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MOVEMENTS AND SPATIAL RELATIONS OF *RANA PIPIENS* IN SPRING AND SUMMER IN NORTHERN MICHIGAN

by
Jim Walter Dole

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in the
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Doctoral Committee:

Professor Frederick H. Test, Chairman
Professor Frederick E. Smith
Professor Charles F. Walker
Associate Professor Robert Zahner

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Introduction

In the past two or three decades, field studies of the movements and spatial relations of vertebrates have been published in ever increasing numbers. Although birds and mammals have received much attention, the cold-blooded terrestrial vertebrates, largely neglected in this respect until the last 10-12 years, have not been so thoroughly investigated. Field data on the dynamics of amphibian and reptile populations are much needed, for our knowledge of vertebrate population ecology is based almost entirely on studies of birds, mammals and, to a lesser extent, fish.

Perhaps the most complete records of the movements of any poikilotherm were those obtained by Stickel (1950) of the Box Turtle (Terrapene carolina) by mapping the trails of individual animals fitted with a trailing device. Blair (1960) more recently has made a very thorough study of the movements of the Rusty Lizard (Sceloporus olivaceus). Among the more extensive and thorough studies of movements of other reptiles which have been published are those on the snakes Thamnophis sirtalis, T. sauritus, T. butleri (Carpenter, 1952), Crotalus viridis (Fitch, 1949) and Agkistrodon contortrix (Fitch, 1960), the turtles Chrysemys picta (Sexton, 1959) and Gopherus agassizi (Woodbury and Hardy, 1948), and the lizard Eumeces fasciatus (Fitch, 1954).

Among the caudate amphibians the movements of Taricha rivularis (Twitty, 1959, 1961), Batrachoseps pacificus

(Hendrickson, 1954; Cunningham, 1960) and Taricha torosa (Pimentel, 1960) have been perhaps the most studied. Anurans have received somewhat more attention, for in the last ten years extensive studies of movements have been made on Rana clamitans (Martof, 1953b), Scaphiopus holbrooki (Pearson, 1955), Syrrhophus marnocki (Jameson, 1955), Hyla regilla (Jameson, 1956, 1957), Acris crepitans (Pyburn, 1958), Rana nigromaculata (Kikuchi, 1958), Hyla crucifer (Delzell, 1958), Rana pretiosa (Turner, 1960) and Bufo hemiophrys (Breckenridge and Tester, 1961). Also, briefer and more limited studies of movements have been made on Rana temporaria (Savage, 1935), Rana catesbeiana (Raney, 1940), Rana sylvatica (Bellis, 1962), Bufo terrestris (Bogert, 1947), Bufo regularis (Chapman and Chapman, 1958), Bufo punctatus (Turner, 1959), Bufo canorus (Karlstrom, 1962), and Gastrophryne olivacea (Fitch, 1956). Notable by its absence from the above lists, however, is the cold-blooded vertebrate most familiar and important to zoologists in this country, the Leopard Frog, Rana pipiens Schreber, one of the most common laboratory animals in embryological, physiological, and anatomical studies.

Several aspects of the ecology of Rana pipiens have been investigated previously and are well understood. Its breeding behavior, studied by Noble and Aronson (1942) and others, is well known. More recently, W. F. Blair (1961) studied the influence of some environmental factors upon the occurrence of mating. Kilby (1945) made an extensive study of the food and feeding habits of Rana pipiens sphenocephala,

and Drake (1914), Force (1925) and Knowlton (1944) have published shorter studies on this aspect of the ecology of the species. Water regulation in an aquatic environment has been investigated by Adolph (1927-1933), Thorson and Svihla (1943), Thorson (1955, 1956) and others. The influence of certain environmental factors upon embryological and larval development also has been studied by Moore (1949, 1950), and more recently by Richards (1958), Ruibal (1962) and Rose (1960); post-metamorphic growth was investigated briefly by Ryan (1953).

The movements and spatial relations of Rana pipiens, aspects of its ecology affecting every phase of the lives of the animals, have not, however, been thoroughly investigated. Only brief notes on movements, mostly obtained incidental to other work, have been published. Ryan (1953), studying growth, reported the recovery of Leopard Frogs at distances of up to 150 yards from the place where first captured. Fitch (1958) in his general survey of vertebrates on the University of Kansas Natural History Reservation, found no evidence that Leopard Frogs had home ranges, and reported that young Rana pipiens dispersed during and after rains. Whitaker (1961), in a study of Zapus hudsonicus, trapped young Leopard Frogs in mouse traps as they dispersed through woods, mostly during rains. Scott (1938) and Carpenter and Delzell (1951) recorded Leopard Frogs killed on highways after precipitation, apparently having moved there during the rain. Cummins (1920), in his study of anurans in a southern Michigan pond, obtained

information on the breeding migrations of Rana pipiens. Wright and Wright (1949) and Breckenridge (1944) include brief notes of mass movements in fall and spring in their general treatments of the life history of this species.

Several factors indicated that a more thorough investigation of the movements of Rana pipiens would be worthwhile. The widespread distribution of the species, from northern Canada to Panama, far more extensive than any other North American anuran, might be indicative of a greater degree of vagility than occurs in other frogs. Its considerable variation and occupation of a wide diversity of environments indicate a high degree of adaptability; a more complete knowledge of its habits might provide a better understanding of its ability to thrive in so many different ecological situations. In addition, its terrestrial habits, better developed than in any other ranid which has been studied, its extensive occupation of grassland, its abundance, and the ease with which it can be captured, make the Leopard Frog an ideal animal for a study of movements.

