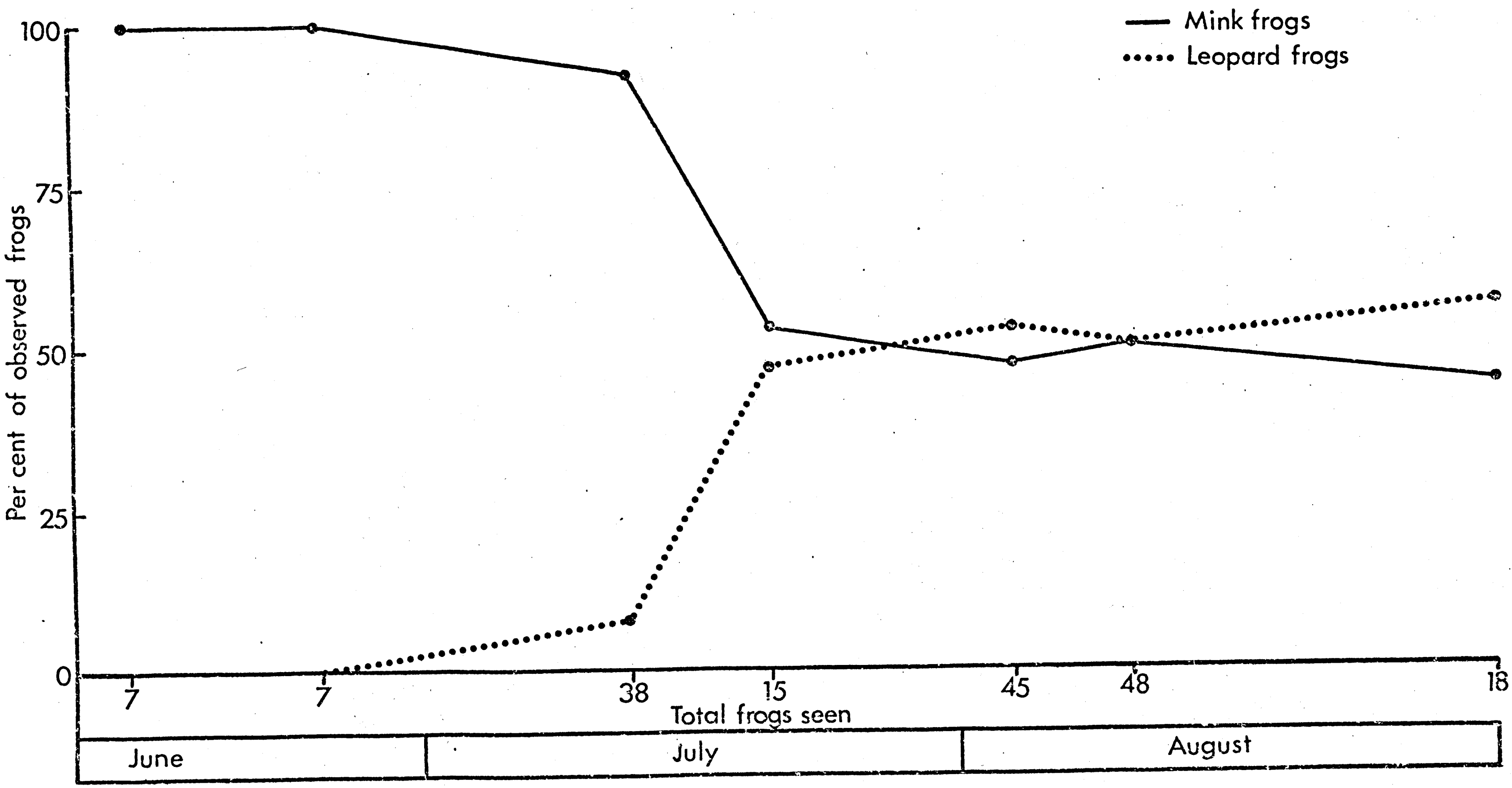


Figure 8. Variation during 1967 in the relative abundance of mink frogs and leopard frogs in French Creek Bay, Itasca State Park, Minnesota.

Dr. J.C. Underhill from Lake Itasca in 1963 is the only known specimen of the species from Itasca State Park. However, populations of green frogs occur in several lotic environments eight to twelve miles south of the park. According to a distribution map in Breckenridge (1944), these are the westernmost green frog populations in Minnesota.

Conant (1958) described the green frog's habitat in a large part of its range as the edge of any water body, flowing or still. This habitat description is certainly valid in eastern Minnesota where green frogs are found along the shores of many different aquatic situations. In many areas within its range, however, the green frog is only characteristic of brooks and small streams (Conant, 1958). The region south of Itasca State Park is such an area for here green frogs are found exclusively along flowing waters.

The green frogs in the Itasca region share their lotic environments with mink frogs, at least during the summer breeding season. In 1966 and 1967, on the basis of collections and calls, the male ratio of green frogs to mink frogs was estimated as 3:1 at two breeding sites: a backwater pond adjacent to Hay Creek 0.2 mile east of the Hubbard County 88 bridge, and a Typha and Zizania marsh bordering Hay Creek 0.1 mile west of the U.S. 71 bridge. Because the location of non-breeding green frogs was not investigated, the amount of overlap in the habitat niches of the two summer-breeding frogs was not determined. Relationships between sympatric mink frog and green frog populations need to be thoroughly studied (Moore, 1952).

FOOD NICHE

Some authors understand the term "ecological niche" to mean an organism's nutritional role in the community (Weatherly, 1963; Smith, 1966). Others define the term as the sum total of the activities and relationships of an organism in an ecosystem, but emphasize the organism's feeding activities and trophic relationships as the most important aspects of the organism's niche (Savage, 1958; Odum, 1959). Consequently, the food niche is often studied as the most important subdivision of the overall ecological niche.

Garnier (1883) portrayed tadpoles of R. septentrionalis as scavengers on the animal tissue of dead fish and tadpoles. Wright (1932) repeated Garnier's statements. Melancon (1950) depicted R. septentrionalis tadpoles as carrion eaters. However, Garnier (1883) also mentioned that R. septentrionalis tadpoles often contain the same "muddy matter" found in all species of tadpoles.

Mink frogs have been known to take small fish, millipedes, water insects, and flies (Garnier, 1883, Pope 1915). Knudsen (1958) listed mayflies and Donacid beetles as important natural prey. Knudsen also suggested that larger adults may occasionally take small frogs, since two captive mink frogs ate small Hyla crucifer kept in the same pen.

In order to define the food niche of R. septentrionalis in the Itasca region, feeding animals were observed and the stomach contents of several collected specimens were examined. All tadpoles and frogs used for stomach content analysis were killed within two hours of capture and placed in ten percent formalin. At a convenient time the tadpoles were staged following the Taylor and Kollros (1946) series for Rana pipiens. The stomachs and intestines of the tadpoles were removed and examined for food presence and types. The stomachs of frogs were removed and their contents identified. Since food items were often broken up and could only be identified by recognizable fragments, most prey organisms were determined only to family or order.

Food Habits of Tadpoles

The stomach and intestinal contents of tadpoles taken in this study indicated an algal diet. R. septentrionalis tadpoles were never observed feeding on dead animals, although many dead fish, tadpoles, and frogs were observed in aquatic habitats with large tadpole populations. R. septentrionalis tadpoles appeared to be primarily herbivorous.

R. septentrionalis tadpoles ceased feeding during Stage XX when the forelimbs appeared and the mouth began widening. Transforming frogs fasted while in Stage XXI. On 10 July 1967 a pair of mating Coenagrionidae adults were observed resting on the head of a Stage XXI mink frog for periods of five and ten seconds. The frog made absolutely no movement. On 15 July a Hydrometra martini adult was observed walking across the head of a Stage XXI frog. The sole reaction of the frog was a blinking of its eyes. These two instances of insects on the heads of Stage XXI frogs contrast markedly with a third observation. On 25 June a Coenagrionidae adult was noted as it landed on the head of an adult frog. The damselfly immediately disappeared into the frog's mouth.

Mink frogs began feeding on an adult diet during Stage XXII. Twenty millimeters was the longest tail length found for a frog whose stomach contained insects. Of twelve mink frogs with tail lengths from 8 to 20 mm., ten (83%) were found with ingested food. Jenssen (1967) found 7 mm. to be the longest tail length for a *Rana clamitans* which had begun an adult diet. Munz (1920) recorded the maximum tail length for frogs with ingested animal prey as 2 mm. in *R. sylvatica*, 5 mm. in *R. palustris*, 15 mm. in *R. pipiens*, and 65 mm. in *R. catesbeiana*. Within the 8 to 20 mm. tail length class Munz reported ingested food in four (15%) of 27 *R. pipiens* and in five (29%) of 17 *R. catesbeiana*.

The above data suggest that mink frogs begin an adult diet earlier during their period of metamorphosis than do most other northern ranids. Bovbjerg and Bovbjerg (1964) listed Stage XXIII as the earliest feeding stage of *R. pipiens*. Jenssen (1967) indicated that *R. clamitans* does not start ingesting insects until Stage XXIII. *R. septentrionalis*, on the other hand, begins an adult diet while in Stage XXII.