Previous information on the movements of anurans has been obtained almost entirely through repeated recaptures of individuals, hence in most cases only the magnitude of movement could be determined; the nature of activity between captures usually was not known. In the present study, however, the movements of individuals were followed by means of a trailing device, permitting a much more precise record of daily activity than has previously been possible with amphibians. In addition, an analysis was made of the spatial

relations within populations, a phase of the population ecology of amphibians which has received little study, for only a few investigators (e.g. Pearson, 1955) have attempted to analyze their data so as to permit a quantitative definition of home range, or to determine the effects of environmental conditions upon spacing. Likewise, the seasonal shifts of individuals from one habitat to another, and the effects of climatic and seasonal changes upon the dispersion of populations, investigated only rarely in the past (e.g. Turner, 1960), were studied. Much effort was also devoted to an investigation of the movements of young frogs, for, except in a very few studies (e.g. Jameson, 1955, 1956), the dispersal of young has been largely ignored.

The purpose then of this investigation was twofold: (1) to increase our understanding of the ecology of one of the most abundant vertebrate members of the pond and grassland communities in much of North America, and (2) to obtain additional factual data to provide a broader basis for generalization concerning the dynamics of vertebrate populations. The information obtained should also have importance in fields other than ecology. Emphasis in genetics in recent years has shifted more and more toward studies of populations; Rana pipiens should prove a useful animal for such work. Moore (1944-1950) has, in fact, shown this species, with its considerable geographic variation, to be valuable for studies of the process of speciation. Certainly some knowledge of the vagility of these animals is essential if such studies

are to be of maximal use, for the rate of gene flow and genetic drift, hence the rate of divergence of populations, are dependent upon the rate of exchange of animals between the breeding groups. Perhaps also the information gathered will prove useful to taxonomists who are still actively debating the taxonomic status of the various groups of this species.

Life History

To enable the reader to fit the subsequent detailed study of their activities into its proper relation in the life of the individual animals, a brief review of the major aspects of the life history of Rana pipiens is presented here. What is said applies mainly to the species in northern Michigan; the details vary somewhat in other parts of the United States, especially far to the south where the animals may be active all year.

Generally in late April, as the ice melts and warmer weather arrives, Leopard Frogs emerge from their winter hibernacula in the bottoms of ponds and streams, or sometimes protected places in terrestrial situations. They are among the earliest frogs to breed. Their choruses may often be heard well into May emanating from the weedy ponds and marshes which they use for breeding purposes.

Usually courtship and egg-laying closely follow emergence from hibernation. Eggs hatch in one and one-half to three weeks depending upon temperatures. After hatching, the tadpoles remain attached to the jelly mass or other objects for several days before they begin feeding throughout the pond.

The length of the larval period depends to a large extent on the temperature regime of the pond during spring and early summer, but transformation usually begins in late July

or early August and may continue well into the latter part of the summer. In the present study the earliest transformation of young occurred in 1960 when emerging frogs were seen at Sedge Point on July 11. In 1961 tadpoles were still transforming as late as August 22. After metamorphosing, the young frogs tend to remain in close proximity to the ponds, but on favorable nights may move great distances from their place of hatching. If survival to metamorphosis is high, very large numbers, often still with stubs of tails up to 15 mm long, may emerge at once and spread over the countryside.

At transformation young frogs vary from 17 to 31 mm, the average being about 22-23 mm. Growth during the first season is rapid, but because of the short time available the young frogs seldom reach more than 40 mm in length before hibernating in the fall. During the second season growth also proceeds at a rapid rate and by the end of their second summer the animals have reached adult size and are sexually mature, ready to breed in the spring of their third season (i.e. when two years old). In this paper newly metamorphosed frogs, those in their first season, will be termed young-of-the-year, or simply young. Second-season frogs are called subadults, for though they do not become sexually mature until the end of summer, their behavior is closely similar to that of the adult frogs. Sexually mature adults in their third season and beyond are indistinguishable as to age, but in general the largest individuals of each sex are probably the oldest.

After spending the spring in the ponds subadult and adult Leopard Frogs abandon the water in early summer for the fields. During July and August they commonly occupy moist meadows, hay fields and pastures, and grassy woodlands. Though found occasionally along streams and around ponds at this time, older frogs generally are quite independent of standing water in summer. They may occasionally be found sitting upon elevated objects such as logs, boards, etc. but most of their time is spent sitting on the soil; they are not arboreal. In general, Leopard Frogs are most active at night. Major movements are confined almost entirely to the dark part of the diel period, though the animals may shift short distances within their local areas in daylight. Feeding occurs both in the daytime and at night, hunger and the presence of suitable food (mostly arthropods) apparently being the only important factors determining when individuals will eat.

When temperatures fall in late September or October, Rana pipiens movesto the hibernating sites. They may remain in and around the ponds for some time, but retreat to the bottom as water temperature falls near freezing.

Study Areas

The field work of this study was done in the years 1960-62 at two areas in the vicinity of The University of Michigan Biological Station, Cheboygan County, near the northern tip of the Lower Peninsula of Michigan. This region is glacial terrain characterized generally by low undulating relief occasionally broken by detached hills and ridges and ranging from 180-240 m above sea level. The general climate of this area, flanked on two sides by lakes Michigan and Huron, is under the tempering influence of these large bodies of water.

Budzinski's Pasture

This study area was a 4.25 hectare pasture on the farm of Mr. Albert Budzinski on Indian Trail Road 8 km east of the Biological Station. It contained an abandoned gravel pit and a small marsh (Fig. 1), both having water most of the summer and together supporting a large population of frogs.

Five distinct zones of vegetation were evident, reflecting largely the moisture content of the soil (Fig. 2). Within and immediately surrounding the marsh proper was a zone of dense sedges, mainly *Eleocharis* sp. but with occasional *Carex retrorsa* with an average height of about 50 cm. Two compact clumps of *Acorus calamus* occurred at the edge of the marsh.

Surrounding the dense sedge zone was a larger one of a dense, mixed stand of grasses and sedges, averaging about 70 cm high. The dominant grasses were *Poa pratensis* and *Glyceria*

Figure 1 (Top) Budzinski's gravel pit, July 27, 1961, showing largest pond and blind from which some observations were made. Looking southward, part of pasture, and an area of sumac beyond, are visible in background. (Middle) Budzinski's marsh in summer (August 4, 1962), looking southwest from northwest corner of gravel pit. Alder-White cedar swamp in which some frogs were trailed is in background. (Bottom) Budzinski's marsh from approximately same location showing extent of water on April 27, 1962.