Feeding Behavior of Frogs

Heatwole and Heatwole (1968) described the feeding behavior in terrestrial toads as consisting of three responses: turning the head and/or body toward the prey, walking to within striking distance of the prey, and capturing and swallowing the prey.

All observed feedings by mink frogs followed the same sequence of responses. First, the frog oriented its body so that it directly faced the prey. Some frogs were noted orienting to large prey located over seven feet away.

Second, the frog swam slowly toward the prey by making alternate strokes with its hind legs while keeping its quarry in sight. If the prey was at an initial distance of more than two feet the frog would usually move toward its mark by submerging its head and making simultaneous kicks with both rear legs. In either case the frog would end up within striking distance. Of course, if the frog was already within striking distance at the end of the first orienting response, the second stalking response was omitted.

The final response was the capturing of the prey by means of a quick lunge. The open mouth of the frog would often take in adjacent floating vegetation along with the prey.

A feeding mink frog generally began and ended its pursuit in the Water Surface Vertical Layer. On two occasions, however, the prey were located in the Transition System adjacent to the water. In these cases the stalking frogs crawled onto the soil of the transition zone before leaping toward the prey. On two other occasions frogs already sitting out of the water in the Transition System caught insects by means of four and eighteen inch jumps. These two frogs remained in the transition zone following their meals.

Food Habits of Frogs

Table 5 lists the food items recorded in all of the mink frog stomachs examined in this study. Animal material was found in all of the stomachs examined, while plant material appeared in 90.5% of the stomachs. Most of the vegetative matter consisted of duckweeds. One stomach contained 48 Lemna minor, another held 40 L. trisulca, and a third was filled with 20 Spirodela polyrhiza. The presence of plant material in adult ranids is usually ascribed to chance ingestion. Either vegetative material is taken accidentally along with captured animal prey, or the material is eaten mistakenly when wind-caused movements trigger the frog's food-catching response (Turner, 1959; Linzey, 1967; Korschgen and Baskett, 1963). The movement of floating conifer needles and seeds (and bird feathers) may have led to their capture by mink frogs. One frog was observed catching a floating Picea mariana seed and spitting it out. Most ingested plant material, however, probably was consumed along with animal prey captured at the water surface. It is not known if plant material may be used as a food source by frogs.

Ingested animals showed a great diversity in size. The largest prey recorded was a 67 mm. Aeshnidae adult with a 94 mm. wingspread which was found in the stomach of a 60 mm. frog. Such a large dragonfly probably represents the upper size limit of acceptable animal prey. In fact, two of three observations of mink frogs catching large Aeshnids ended with the escape of the dragonfly from the grasp of the captor. It should be noted that the

TABLE 5. TAXONOMIC DISTRIBUTION OF FOOD ITEMS IN 74 STOMACHS OF MINK FROGS COLLECTED IN ITASCA STATE PARK AND VICINITY, MINNESOTA

Animals
- Arthropoda
  - Insecta
    - Collembola
      - Poduridae
      - Sminthuridae
    - Ephemeroptera (la. & ad.)
    - Odonata
      - Aeshnidae
      - Libellulidae (la. & ad.)
      - Lestidae
      - Coenagrionidae (la. & ad.)
    - Orthoptera
      - Gryllidae
    - Hemiptera
      - Corixidae
      - Pleidae
      - Gerridae
      - Veliidae
      - Tingidae
      - Mesoveliidae
      - Hebridae
    - Homoptera
      - Cicadellidae
      - Aphididae
    - Neuroptera
      - Sisyridae
    - Coleoptera
      - Cicindelidae
      - Carabidae
      - Dytiscidae (la. & ad.)
      - Hydrophilidae (la. & ad.)
      - Staphylinidae
      - Cucujidae
      - Coccinellidae
      - Chrysomelidae
      - Curculionidae
    - Trichoptera
      - Psychomyiidae
      - Limnephilidae
      - Leptoceridae (la. & ad.)
    - Lepidoptera
      - Pyralidae
      - and others (la. & ad.)
    - Diptera
      - Tipulidae
      - Culicidae
      - Chironomidae (la., pu., & ad.)
      - Mycetophilidae
      - Stratiomyidae
      - Empididae
      - Dolichopodidae
      - Syrphidae
      - Sciomyzidae
      - Ephydridae
      - and others
    - Hymenoptera
      - Tenthredinidae (la.)
      - Braconidae
      - Ichneumonidae
      - Mymaridae
      - Formicidae
      - Vespidae
  - Arachnida
    - Araneida
    - Acarina
  - Crustacea
    - Amphipoda
  - Diplopoda
- Mollusca
  - Gastropoda
    - Pulmonata
- Chordata
  - Aves (feathers)

Plants
- Tracheophyta
  - Gymnospermae
    - Pinaceae
      - *Picea mariana* (seeds & leaves)
      - *Larix laricina* (leaves)
  - Angiospermae
    - Lemnaceae
      - *Spirodela polyrhiza*
      - *Lemna trisulca*
      - *Lemna minor*
    - Ceratophyllaceae
      - *Ceratophyllum demersum* (leaves)
  - Unidentified seeds

two unsuccessful frogs were smaller than the successful captor, a 55 mm. female.

Several animals 2 mm. or less in length were found in the 74 stomachs examined. Veliidae adults and nymphs were found in 27 stomachs. In the Itasca region these tiny insects were abundant near the shores where they often occurred in surface swarms. These swarms undoubtedly produced a sufficient amount of mass and movement to attract feeding mink frogs. One frog contained 275 Veliids while eight other frogs each held more than 50. On the other hand, twelve frogs had ingested only one or two Veliids. It is doubtful that a single Veliid would evoke a food-catching response. When only one or two Veliids occurred, they most likely had been fortuitously ingested along with larger prey taken at the surface. Most of the still smaller Collembola and Pleidae individuals probably were also accidentally caught. Only one or two Collembolans were found in 15 of the 23 stomachs containing these organisms. A single Pleid was recorded from six of the seven frogs which held Pleids.

The food niche of a species is largely determined by its habitat niche. Rana clamitans tadpoles ingest whatever entomostracans and algal species are present in their local habitats (Jenssen, 1967). In general, adult ranids eat anything of proper size which moves within range. Therefore, a frog's diet is largely a reflection of the availability of prey organisms in the frog's local habitat. Diet differences between individuals or populations of the same Rana species have usually been correlated with habitat differences (Tyler, 1958; Korschgen and Baskett, 1963; Jenssen and Klimstra, 1966).

The stomach contents of mink frogs collected from Bog D Lake on 7 August 1967 (Table 6) and those of frogs taken four miles away from French Creek Bay on 4 and 11 August 1967 (Table 7) showed obvious differences. Ingested vegetation in the Bay frogs included Spirodela polyrhiza and Lemna trisulca. Neither of these duckweeds were found in the Bog D frogs. But some of the Bog D frogs had taken Larix needles while none of the Bay frogs had done so. These results were due to the presence or absence of the plant species in the local habitats. Although Lemna minor, L. trisulca, and Spirodela polyrhiza were abundant in the Ceratophyllum demersum mats of French Creek Bay, only L. minor was present in the C. demersum mats of Bog D. A zone of tamaracks completely surrounded Bog D Lake; Larix needles were easily blown into the lake. The nearest tamaracks to French Creek Bay were located 700 feet away.

A comparison of the animal prey shows there was a much greater percent frequency of occurrence of Gerridae, Coleoptera larvae, and Pulmonata in the Bay frogs. Conversely, there was a more frequent occurrence of Veliidae in the Bog D frogs. Most Bog D frogs were found on vegetation mats within five feet of the shoreline, while most Bay frogs were taken from mats located more than twenty feet offshore. Consequently, the stomachs of the Bay frogs held a much larger percentage of aquatic organisms, e.g. aquatic Coleoptera larvae and pulmonate snails. The occurrence

TABLE 6. INGESTED MATERIAL FOUND IN 18 MINK FROGS, MEAN SNOUT-VENT LENGTH 52.5 MM., COLLECTED 7 AUGUST 1967 IN BOG D, AND IN 19 MINK FROGS, MEAN SNOUT-VENT LENGTH 56.3 MM., COLLECTED 25 JUNE, 13 AND 21 JULY 1967 IN FRENCH CREEK BAY, ITASCA STATE PARK, MINNESOTA

	Bog Mink Frogs (N=18)			Bay Mink Frogs (N=19)		
Ingested Material	No. of Stomachs	% Freq.	No. of Items	No. of Stomachs	% Freq.	No. of Items
Collembola	2	11.1	2	8	42.1	31
Odonata						
Aeshnidae ad.	1	5.6	1	--	-----	--
Libellulidae ad.	1	5.6	1	5	26.3	8
Lestidae ad.	1	5.6	1	--	-----	--
Coenagrionidae ad.	5	27.8	7	14	73.7	31
Libellulidae la.	--	-----	--	2	10.5	2
Coenagrionidae la.	--	-----	--	9	47.4	18
Hemiptera						
Corixidae	6	33.3	7	--	-----	--
Pleidae	3	16.7	5	--	-----	--
Gerridae	4	22.2	4	1	5.3	1
Veliidae	16	88.9	1295	3	15.8	3
Hebridae	--	-----	--	1	5.3	1
Homoptera						
Cicadellidae	5	27.8	6	1	5.3	1
Aphididae	1	5.6	1	--	-----	--
Neuroptera						
Sisyridae ad.	1	5.6	1	--	-----	--
Coleoptera						
adults	6	33.3	9	6	31.6	10
larvae	1	5.6	1	--	-----	--
Trichoptera						
adults	3	16.7	3	14	73.7	99
larvae	3	16.7	3	1	5.3	1
Lepidoptera						
larvae	4	22.2	5	--	-----	--
Diptera						
adults	12	66.7	26	7	36.8	9
pupae	2	11.1	2	6	31.6	11
Hymenoptera						
adults	5	27.8	17	2	10.5	3
larvae	4	22.2	7	--	-----	--
Araneida	11	61.1	16	2	10.5	4
Acarina	1	5.6	1	--	-----	--
Pulmonata	3	16.7	3	2	10.5	2
Feather	--	-----	--	1	5.3	1
Larix laricina leaf	5	27.8	8	--	-----	--
Spirodela polyrhiza	--	-----	--	12	63.1	92
Lemna trisulca	--	-----	--	7	36.8	16
Lemna minor	7	38.9	116	6	31.6	67
Ceratophyllum demersum leaf	7	38.9	19	9	47.4	20
Seed	5	27.8	7	2	10.5	6

TABLE 7. INGESTED MATERIAL FOUND IN 23 MINK FROGS, MEAN SNOUT-VENT LENGTH 60.8 MM., AND IN 23 LEOPARD FROGS, MEAN SNOUT-VENT LENGTH 62.3 MM., COLLECTED 4 AND 11 AUGUST 1967 IN FRENCH CREEK BAY, ITASCA STATE PARK, MINNESOTA

Ingested Material	Mink Frogs (N=23)			Leopard Frogs (N=23)		
	No. of Stomachs	% Freq.	No. of Items	No. of Stomachs	% Freq.	No. of Items
Collembola	11	47.8	45	1	4.3	1
Odonata						
Aeshnidae ad.	1	4.3	1	--	-----	--
Libellulidae ad.	5	21.7	5	3	13.0	6
Coenagrionidae ad.	4	17.4	7	3	13.0	3
Unidentified ad.	--	-----	--	1	4.3	1
Coenagrionidae la.	--	-----	--	1	4.3	1
Unidentified la.	1	4.3	1	--	-----	--
Hemiptera						
Corixidae	1	4.3	1	--	-----	--
Pleidae	4	17.4	4	1	4.3	3
Gerridae	12	52.2	22	8	34.8	10
Veliidae	6	26.1	7	2	8.7	2
Mesoveliidae	1	4.3	1	--	-----	--
Pentatomidae	--	-----	--	4	17.4	5
Unidentified	3	13.0	4	1	4.3	1
Homoptera						
Cicadellidae	1	4.3	1	2	8.7	2
Aphididae	1	4.3	1	--	-----	--
Coleoptera						
adults	11	47.8	14	7	30.4	10
larvae	14	60.9	28	3	13.0	5
Trichoptera						
adults	8	34.8	10	1	4.3	1
larvae	1	4.3	1	--	-----	--
Lepidoptera						
adults	5	21.7	7	8	34.8	11
larvae	1	4.3	1	4	17.4	4
Diptera						
adults	12	52.2	27	11	47.8	17
pupae	6	26.1	8	1	4.3	1
larvae	2	8.7	3	2	8.7	2
Hymenoptera						
adults	12	52.2	17	14	60.9	24
Araneida	8	34.8	8	11	47.8	17
Acarina	2	8.7	2	1	4.3	1
Pulmonata	11	47.8	23	15	65.2	34
Picea mariana leaf	1	4.3	1	--	-----	--
Spirodela polyrhiza	14	60.9	97	9	39.1	41
Lemna trisulca	14	60.9	148	14	60.9	39
Lemna minor	6	26.1	49	6	26.1	11
Ceratophyllum demersum leaf	15	65.2	73	7	30.4	11
Seed	6	26.1	6	2	8.7	2

of more Veliids in frogs from the 0.8-acre Bog D Lake and more Gerrids from Lake Itasca's French Creek Bay was to be expected. In general, Veliids occupy more secluded or protected aquatic habitats than their relatives the Gerrids (Usinger, 1963).

A ranid's diet will change seasonally even if the animal continues to occupy the same habitat (Turner, 1959; Brooks, 1964; Linzey, 1967). The ingested organisms in French Creek Bay mink frogs collected on 25 June, 13 and 21 July 1967 (Table 6) were quite different from the prey of the Bay frogs collected on 4 and 11 August 1967 (Table 7). A large number of Trichoptera adults and Coenagrionidae larvae and adults were counted in the June and July frogs. The numbers of these same organisms were much smaller in the August frogs. The latter frogs, however, showed a larger intake of other prey: Pulmonata, Gerridae, Coleoptera larvae, and Hymenoptera adults. The seasonal variation in diet undoubtedly coincided with the life cycles and seasonal movements of the prey organisms.

Comparative Summer Food Niches

Frogs are usually characterized as opportunistic predators without any food preferences. Different frog species of the same size class in the same local habitat generally eat the same prey organisms. Inger and Greenberg (1966) described very similar food niches in three _Rana_ species which occupied almost identical habitat niches. Marshall and Buell (1955) found that the Bog D populations of _Rana pipiens_ and _R. sylvatica_ overlapped extensively in the Tamarack Zone (Figure 7A). A stomach analysis study revealed that similar prey were taken by the sympatric frogs (Table 8A).

The Bog D population of R. pipiens also overlaps with that of R. septentrionalis. During August 1967 and 1968, leopard and mink frogs were present together on vegetation mats in the Bog D Aquatic Zone (Figure 7B). On 7 August 1967, seven leopard frogs and eighteen mink frogs were collected from the Aquatic Zone for stomach content analysis. The mean snout-vent length of the leopard frogs was 48.6 mm. while that of the mink frogs was 52.5 mm. Most of the frogs were taken from within five feet of the shoreline.

A total of 55 identifiable animals were found in the leopard frog stomachs while 1424 (including 1295 Veliids) animals were counted in the mink frog stomachs. Table 8B summarizes the data by listing the number of stomachs in which the most abundant foods for each species were found. With the exception of Araneida, the most abundant food items in the leopard frogs and in the mink frogs were not the same. Cicadellidae individuals were found in five leopard frogs and in five mink frogs. Adult Formicidae and Ichneumonidae were each found in three leopard frogs and in two mink frogs. The frequencies of occurrence of Cicadellids, Formicids, and Ichneumonids were greater in the seven leopard frogs than in the eighteen mink frogs. Conversely, the frequencies of occurrence of Veliidae, Corixidae, and Chironomidae were much greater in the mink frogs. No Veliids or Corixids and only one Chironomid were found in the leopard frogs.

TABLE 8. NUMBER OF STOMACHS CONTAINING THE MOST ABUNDANT FOOD ITEMS FOUND IN EACH RANID A) DURING AUGUST 1951, 1952, AND 1953 IN THE TAMARACK AND SEDGE MAT ZONES (FROM MARSHALL AND BUELL, 1955), AND B) DURING AUGUST 1967 IN THE AQUATIC ZONE, BOG D, ITASCA STATE PARK, MINNESOTA

A.

	Wood Frog		Leopard Frog		Mink Frog	
Tamarack	(29)*		(22)		(0)	
	Formicidae	12	Formicidae	5		
	Carabidae	9	Araneida	5		
	Ichneumonidae	5	Ichneumonidae	3		
Sedge Mat	(1)		(32)		(0)	
	Formicidae	1	Formicidae	12		
	Carabidae	1	Araneida	11		
	Cicadellidae	1	Ichneumonidae	9		

B.

	Wood Frog		Leopard Frog		Mink Frog	
Aquatic	(0)		(7)		(18)	
			Cicadellidae	5	Veliidae	16
			Formicidae	3	Araneida	11
			Araneida	3	Chironomidae	7
			Ichneumonidae	3	Corixidae	6

*Figures in parentheses show number of stomachs containing food items.

During August 1967 and 1968, leopard and mink frogs also occurred together on vegetation mats in French Creek Bay (Figure 8). On 4 August 1967, eleven leopard frogs and twelve mink frogs were collected for stomach analysis. On 11 August, samples of twelve leopard frogs and eleven mink frogs were taken. The mean snout-vent length of the leopard frogs was 62.3 mm. while that of the mink frogs was 60.8 mm. Most of the frogs were collected more than twenty feet offshore.