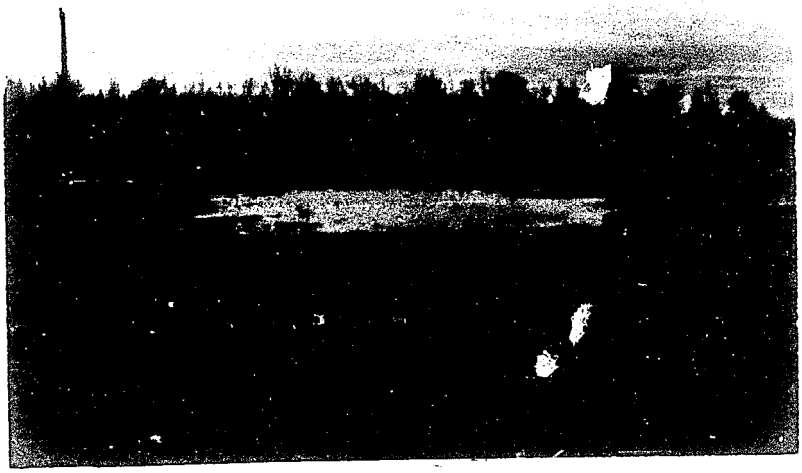


FIGURE 1

Figure 2 Map of Budzinski's pasture showing dominant vegetation. Marsh is at center left, gravel pit at top center. Soil within the outer boundaries of Poa-Glyceria zone was permanently moist throughout summers.

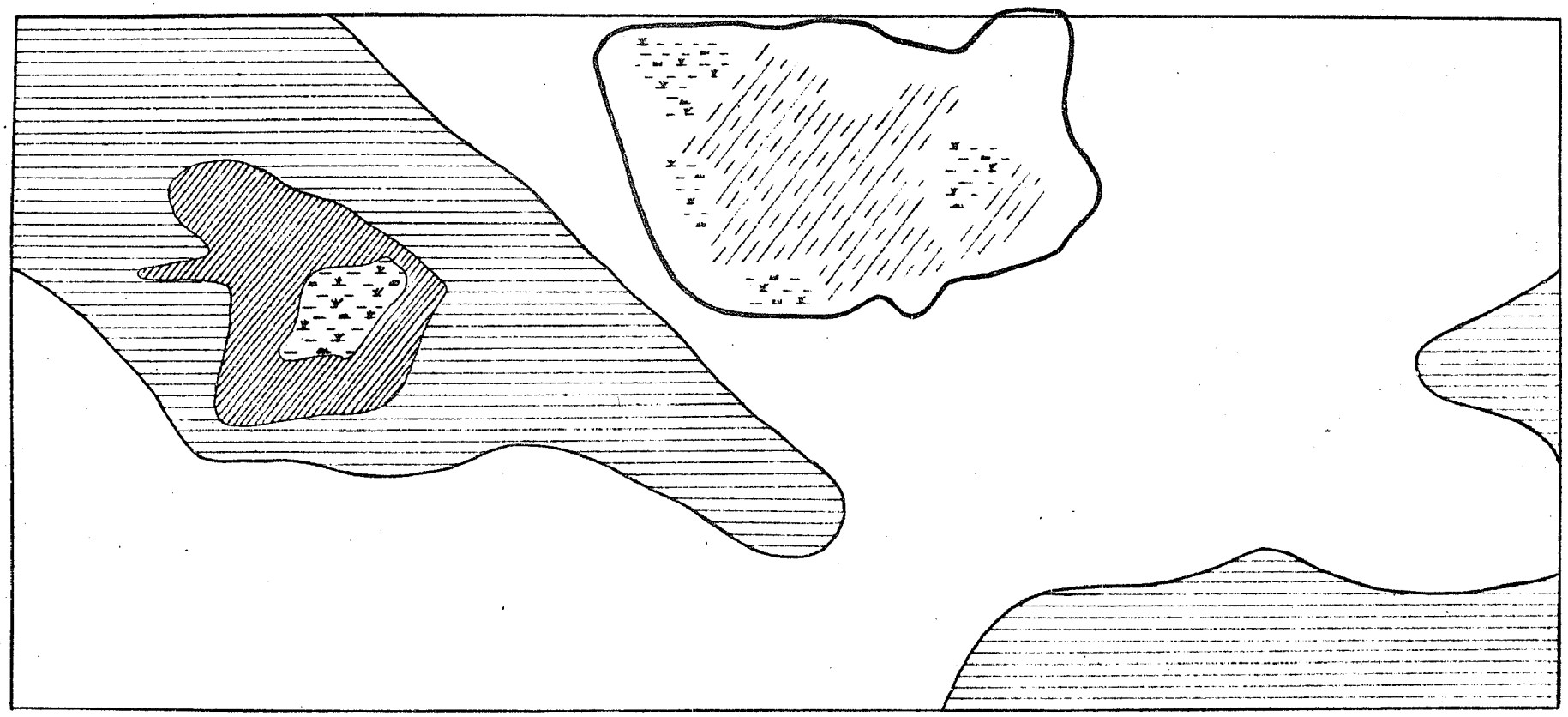

ELEOCARIS-CAREX
POA-GLYCERIA
CAREX-GLYCERIA
SALIX-CAREX
AGROPYRON-POTENTILLA
N
A. BUDZINSKI'S PASTURE
50 METERS

FIGURE 2

sp. and the most common sedges Carex flava, C. retrorsa and Eleocharis sp. in descending order of importance. Several species of mint (Labiatae) also occurred in this region.

Bounding the sedge-grass zone was an area of almost pure grass (Glyceria), with a few scattered clumps of Poa. The vegetation in this region was very dense with an average height of about 70 cm. Smaller areas in the southeast corner and the east side of the pasture supported similar vegetation.