A total of 162 identifiable animals were recorded from the 23 leopard frog stomachs, and 249 identifiable animals were found in the 23 mink frog stomachs. Table 7 lists the organisms recorded in the stomachs examined. Overall, the diets of the French Creek Bay leopard frogs and mink frogs were similar in taxonomic composition and prey numbers. Yet there were some significant differences in the diets. More Trichoptera adults, Coleoptera larvae, Collembola, and vegetation were ingested by mink frogs than by leopard frogs. Trichoptera adults were present both above and at the water surface. Trichoptera adults were recovered from eight (34.8%) of the mink frogs, but only from one (4.3%) of the leopard frogs. The larvae of Hydrophilid beetles were present just beneath the water surface of the bay in thick vegetation mats. Hydrophilidae larvae constituted 25 of the 28 larval Coleopterans eaten by fourteen mink frogs, and four of the five larval Coleopterans eaten by three leopard frogs. Collembolans and vegetation were probably accidentally swallowed along with surface prey. A total of 45 Collembolans, To: MII

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THE ECOLOGY AND LIFE HISTORY OF THE MINK FROG...
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294 duckweeds, and 73 _Ceratophyllum demersum_ leaves were found in the mink frogs. One Collembolan, 91 duckweeds, and eleven _C. demersum_ leaves were recovered from the leopard frogs.

Zweifel (1955) stated that since ranids eat anything of proper size which moves within range, different species of _Rana_ occupying the same region will necessarily have slightly different habitat preferences. In the Itasca region, mink frogs were almost always restricted to aquatic habitats, occurring in terrestrial habitats only during movements between water bodies. Leopard frogs were found primarily in areas dominated by grass-like plants, although leopard frogs inhabited wooded and aquatic habitats as well.

Both leopard frogs and mink frogs were found on 7 August 1967 in the Bog D Aquatic Zone. Stomach content analysis revealed that the most abundant foods of the Aquatic Zone leopard frogs were terrestrial in origin and largely identical to those food items found in leopard frogs from the Sedge Mat and Tamarack Zones (Table 8). The mink frogs, on the other hand, primarily ingested aquatic organisms which were common at the water surface of Bog D Lake. The Bog D mink frogs obviously fed in the Aquatic Zone in which they also rested, while the sympatric leopard frogs apparently fed in the adjacent Sedge Mat Zone, a typical habitat of _Rana pipiens_.

The leopard frogs in French Creek Bay during August 1967 rested much further offshore than those in Bog D. Consequently, the diet of the Bay leopard frogs contained more aquatic food items and approximated the diet of sympatric mink frogs (Table 7). Bay leopard frogs and mink frogs contained similar numbers of all major food items except Hydrophilidae larvae and Trichoptera adults. The higher incidence of the latter two aquatic prey in the mink frogs may reflect interspecific differences in either food preference or feeding behavior.

Cott (1940) presented a great deal of experimental evidence showing that anurans are able to discriminate in their choice of prey. Cott concluded that differential food preferences are responsible for dissimilar stomach contents in sympatric species of frogs. Perhaps in French Creek Bay the leopard frogs avoided larval Hydrophilids and adult Trichopterans. However, it is not known what factors would make these two prey less palatable to leopard frogs than to mink frogs.

Interspecific differences in feeding behavior may also account for the greater utilization of certain prey by one species (Klimstra and Myers, 1965). For example, the major summer foraging zones of the white-breasted nuthatch, Sitta carolinensis, are all included within some of the major foraging zones of the hairy woodpecker, Dendrocopus villosus, in Colorado ponderosa pine forests (Stallcup, 1968). In the areas of overlap the hairy woodpecker most often takes food from the surface of the bark, while the white-breasted nuthatch forages both on the surface and beneath flakes of bark. The white-breasted nuthatch utilizes more of its relatively restricted habitat for feeding than does the greater-ranging hairy woodpecker. In eastern deciduous forests the towhee, Pipilo erythrophthalmus, feeds primarily on the forest floor while the catbird, Dumetella carolinensis, obtains only some of its food there. As might be expected, the ground foraging behavior of the towhee is much more efficient than that of the catbird (Klopfer, 1962).

In the Itasca region during August the feeding area of Rana pipiens encompassed both aquatic and terrestrial habitats while that of R. septentrionalis included only aquatic habitats. In aquatic areas of overlap the foraging behavior of the aquatic mink frog may have been more efficient than that of the widely-ranging leopard frog. Specifically, mink frogs may have had a greater awareness of prey at the water surface since mink frogs usually rest with their eyes just above the surface. The comparatively large amount of Collembolans and vegetation ingested by the mink frogs in French Creek Bay indicated a more frequent occurrence of surface feeding by the mink frogs than by the leopard frogs. Collembolans and vegetation are thought to be fortuitously ingested along with larger prey taken from the water surface. Examples of larger prey would include larval Hydrophilids which were present just beneath the water surface in the vegetation mats, and adult Trichopterans which emerged from their pupal cases at the surface, laid eggs at the surface, and often were caught in the surface film. In short, the higher incidence of Hydrophilidae larvae and Trichoptera adults in mink frog stomachs may have been due to a better utilization of water surface prey by mink frogs than by sympatric leopard frogs.

PARASITISM

In addition to habitats and foods, enemies are also basic elements of an animal's ecological niche (Elton, 1927; Savage, 1958: Kendeigh, 1961). Both parasites and predators largely determine an organism's position in an ecosystem.

The mink frog harbors a great number of parasites, probably because it is a year-around resident of the Aquatic System. Bouchard (1951) found that every species of platyhelminth parasite recovered in five host species of Maine amphibia also occurred in _R. septentrionalis_. No change in the parasite fauna of the mink frog was noted during a four month (May -- August) study period. Obviously, infection and re-infection is a constant process in the aquatic host (Bouchard, 1951).

Among protozoan parasites of the mink frog, Metcalf (1923) recorded one scant infection of _Opalina_ sp. in a specimen from Lucknow, Ontario. Camara and Buttrey (1961) found 19 species of enteric protozoa in _R. septentrionalis_ from the Itasca region. Walton, in his inclusive review of the parasites of amphibians (Walton, 1964a, 1964b, 1966), catalogued all of the mink frog parasites mentioned in the three papers cited above. In addition, he listed the trematode _Megalodiscus americanus_ as a parasite of the mink frog (Walton, 1964b). Since Walton in the same paper subsequently failed to list _R. septentrionalis_ as one of the many hosts of _M. americanus_, and as no other reference to this species as a mink frog parasite has been found in a thorough search of the literature, this author is inclined to believe that the inclusion of the trematode was simply an error in cataloguing.

In addition to the published studies cited above, Dr. Clarence E. Harms investigated helminth parasites of mink frogs taken from the Itasca region in 1963 (Harms, unpublished manuscript). Harms found one genus of Acanthocephala, one genus of Nematoda, and eight genera of Trematoda in the mink frogs which he examined. Harms also recorded the presence of the cestode _Ophiotaenia olor_ (Ingles, 1936) Yamaguti, 1938 (=_Crepidobothrium olor_ Ingles, 1936) in the intestines of "several dozen" mink frogs from Lake Itasca. The only other known host of this tapeworm is _Rana aurora_ (Walton, 1964b).

The incidence of _O. olor_ in mink frogs from Lake Itasca was determined in 1967 in conjunction with a study of stomach food contents. The 41 frogs examined for tapeworms were taken from French Creek Bay during the period 13 July through 1 September. The frogs were killed within two hours of capture and placed in ten percent formalin. At a convenient time their intestines were removed and examined for the presence of _O. olor_.

Specimens of _O. olor_ were found in 16 (39%) of the 41 frogs examined. The tapeworms were found in nine (56%) of 16 males and in seven (28%) of 25 females. A four-fold Chi-square test failed to show a significant difference between the incidences of infection on the two sexes (Chi-square = 3.272; $.10 > P > .05$).

The life-cycle of _O. olor_ is not completely known. Ingles (1936) was successful in observing the development of _O. olor_ procercoids in copepods, but did not pursue the development of the plerocercoid and adult stages. The life-cycles of other frog-inhabiting Ophiotaenids involve the accidental ingestion of an intermediate entomostracan host by an anuran host. In one type of life-cycle a copepod is the only intermediate host (Thomas, 1931; Yamuguti, 1943). In such a life-cycle the plerocercoid develops either in the copepod or in the definitive frog host (Wardle and McLeod, 1952). Another life-cycle involves two intermediate hosts: a microcrustacean, and a tadpole or young frog which ingests the first intermediate host (Thomas, 1934; Noe C. and Lira L., 1946). In the latter life-cycle the second intermediate host is subsequently caught and eaten by the definitive frog host.

Fortuitous ingestion of an infected copepod by a mink frog is very possible. The capture of an animal prey at the water surface by a mink frog often results in the accidental consumption of many smaller aquatic organisms. A mink frog may easily ingest a copepod serving as an intermediate host for O. olor. The existence of a second intermediate amphibian host in the life-cycle of O. olor is unlikely. No vertebrates were found in a stomach analysis study of 74 mink frogs, 40 of which were taken from areas where metamorphosing and juvenile mink and leopard frogs were common. In short, the food habits of the definitive host R. septentrionalis suggest that copepods serve as the only intermediate hosts for O. olor in Lake Itasca.

PREDATION

Previous ecological studies have identified only vertebrates as predators of *R. septentrionalis*. According to Wright (1932), the newt, *Notophthalmus viridescens*, is a serious predator of eggs and hatching embryos. Known predators of *R. septentrionalis* tadpoles and frogs are the great blue heron, *Ardea herodias*, and other Ciconiiformes (Wright, 1932), the green frog, *Rana clamitans* (Moore, 1952), and a snake, probably *Thamnophis sirtalis* (Hoopes, 1938).

All of the above carnivores occurred in mink frog habitats in the Itasca region. Great blue herons were often observed taking *R. septentrionalis* tadpoles and adults (Hedeen, 1967). Captive green frog adults regularly fed on metamorphosing *R. septentrionalis* tadpoles.

Other vertebrate predators included larvae of the tiger salamander, *Ambystoma tigrinum*, which readily ate tadpoles taken from the same pond. Raccoons, *Procyon lotor*, were observed attempting to catch mink frogs on two occasions. Raccoons probably are not major predators of *R. septentrionalis*, since frogs constitute only 0.2% by volume of the diet of raccoons in north-central Minnesota (Schoonover and Marshall, 1951).

Several other vertebrates may also prey on *R. septentrionalis* eggs, tadpoles and frogs in the Itasca region. Mature tadpoles taken from water bodies with large populations of the five-spined stickleback, *Culaea inconstans*, were often missing up to half of their tails. While defending their nests, the aggressive male sticklebacks apparently bit off pieces of the tadpoles' tails. These pugnacious little fish are destructive even to fishes of larger size (Forbes and Richardson, 1920), and so they might easily kill and consume small *R. septentrionalis* tadpoles. Other known tadpole-eating fishes which occurred in mink frog breeding habitats were the mud minnow, *Umbra limi*, and sunfish, *Lepomis* spp. (Voris and Bacon, 1966). Northern pike, *Esox lucius*, and largemouth bass, *Micropterus salmoides*, probably were predators of mink frogs in the deeper water bodies (Ferguson *et al.*, 1965).

Martof (1956b) reported that green frog eggs were eaten by the painted turtle, *Chrysemys picta*, and the snapping turtle, *Chelydra serpentina*. Both of these turtles frequented mink frog breeding areas in the Itasca region and may have consumed mink frog eggs. Pope (1939) stated that *C. serpentina* also eats tadpoles and frogs. In May 1967 a submerged snapping turtle was observed taking breeding *Bufo americanus* males from the water surface. Snapping turtles probably also preyed upon *R. septentrionalis* frogs and tadpoles.

Due to its feeding habits and habitats, the belted kingfisher, *Megaceryle alcyon*, was suspected to be a predator of *R. septentrionalis* tadpoles. Belted kingfishers are known to feed on large *Rana catesbeiana* tadpoles (Terres, 1968). Karlstrom (1962) listed the coyote, *Canis latrans*, as a predator of adult *Bufo canorus*. On the rainy evening of 12 September 1967, two coyotes were observed on a paved road just north of Itasca State Park as they captured migrating leopard frogs.

Coyotes may likewise have taken migrating mink frogs. The mink frog's namesake might also have been one of its predators. The diet of the amphibious mink, Mustela vison, usually includes frogs (Dearborn, 1932; Gunderson and Beer, 1953).

Invertebrate predators of R. septentrionalis belong to two classes, Insecta and Hirudinea. Insects constitute most of the diet of mink frogs, but R. septentrionalis tadpoles surely serve as food for many insects. Two giant water bugs, Lethocerus americanus, were found sucking the body fluids from metamorphosing tadpoles. Other aquatic insects known to prey on tadpoles were also present in breeding habitats of the mink frog: Belostoma fluminea, Notonecta spp., Ranatra fusca, several species of larval Odonata, larval Gyrinidae, larval Hydrophilidae, and larval and adult Dytiscidae (Hungerford, 1919; Wilson, 1923; Pennak, 1953).

Leeches are another important group of aquatic predators. Many species of leeches occur in the Itasca region, but only Macrobdella decora was observed feeding on R. septentrionalis. Four active mink frogs were caught with attatched M. decora individuals. Leeches were found on three tadpoles, two of which had died. M. decora is also known to feed on frog eggs (Moore, 1923).

ESCAPE BEHAVIOR

Unsuccessful attacks by *Macrobdella decora* on mink frogs were noted on three occasions. At the instant the partly-submerged frogs were touched by the swimming leeches, they leaped to the edge of the sedge mat where they subsequently rested almost completely out of the water. One of the frogs jumped three times before reaching the sedge mat, each jump being triggered by the pursuing leech.

Mink frogs escaping from above-surface disturbances usually dove underwater. The escape behavior of 312 frogs resting at the water surface was noted during the summers of 1966 and 1967. When confronted by an observer, 86.5% of the frogs dove underwater, 7.7% swam underwater for a short distance and then surfaced, and 5.8% hopped into nearby terrestrial vegetation. There was little difference between the escape behavior of frogs approached from land by foot and that of frogs approached from water by boat. Of 127 frogs confronted by an observer on land, 86.6% dove, 9.5% swam, and 3.9% hopped. Of 185 frogs confronted by an observer on water, 86.5% dove, 6.5% swam, and 7.0% hopped.

The frogs that dove underwater usually concealed themselves in submerged vegetation or in the bottom mud. They remained hidden for periods ranging from 30 seconds to 26 minutes. Upon returning to the surface, the frogs exposed only their eyes and snouts above water. At the slightest movement by the observer the alert frogs again dove underwater.

The escape behavior of a frog is closely related to its preferred habitat. Little water is available in the bog forests of Itasca State Park during the summer months. Consequently, very few of the resident Rana sylvatica individuals escape into water (Marshall and Buell, 1955; Bellis, 1961b). Even when water is available, the escape behavior of the terrestrial wood frog differs from that of the aquatic mink frog. A wood frog popula-rion located around the shore of a temporary pond in Michigan showed the following escape methods: 39.6% of the frogs dove, 47.8% swam, 1.2% hopped overland, and 11.4% hopped over the water on surface litter and muck (Heatwole, 1961). In contrast to the escape behavior of mink frogs, more escaping wood frogs swam near the water surface than dove to the bottom. Escaping wood frogs also hopped over surface substrata, an escape route never used by observed mink frogs.

When confronted by an observer, Rana pipiens on floating vegetation mats escaped either by hopping over the mats or by swimming to other mats. Sympatric mink frogs usually dove under-water immediately. Leopard frogs inhabiting field habitats often escaped by jumping into adjacent aquatic habitats. But most of the terrestrial leopard frogs that escaped into water bodies immediately returned to shore. This aversion to water in terrestrial leopard frogs has been noted in other leopard frog populations in Minnesota (D.J. Merrell, personal communication) and in Florida (Barbour, 1920). Neither Rana sylvatica nor R. pipiens use water as an escape cover as frequently as does R. septentrionalis.

"RED LEG"

During the summers of 1966 and 1967, eighteen dead and dying *R. septentrionalis* tadpoles and six dead mink frogs were found without any external marks of predation. On thirteen of the tadpoles and two of the frogs the symptoms of "Red Leg" were observed: pink skin and extreme edema in the abdominal region and legs (Emerson and Norris, 1905). "Red Leg" is a usually fatal disease found in frogs infected with bacteria of the type *Aeromonas* (Reichenbach-Klinke and Elkan, 1965). "Red Leg" appears commonly among stock frogs held in laboratories. Natural occurrences of the disease have been previously recorded in populations of *Bufo americanus* (Dusi, 1949) and *Rana clamitans* (Martof, 1956b).

THERMAL ECOLOGY

Environmental temperatures greatly affect the distribution and survival of a species. Consequently, temperature is one of the important physical factors included in an animal's niche (Dumas, 1956; Hutchinson, 1957). The effect of environmental temperatures on R. septentrionalis has been noted in two previous studies. Brattstrom (1963) reported that four mink frogs had a mean body temperature of 28.8°C. while basking in the sun on 25.0°C. rocks and in 22.0°C. air. Dean (1966) concluded that 36°C. is the LD_{50} temperature of Itasca State Park mink frogs submerged in warmed water for one hour.

During the period 25 -- 28 May 1967 body temperatures were taken of partly-submerged mink frogs caught in Itasca State Park. The temperatures were taken by means of a Schultheis quick recording thermometer calibrated in divisions of 0.2°C. The bulb of the thermometer was inserted cloacally immediately after a frog was secured. Approximately ten seconds were required to obtain a temperature reading. Frogs held longer than twenty seconds showed a rising body temperature due to heat conduction from the captor's hands. Body temperatures were not taken when captures involved too much handling or a chase. The temperatures of the air and water which immediately surrounded a frog were recorded. Light conditions were listed as sunny, shady, or cloudy. No frogs were taken at night.