The soil within these three zones, extending to the outer margin of the Poa-Glyceria zone, remained wet throughout the entire summer even though all the water in the marsh disappeared. The moisture content of the soil gradually decreased from the marsh outward along the gradual uphill gradient and this change in wetness was reflected in the gradual changes in the vegetation. The boundary of this permanently wet soil was quite marked and coincided almost exactly with the outer margin of the Poa-Glyceria zone. The soil moisture boundary receded less than 1 m in July and August of 1962.

By far the largest zone in the field was located along a dry ridge which ran diagonally across the pasture, 5-6 m above the lowest part of the field (marsh). Here the dominant plant was the grass Agropyron repens, but Potentilla recta, Crysanthemum leucanthemum, Trifolium pratense, and Vicia villosa were also very common throughout the area. Vegetation here was more sparse and less tall (average about 50 cm) than in the wetter regions.

The gravel pit, unused since before 1960, supported a flora distinct from the other zones. Sedges of the genus Carex were the dominant plants of the ground stratum, growing in small clumps interspersed with bare sandy soil over the entire gravel pit. Small willows (Salix sp.) up to 1 m tall were scattered over the entire pit while one clump of Typha sp. grew in its deepest part. The lowest parts of the pit also produced luxuriant growths of Eleocharis sp., and in the deepest part, which retained water all summer, Chara sp. and Potomogeton sp. grew. The bottom of the gravel pit generally remained moist throughout the summer even after most of its water had disappeared. The steeply sloping walls of the pit were of exposed gravel and sand bearing only scattered grasses and forbs. In the northwest corner the wall of the pit was more than 3 m high but elsewhere was lower.

During early spring after the snow had melted both the gravel pit and marsh contained several feet of water. In April, 1962, the marsh contained 1 m of water, while the greatest depth of the gravel pit was about 1.5 m. During the summer months, however, the water level fell gradually and it commonly disappeared entirely in the marsh. In 1961 and 1962 the marsh had dried completely by late July but in 1960, an exceptionally rainy year, it still contained more than 30 cm of water at the end of August. The gravel pit followed a similar pattern of water level fluctuation. Its bottom was nearly completely covered in the spring but as summer progressed the level dropped until only one small pool approximately 4 x 5 m remained

near its west end in 1961 and 1962. In 1960, as with the marsh, the water was still about 50 cm deep in August.

The marsh and gravel pit were entirely dependent upon precipitation as a source of water as there were neither inlets nor outlets. After particularly heavy summer rains the water level often rose several inches temporarily but the ponds usually regained their former level within a week. The extent of the water at intervals through the spring and summer of 1962 is shown in Fig. 3.

Throughout the summer of 1960 the pasture was not used for farming activities and the grass and sedges grew rank in the low wet areas of the field. In late July, 1961, the southern half of the field was mowed for hay. This procedure was limited to the dry ridge and did not appreciably affect the bulk of the frog population which largely occupied the low wet northwest corner, though some frogs were injured or killed in the southeast corner.

In June and July of 1962 cattle were grazed in the pasture. They were removed on July 17, but not until they had cropped the usually tall grass to a height of 20-25 cm. The sedges, which they refused to eat, were not appreciably disturbed and, together with the remaining grasses, seemed to provide adequate cover for the frogs. The frogs were not appreciably disturbed by the activities of the cattle which moved about slowly, and, in fact, the cattle tended most of the time to graze along the drier ridge where no frogs lived.

Several other amphibians bred in these same ponds but only the Green Frog, Rana clamitans, could commonly be seen in

Figure 3 Change in water levels of ponds in Budzinski's pasture as water receded in spring and summer of 1962. Water in marsh (center left) dried completely about July 23-24. Small puddles were present on south side of pasture until shortly after May 6.