Table 9 lists the body temperatures of 27 mink frogs caught in Itasca State Park. The body temperatures of the

TABLE 9. BODY TEMPERATURES OF MINK FROGS CAUGHT IN ITASCA STATE PARK, MINNESOTA

Date	Time	Temperature °C. Body	Air	Water
25 May 1967	1125	24.2	21.9	24.3
	1215	23.7	21.8	20.4
	1230	23.8	21.9	19.1
	1410	24.3	22.9	19.1
	1505	24.0	23.4	24.2
	1550	26.8	23.1	26.2
	1610	26.0	24.0	22.9
26 May 1967.	1215*	19.9	19.4	20.9
	1235*	21.0	21.5	20.0
	1250	21.8	21.3	19.7
	1310	21.7	19.4	19.9
	1350	27.1	21.0	25.6
	1410	25.9	21.2	25.2
	1455	26.0	21.2	23.3
	1600	27.1	21.3	22.9
	1625	22.5	20.6	21.8
	1915	16.2	15.2	14.6
27 May 1967	1230	21.7	19.3	21.4
	1240	21.1	19.5	21.7
	1540	26.4	22.3	23.4
	1620	24.6	21.6	22.4
	1710	21.8	19.5	18.1
28 May 1967	1130	21.5	19.1	17.2
	1150	22.9	19.2	19.7
	1200**	17.1	19.0	16.0
	1215	20.2	19.1	17.3
	1235**	19.0	19.0	17.5

*Cloudy
**In shade

poikilothermous mink frogs varied widely, as the histogram of Figure 9 clearly shows. Brattstrom (1963) listed 25.7°C. as the minimum voluntary temperature of the species. The 16.2°C. body temperature of a mink frog found on 26 May 1967 lowers the known minimum voluntary temperature by 9.5°C.

The internal temperature of a poikilotherm varies in relation to environmental temperatures. Body temperatures of partly-submerged mink frogs approximated ambient water and air temperatures (Figures 10 and 11). Animals collected under sunny conditions usually had body temperatures that exceeded the environmental temperatures. Solar radiation served to raise a frog's internal temperature above the level determined by heat conduction from surrounding air and water. By selecting a microhabitat in which radiant heat and air and water temperatures are at a maximum, a mink frog may maintain its body temperature at the highest level possible under local environmental conditions. Of course, there is an internal temperature level beyond which further heating would prove dangerous to the frog. The maximum voluntary temperature of R. septentrionalis is listed as 30.5°C. by Brattstrom (1963).

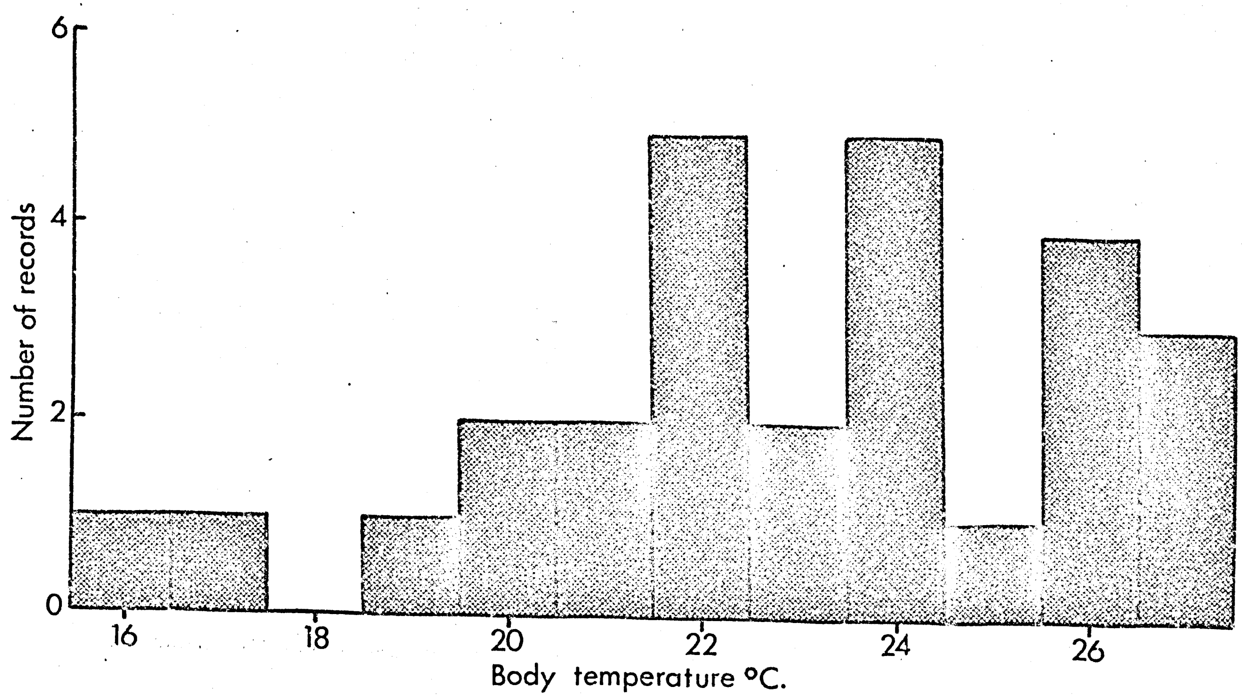

Figure 9. Body temperatures of mink frogs caught 25 -- 28 May 1967 in Itasca State Park, Minnesota.

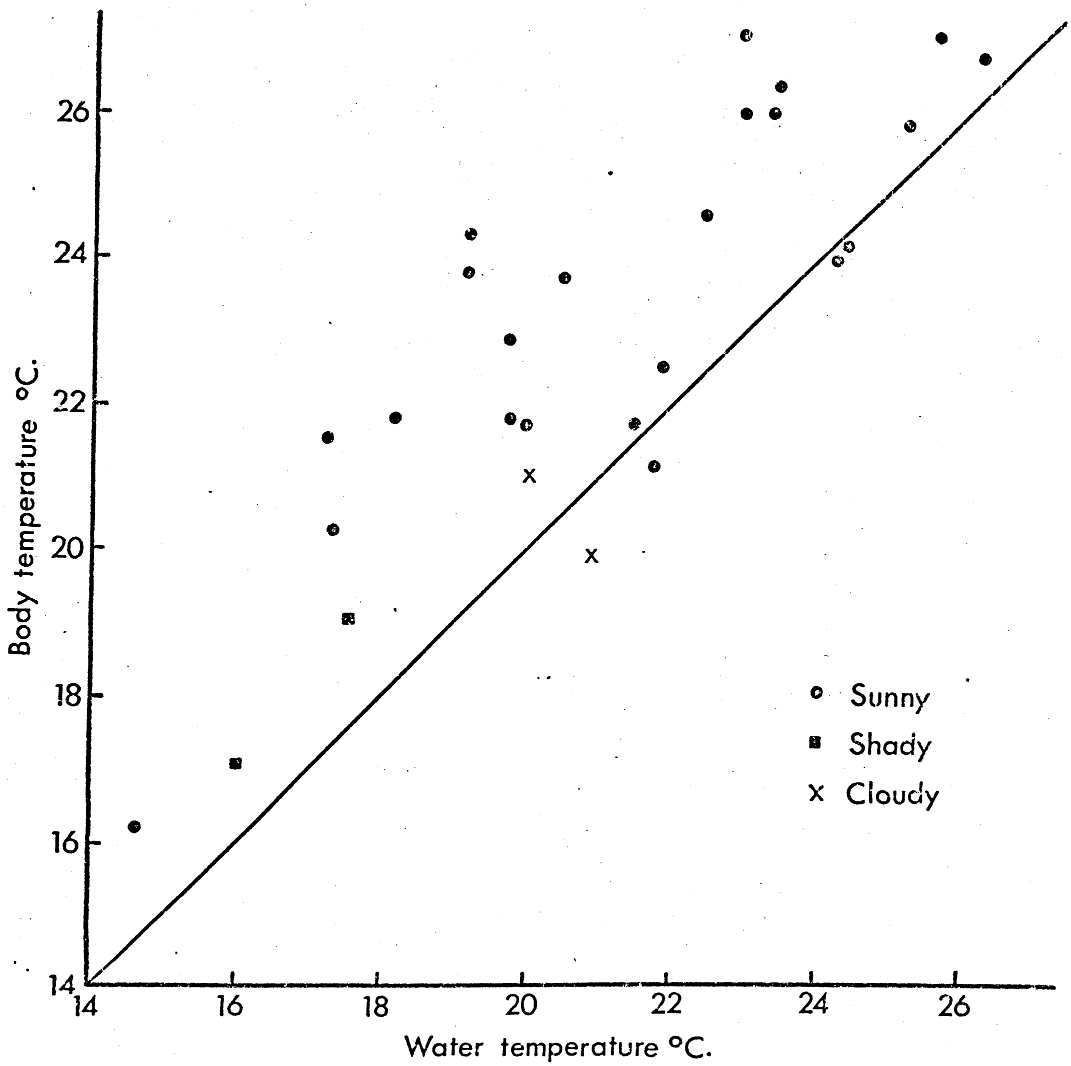

Figure 10. Body temperatures of mink frogs plotted against ambient water temperatures. Solid line indicates where body temperature equals water temperature.