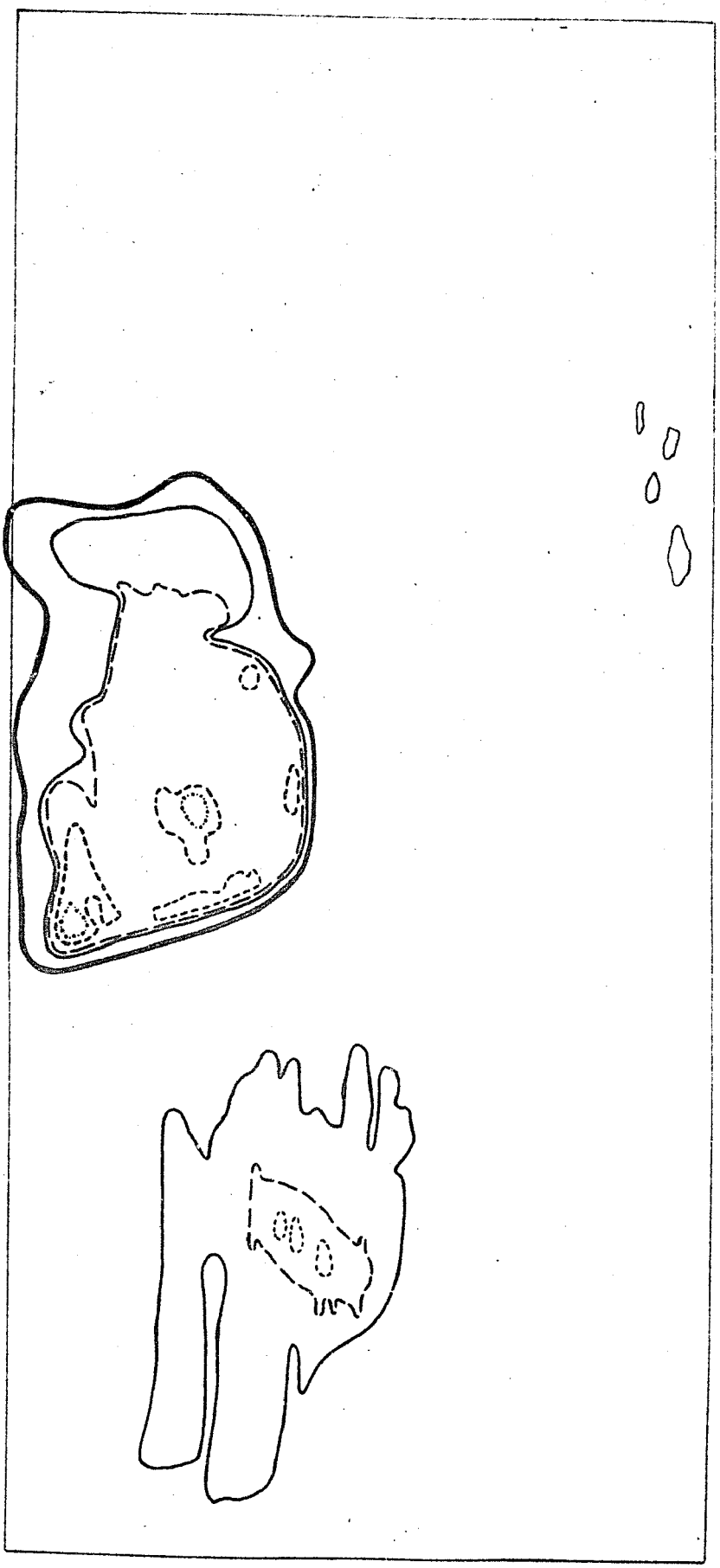

N
A. BUDZINSKI'S PASTURE
50 METERS
MAY 5,1962
JUNE 15,1962
JULY 20,1962
AUG. 20,1962

FIGURE 3

summer, 20 to 25 sitting in and around the water in the gravel pit. The American Toad, Bufo terrestris americanus, Spring Peeper, Hyla crucifer, and Common Tree Frog, Hyla versicolor, all shared the pond in the spring for breeding, and the newly metamorphosed young, especially Bufo, were conspicuously abundant for short periods after emergence. No salamanders were known to breed in the area.

The most common reptiles were Ribbon Snake, Thamnophis sauritus, and Garter Snake, T. sirtalis, large numbers inhabiting the gravel pit and the moist areas of the field. The Green Snake, Opheodrys vernalis, and Dekay's Snake, Storeria dekayi, were also seen on occasion. No turtles were found.

Several birds nested in the field and gravel pit at various times. The most conspicuous were the Red-wing, Agelaius phoeniceus, Bobolink, Dolichonyx oryzivorus, Eastern Meadowlark, Sturnella magna, Savannah Sparrow, Passereulus sandwichensis, and Vesper Sparrow, Pooecetes gramineus. The only mammals known to inhabit the field were the Thirteen-striped Ground Squirrel (Citellus tridecemlineatus), Meadow Vole (Microtus pennsylvanicus), Pine Vole (Pitymys pinetorum), Masked Shrew (Sorex cinerus) and Short-tailed Shrew (Blarina brevicauda). Several apparently abandoned Woodchuck (Marmota monax) burrows were noted but no animals were seen. Occasionally White-tailed Deer (Odocoileus virginianus) came to the marsh for water.

Insects, an important source of food for frogs, were common throughout the summer. Grasshoppers, crickets, and leaf-hoppers were the most conspicuous in the field but

numerous beetles, flies, bees, true bugs, dragon-flies and other insects were always abundant, especially nearer water. Spiders, too, were abundant.

Sedge Point

The second study area, chosen because it offered ecological conditions considerably different from those on Budzinski's farm, consisted of the region immediately surrounding two beach pools at Sedge Point on the northern shore of Douglas Lake, Cheboygan County, Michigan (Fig. 4). The area around the beach pools was a roughly triangular point of land projecting southward into Douglas Lake, surrounded on the east and southwest by the lake and on the north by a maple woods. According to Gates (1948) the beach pools were formed by currents set up by the winds which swept along the unprotected shore of the point. As more and more sand was deposited in the form of bars along the point the water trapped behind was cut off completely from the lake to form the two major beach pools there now. During the three years of this study a new and much smaller beach pool was cut off from the lake just east of the present ones.

Built up by the lake currents, the substrate of the point was almost pure sand. Only in the region of old beach pools had a few inches of organic material been deposited over it. Elsewhere only a thin layer of dead vegetation was generally present where plants grew in abundance.

The pools have been invaded slowly by the surrounding vegetation and gradually filled in by both sand and organic

Figure 4 (Top) Shore of Douglas Lake east of the study area, August, 1960. Sedge Point extends southward (toward the left in photograph) into lake. East beach pool is among trees in upper right; west pool is beyond. (Middle) East beach pool at Sedge Point in August, 1960 looking northward from its south end. Maple wood, with some white pines at edge, in background. (Bottom) East beach pool (background) and region between two beach pools flooded in spring. Looking northeastward from between east and west pools April 27, 1962.

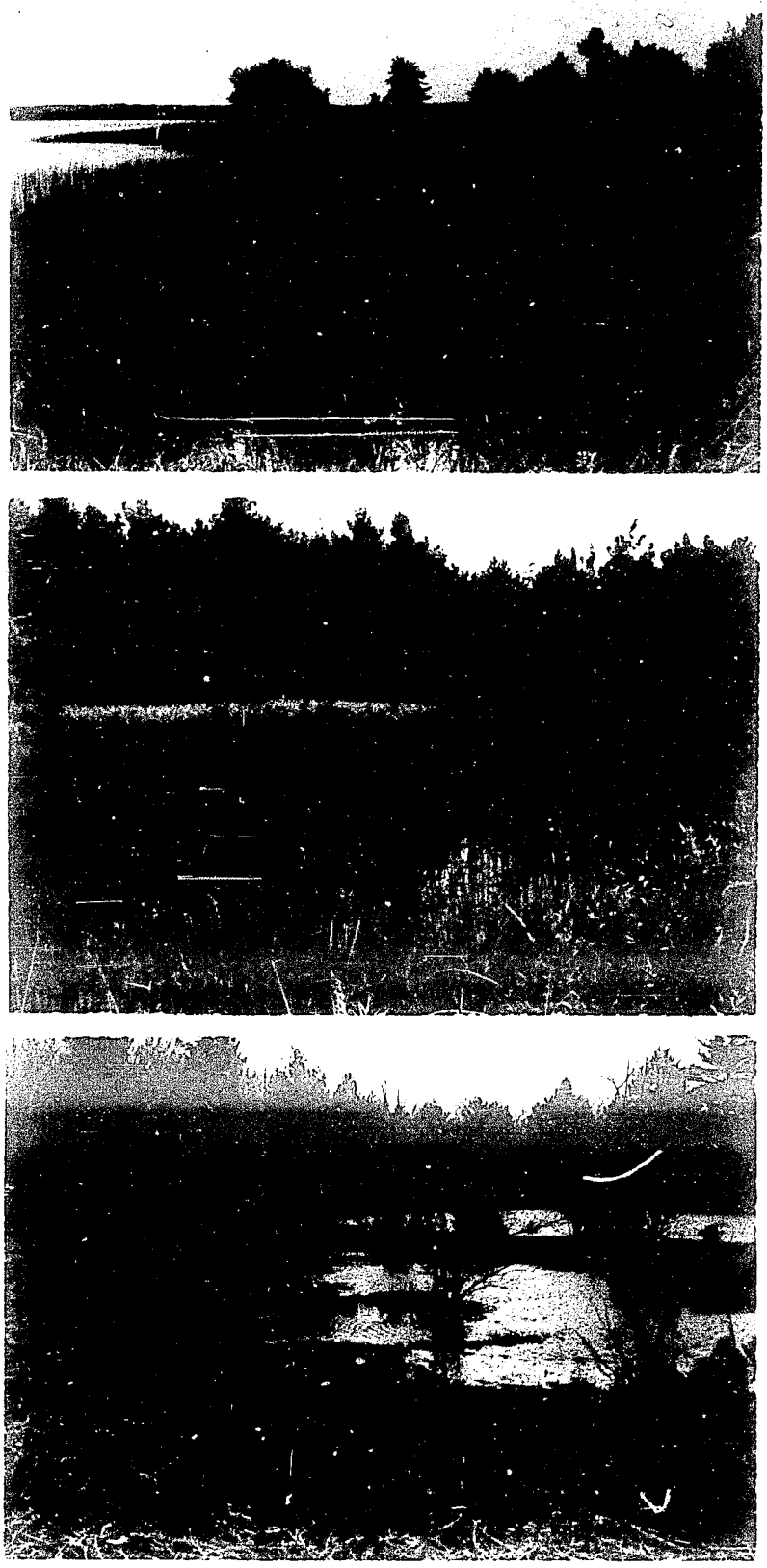


FIGURE 4

material. The bottoms of both pools were covered with a 20-25 cm layer of decaying organic material on top of the sand. Each pool was about 1-1.5 m deep at its deepest point during early spring.

The vegetation on the point was predominantly grass and sedges (Fig. 5). Shore-grass (Spartina sp.) grew in dense stands up to 1 m tall between the beach pools and on the north and south ends of the east pool. Intermixed with the grass nearly everywhere was a luxuriant growth of poison ivy (Rhus radicans). On the east side of the point the grass was sparser with more bare sand exposed. A fair growth of small willows (Salix sp.), milkweed (Asclepias sariaca), Equisetum sp. and Rhus radicans grew along the east edge of the east pool. Along the south side of the larger west pool was a narrow band of small red maples (Acer rubrum), white pines (Pinus strobus) and willows (Salix sp.) with sparse shore-grass and poison ivy in some places.

The pools themselves supported a luxuriant growth of vegetation. Sedges (Scirpus validus and S. americanus) were by far the most common aquatic plants, growing often in dense stands along the margins of both pools. Iris versicolor and Typha angustifolia were intermixed with the sedges in some localities. Nuphar advena was a common aquatic in the west pool, but was less abundant in the east pool.

The western half of the large west pool was much shallower than the eastern end, reaching only 30-40 cm in depth, and in late summer it was completely separated from the deeper eastern half. Here grew a dense, heterogeneous mixture of aquatic

Figure 5 Dominant vegetation at Sedge Point, Douglas Lake. Outlines of beach pool depressions and lake shore are shown by heavy lines.