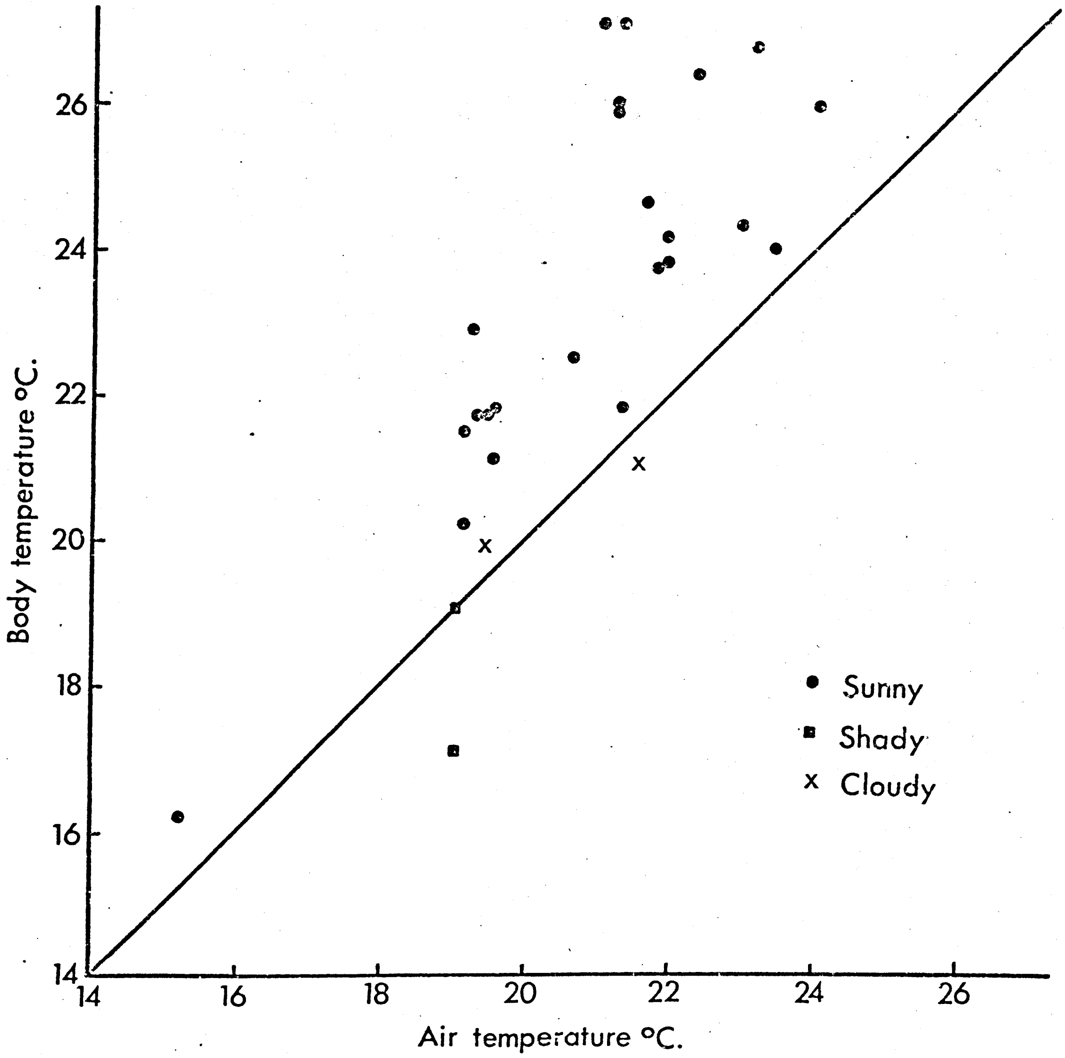

Figure 11. Body temperatures of mink frogs plotted against ambient air temperatures. Solid line indicates where body temperature equals air temperature.

DISTRIBUTION IN MINNESOTA

Breckenridge (1944) listed nine Minnesota county records of *R. septentrionalis*: Ramsey, Crow Wing, Beltrami, Itasca, Carlton, St. Louis, Cook, Lake, and Clearwater. Mink frogs were recorded from eighteen Minnesota counties during the years 1966 -- 1968 (Table 10), including three of the counties mentioned above (Cook, Lake, Clearwater). According to the vegetation map by Kuchler (1964), all of the recorded Minnesota localities of *R. septentrionalis* are situated within the portion of the state's forested region located north of 45° N. latitude. Mink frogs never have been recorded from the prairie formations in western Minnesota, although males were heard in Mahnomen County within 1.5 miles of the tallgrass prairie (see local vegetation map in McAndrews, 1966).

TABLE 10. MINNESOTA COUNTIES IN WHICH MINK FROGS WERE RECORDED DURING THE YEARS 1966, 1967, AND 1968. ALL COLLECTED FROGS ARE DEPOSITED AT THE JAMES FORD BELL MUSEUM OF NATURAL HISTORY, MINNEAPOLIS, MINNESOTA

Cook Co........	Three juveniles were collected from a small lake at the base of Mt. Josephine on Hat Point, 0.5 mi. northwest of Co. 73, on 22 Aug. 1967.
Lake Co........	Several frogs were taken from Baptism R. next to Co. 7, 4 mi. north of Finland, on 21 Aug. 1967.
Clearwater Co..	Several frogs were heard and collected during 1966, 1967, and 1968 at many localities in Itasca State Park. Frogs were also heard at Upper and Lower Rice L., Heart L., and Roy L.
Hubbard Co.....	Several frogs were heard and collected during 1966, 1967, and 1968 at many localities in Itasca State Park. Frogs were also heard at L. Alice, L. George, Lac Mer, Island L., and Potato L.
Becker Co......	Six adults were collected from Hay Creek near the Co. 32 bridge on 17 July 1967. Frogs were heard at Two-Island L., Bad Medicine L., Juggler L., Elbow L., and Tulaby L. on 9 and 20 July 1967.
Wadena Co......	One juvenile was taken from Shell R. near the Co. 23 bridge on 14 Sept. 1967.
Cass Co........	Seven juveniles were collected from a roadside ditch along the south side of State 34, 7.2 mi. west of State 84, on 2 Sept. 1967.
Aitkin Co......	Three adults were collected from a pond along State 65, 5.7 mi. north of Libby, on 2 Sept. 1967.
Mille Lacs Co..	Two adults were taken from Rum R. next to U.S. 169, 4 mi. south of Onamia, on 12 Sept. 1967.
Anoka Co.......	One transforming frog was taken from Cedar Bog L. on 5 July 1968. Frogs were heard at Fish L. on 3 July 1968.
Morrison Co....	Two females were observed in a small pond along the west side of U.S. 10, 2.6 mi. south of Lincoln, on 12 Sept. 1967.
Kanabec Co.....	One female was observed in a stream at State 65, 1.0 mi. north of Woodland, on 2 Sept. 1967.
Chisago Co.....	Frogs were heard in the Carlos Avery Game Refuge 0.5 mi. east of Stacey on 4 July 1968.
Isanti Co......	Frogs were heard at Beckman L. on 4 July 1968..
Sherburne Co...	Frogs were heard at a pond on the east side of U.S. 169, 2.3 mi. north of Lake Fremont City, on 9 July 1968.
Benton Co......	Frogs were heard at Little Rock L. on 9 July 1968.
Todd Co........	Frogs were heard at Lawrence L. and Pine Island L. on 9 July 1968.
Mahnomen Co....	Frogs were heard at McCraney L., Capon L., Fowl L., Hart L., and at a pond along the south side of State 113, 0.4 mi. west of Co. 3, on 20 July 1967.

DISCUSSION

The geographical range of *Rana septentrionalis* in Minnesota overlaps with the Minnesota distributions of *R. sylvatica*, *R. pipiens*, and *R. clamitans*. Mink frogs, wood frogs, and leopard frogs are common in the Itasca region. Green frogs also occur in the Itasca region in local, relatively small populations. The coexistence of these four *Rana* species suggests that their ecological niches differ from one another to some extent. An ecological niche is here defined as the sum total of the activities and relationships of a frog in an ecosystem. The important aspects of each ranid's niche are summarized in Table 11. It is the purpose of this discussion to review the elements of the mink frog's niche that set it apart from the niches of the other three ranids in the Itasca region.

R. septentrionalis males were heard calling from late May through early August. The calling frogs were located in permanent aquatic habitats throughout the Itasca region. Calling *R. septentrionalis* males were joined by calling *R. clamitans* males in areas adjacent to lotic environments located eight to twelve miles south of Itasca State Park. The calling period of the green frogs coincided with that of the sympatric mink frogs, indicating a common breeding season. There was some subdivision of the breeding habitat in areas where both species occurred. It has been previously noted in sympatric populations that green frogs lay their eggs in films on the water surface, while mink frogs deposit their eggs in globular masses attached to

TABLE 11. IMPORTANT ELEMENTS OF THE ECOLOGICAL NICHES OF FOUR RANIDS OCCURRING IN ITASCA STATE PARK AND VICINITY, MINNESOTA

	R. septentrionalis	*R. clamitans*	*R. pipiens*	*R. sylvatica*
Calling Period	Late May -- Early August	Late May -- Early August	Mid-April -- Mid-May	Mid-April -- Mid-May
Habitat of Breeding Frogs	Permanent waters	Permanent waters	Permanent and temporary waters	Temporary waters
Egg Mass	Submerged, globular	Surface, film	Submerged, globular	Submerged, globular
Duration of Tadpole Stage	12 -- 13 months	12 -- 13 months	2 -- 3 months	2 -- 3 months
Habitat of Non-breeding Frogs	Permanent and temporary waters	?	Grassy areas; sometimes water	Moist wooded areas
Habitat of Overwintering Frogs	Water	?	Water	Soil
Diet of Non-breeding Frogs	Aquatic	?	Aquatic and terrestrial	Terrestrial

submerged plants (Wright, 1932).