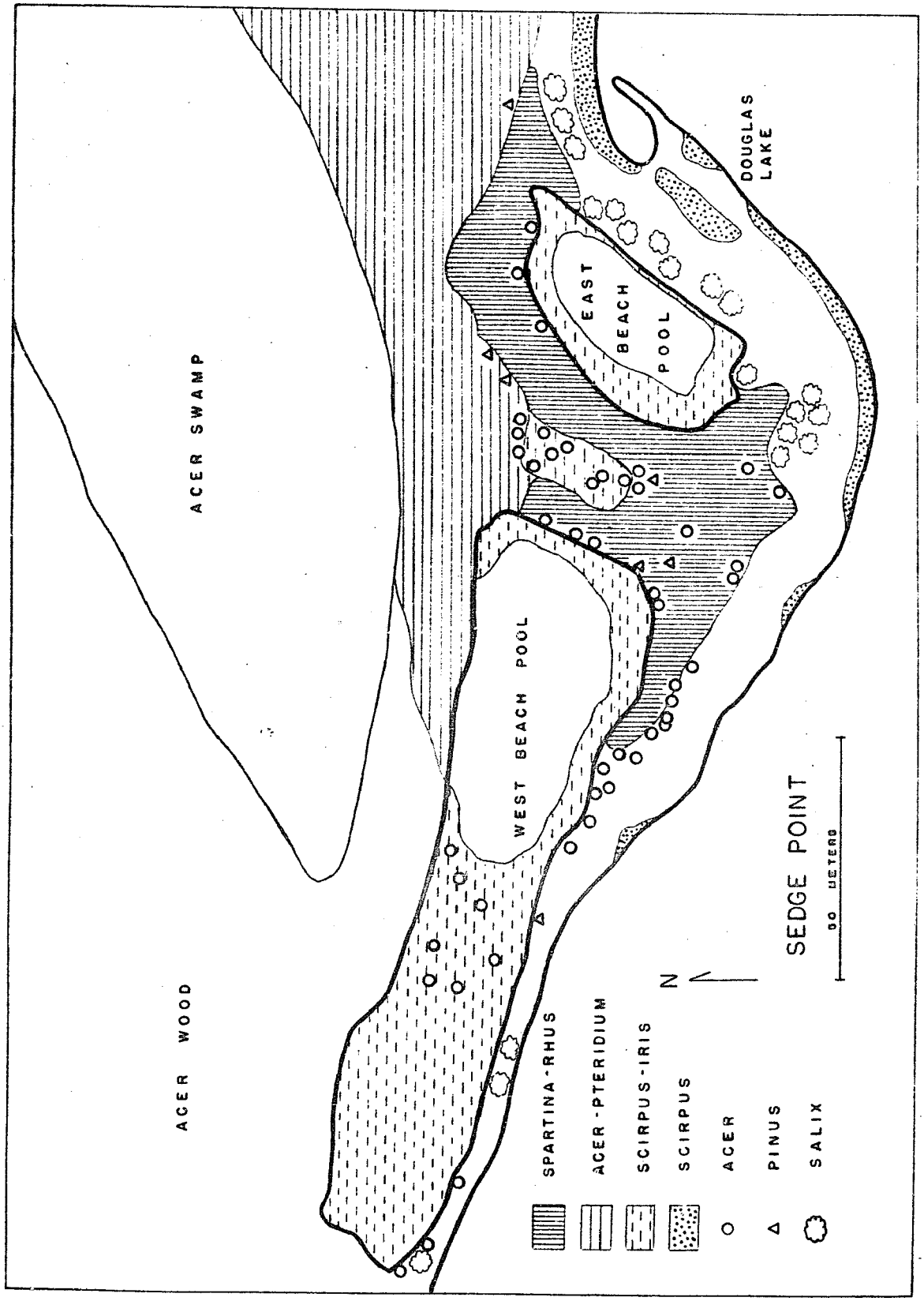

ACER SWAMP
ACER WOOD
EAST BEACH POOL
WEST BEACH POOL
DOUGLAS LAKE
SEDGE POINT
N
SPARTINA-RHUS
ACER-PTERIDIUM
SCIRPUS-IRIS
SCIRPUS
ACER
PINUS
SALIX

FIGURE 5

and semi-aquatic plants including bracken fern (Pteridium aquilinum), sedges (Scirpus validus, S. americanus), Iris versicolor and Spartina sp. Shrub willows (Salix sp.) and several small maples (Acer rubrum) also occurred scattered over the area.

The lake shore east of the point supported a very dense growth of sedges often extending 7 or 8 m into the lake, interspersed occasionally with patches of bare sand (Fig. 4). Where the permanently moist sand of the shore gave way to drier sand the sedges were replaced in some regions by an equally dense stand of Spartina sp. Both the sedges and grass commonly reached 0.8 - 1.0 m in height. The lake shore west of the point, receiving the brunt of the wind and wave action supported only a few very sparse clumps of sedges along the shoreline; it consisted largely of bare cobble-strewn sand extending inland up to 10-12 m in some places.

On the north the study area was bounded by a predominantly maple forest (Acer rubrum and A. saccharum) including within it a large depression representing an old beach pool (Gates, 1948). The depression, 25-30 m north of the west beach pool at its closest point, usually contained 20-30 cm of water in spring; it was dry by late June in 1961 and 1962, but in 1960 water remained until late August. Except for the dominant maples and an occasional patch of moss or Spartina sp. this low area was largely bare of vegetation. Its floor was covered by a thick layer of leaf litter while moss-covered stumps and broken limbs were scattered through it. The drier parts of the woods surrounding the depression supported a dense stand of Pteridium

aquilinum.

The water level of the pools fluctuated directly with the level of Douglas Lake. During high water of early spring the beach pools actually connected at some places with the lake. This was evident in the spring of 1962 when the beach pools covered a considerably larger area than normally (Fig. 6). The low area between the two main pools also filled, becoming a third pool. As summer progressed the level of the lake dropped causing a corresponding lowering of the ponds. The area between the beach pools lost its water, though the soil remained permanently wet, and the beach pools became separate entities, losing their connections with the lake. In the summers of 1961 and 1962 the water level dropped so far that the shoreline of the beach pools receded inward 8-12 m from their normal boundaries, making the pools considerably smaller in area and lowering their depth from the usual 1-1.5 m of early spring to 20-30 cm by late August. The pools have been known to dry up completely, but this did not happen during the period of the study.

Five other species of frogs, Rana clamitans, Hyla versicolor, H. crucifer, Acris gryllus, and Bufo terrestris were known to breed in the ponds but only R. clamitans could be found in numbers through the summer. In 1962 the Wood Frog (Rana sylvatica) produced numerous tadpoles in the woods depression but apparently did not breed here in 1960 or 1961. The Eastern Newt, Notophthalamus viridescens, Spotted Salamander, Ambystoma maculatum, and Jefferson's Salamander, A. laterale, were the only salamanders seen.

Figure 6 Change in water levels of beach pools at Sedge Point, Douglas Lake, as water receded in spring and summer of 1962. Swamp dried about July 1-3.