The egg mass of R. septentrionalis closely resembled the egg masses of R. sylvatica and R. pipiens, two species which bred between mid-April and mid-May in the Itasca region. R. sylvatica normally bred in shallow temporary ponds, while R. pipiens bred in both temporary and permanent waters. R. pipiens tadpoles occurred together with R. clamitans and R. septentrionalis tadpoles in the permanent habitats utilized by all three species for breeding. The sympatric tadpoles may have subdivided their underwater habitat by feeding at different depths, by employing different methods of feeding, or by selecting different foods. At Smartswood Lake in New Jersey, Gosner (1959) found that blue-green algae and diatoms were common in R. clamitans and scarce in R. pipiens, while filamentous algae were plentiful in R. pipiens and scarce in R. clamitans.

Steady increases in the length and weight of tadpoles from hatching to metamorphosis have been reported for R. sylvatica (Herreid and Kinney, 1967) and R. pipiens (Adolph, 1931; Taylor and Kollros, 1946). Both species transformed during July or August of their first summer in the Itasca region. R. septentrionalis tadpoles, however, did not transform until July or August of their second summer. Growth was reduced markedly during the overwintering period of the mink frog larvae. R. clamitans tadpoles also overwintered and transformed during July or August of their second summer. R. clamitans tadpoles located 150 miles southeast of Itasca State Park exhibited little growth during the winter months (Hedeen, unpublished).

The amount of habitat overlap between transformed, non-breeding *R. clamitans* and *R. septentrionalis* is not known. Locations and activities of non-breeding green frogs in the Itasca region were not ascertained. Observations by the author in eastern Minnesota, southern Ontario, and northern New York indicated that green frogs are often riparian while mink frogs are almost completely aquatic. Current studies of sympatric populations in the Adirondacks should delineate postmetamorphic relationships between green frogs and mink frogs (Margaret Stewart, personal communication).

In contrast to the aquatic *R. septentrionalis*, non-breeding *R. sylvatica* usually inhabited moist areas dominated by trees, while non-breeding *R. pipiens* generally occupied areas dominated by grass-like plants. Obviously, mink frogs were preyed upon by swimming and wading predators, *e.g.* leeches and herons, while wood frogs and leopard frogs were preyed upon by more terrestrial animals, *e.g.* garter snakes. Of the three ranids, mink frogs probably had the highest incidence of "Red Leg," since the infective agent *Aeromonas* is transmitted through water (Reichenbach-Klinke and Elkan, 1965). Likewise, *R. septentrionalis* probably harbored a greater number of platyhelminth parasites than either *R. sylvatica* or *R. pipiens*. In the vicinity of Presque Isle, Maine, Bouchard (1951) found cestodes and trematodes in 53 of 57 mink frogs, trematodes in two of 46 wood frogs, and nothing in 16 leopard frogs. The paucity of platyhelminth parasites in R. sylvatica and R. pipiens was due to the lack of intermediate aquatic hosts in the terrestrial environment.

Ranids are opportunistic predators (Zweifel, 1955; Jenssen and Klimstra, 1966). Their diets, like their predators, diseases, and parasites, are largely determined by their habitats. At Bog D in Itasca State Park, the most common prey taken by both R. sylvatica and R. pipiens in the Tamarack and Sedge Mat Zones were ants, spiders, carabid beetles, and ichneumon wasps (Marshall and Buell, 1955). The most common prey taken by R. septentrionalis in the Aquatic Zone were broad-shouldered water striders, spiders, midges, and water boatmen. The dissimilarity in ranid diets reflected a dissimilarity in habitat.

The habitats of the ranids in Itasca State Park outside of their breeding seasons were not entirely separate. For example, both leopard frogs and mink frogs hibernated underwater during the winter months, while wood frogs overwintered in the soil. Many leopard frogs also joined resident mink frogs in aquatic habitats during the latter part of the summer. The immigration of leopard frogs onto floating vegetation during July and August might be attributed to a number of factors: late summer aridity in the terrestrial environment, greater food availability in the aquatic environment, a tendency of adult leopard frogs to occupy regions where crowding is least (Dole, 1965).

One area where the habitats of R. pipiens and R. septentrionalis overlapped during August was on mats of floating vegetation in the Aquatic Zone of Bog D. Although the sympatric animals would be expected to take similar prey, a stomach content analysis of the Aquatic Zone frogs revealed very different diets. The organisms most commonly taken by the mink frogs were those that occurred at the water surface. On the other hand, the most abundant foods of the Aquatic Zone leopard frogs were terrestrial in origin. The mink frogs obviously fed in the Aquatic Zone in which they rested, while the sympatric leopard frogs apparently fed in the adjacent Sedge Mat Zone, a typical habitat of R. pipiens. Most of the vegetation mats in Bog D were located within five feet of the sedge mat, and so the leopard frogs did not have to travel far to find terrestrial prey.

A second area where R. pipiens and R. septentrionalis occurred together during August was in Lake Itasca's French Creek Bay. Most of the frogs in the Bay occupied mats of vegetation located over 20 feet from the sedge mat shoreline. Unlike the frogs in Bog D, R. pipiens and R. septentrionalis in French Creek Bay had very similar diets that primarily consisted of aquatic organisms. However, many more water scavenger beetle larvae, caddisflies, springtails, and plant materials were taken by mink frogs than by an equal number of sympatric leopard frogs. The higher incidence of these food items in R. septentrionalis than in R. pipiens may have reflected interspecific differences in feeding behavior. The water surface foraging behavior of R. septentrionalis, a very aquatic species, was probably more efficient than that of R. pipiens, a semi-aquatic species with a wide habitat range.

SUMMARY

1. Several aspects of the ecology and life history of *Rana septentrionalis* were investigated in the vicinity of Itasca State Park, Minnesota.

2. *R. septentrionalis* had a one-year larval period, although a few individuals may have spent two years in the tadpole stage. Tadpoles showed a marked reduction in growth during the winter months.

3. Metamorphosis took place during July and August. Transforming individuals had an average snout-vent length of 37.2 mm. Some frogs attained body lengths of 60 mm. by the end of August of the first full summer following transformation. Although 72 mm. was the maximum length of both sexes, there were higher frequencies of females in the larger size classes. This size dimorphism may have been due to higher death rates in males or faster growth rates in females.

4. In 150 (98%) of 153 frogs 48 mm. or longer, the ratio of snout-vent length to tympanum diameter was below ten in males and ten or above in females. This ratio was employed as the primary means of sex recognition in the field. Frogs of both sexes smaller than 48 mm. usually had ratios above ten and were classified as subadults.

5. Males became sexually mature during their first full summer following transformation when about 45 to 50 mm. in length. Females became sexually mature during either their first or

second summer when about 54 to 59 mm. in length.

6. Calling males were heard from late May through early August. Breeding took place at night from late June through early August. Calling males in a breeding habitat shifted their locations during the summer calling period.

7. Frogs were found moving across land at night during or immediately following periods of precipitation. Under such environmental conditions the frogs could minimize water loss and maximize water uptake in order to maintain safe body water levels. At all other times mink frogs were confined to aquatic habitats.

8. Mink frogs inhabited both lentic waters and lotic waters without rapid currents. Breeding and hibernating frogs occurred only in permanent habitats. Non-breeding frogs occupied both permanent and temporary habitats during the ice-free season.

9. During July and August, the majority of frogs in West Twin Lake rested with only their eyes and snout above the water surface. The distribution pattern of the West Twin Lake population was influenced by the distribution of water surface substrata on which the frogs rested. Wind also may have affected the frogs' local distribution pattern.

10. R. septentrionalis fed primarily on algae through stage XX, fasted during stage XXI, and commenced on an adult diet during stage XXII (stages based on Taylor and Kollros, 1946). All 74 adult stomachs examined contained animal material.

Accidentally ingested plant material occurred in 90.5% of the stomachs. Diet differences among populations were due to differences in habitat and seasonal food availability.

11. "Red Leg" and the tapeworm Ophiotaenia olor occurred in the aquatic frogs. *R. septentrionalis* food habits suggested that *O. olor* utilizes a single intermediate host during its life-cycle.

12. *R. septentrionalis* had many aquatic and non-aquatic predators. Generally, mink frogs leaped onto shore to escape underwater predators, and dove into submerged vegetation or bottom mud to evade above-surface disturbances.

13. Body temperatures of 27 partly-submerged frogs ranged from 16.2°C. to 27.1°C. Solar radiation served to raise body temperatures above ambient water and air temperatures.

14. Mink frogs were found in 15 Minnesota counties for the first time, bringing the number of Minnesota county records to a total of 24.

15. The geographical range of *R. septentrionalis* in Minnesota overlapped with the Minnesota distributions of *R. sylvatica*, *R. pipiens*, and *R. clamitans*. Aspects of the ecological niche of *R. septentrionalis* were reviewed and discussed in relation to the ecological niches of the three ranids sympatric with the mink frog.

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