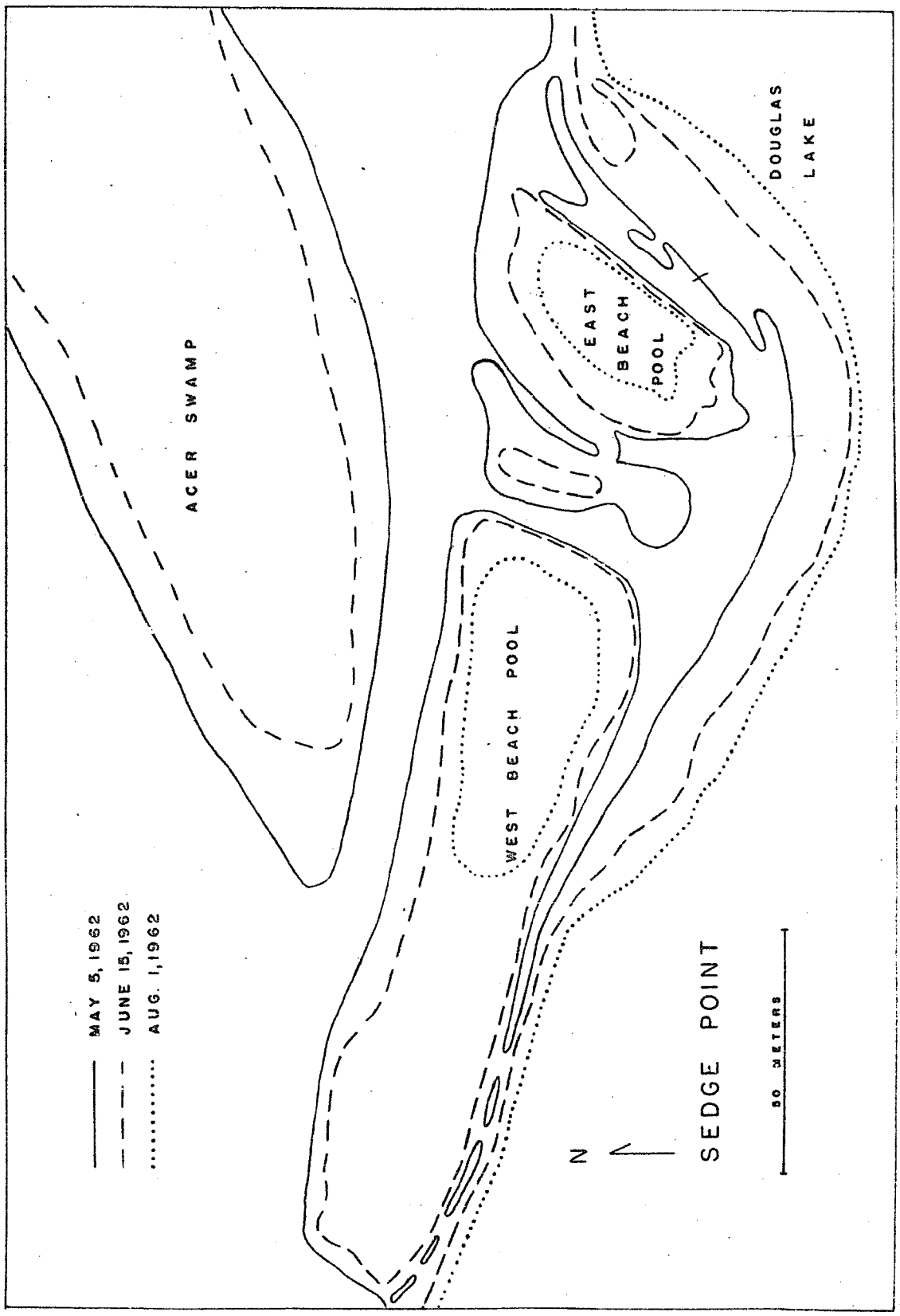

MAY 5, 1962
JUNE 15, 1962
AUG. 1, 1962
ACER SWAMP
WEST BEACH POOL
EAST BEACH POOL
DOUGLAS LAKE
N
SEDGE POINT
50 METERS

FIGURE 6

Several snakes known to be predators on the Leopard Frog were noted; Thamnophis sauritus and T. sirtalis were abundant but the Banded Water Snake (Natrix sipedon) was less common. Dekay's Snake (Storeria dekayi) and the Red-bellied snake (S. occipitomaculata) were also found. Raccoons (Procyon lotor), Muskrats (Ondatra zibethica), Herring Gulls (Larus argentatus), Black Ducks (Anas rubripes), Mallard Ducks (Anas platyrhynchos), Great Blue Herons (Ardea herodias), Kingfishers (Megaceryle alcyon) are all possible predators which frequented the area.

While fish of many types were abundant in Douglas Lake only one was seen in the pools. Several young Bullheads (Ameiurus natalis) were found in the west pool in the spring of 1962, undoubtedly having gained entrance from the lake during the high water period when the lake and pool were connected.

General Methods

Three major methods were used to secure data on populations and movements: intensive, systematic collecting and marking of individual frogs; trapping by means of pit traps placed at strategic locations; and following detailed movements of selected individuals by means of a trailing device.

Census

A census was made by walking slowly back and forth across the study areas systematically covering every portion. While I walked an insect net used to capture the frogs was kept swinging from side to side, if vegetation permitted, so that a swath about 2 m wide was covered. My movements and those of the net served to disturb frogs sitting among the vegetation into jumping. As they jumped they could be easily seen and, once seen, were generally easily captured. In areas with little or no vegetation the net was not used to flush frogs, but instead they were sought out visually. Probing into crevices with the handle of the net occasionally flushed a frog which might otherwise have gone undetected.

To obtain an estimate of the effectiveness of the searching procedure the percentage of recaptures in censuses of four successive weeks in June and July of 1961 and 1962 was determined for each of the study areas. The results are plotted in Fig. 7. In the second census an average of 26.5% (range, 23-32%) of the frogs taken were recaptures from the first

Figure 7 Percentage of recaptured frogs in successive weekly censuses in 1961 and 1962. Heavy line represents the theoretical percentage of recaptures expected if 25% of the frogs present were captured in each census.

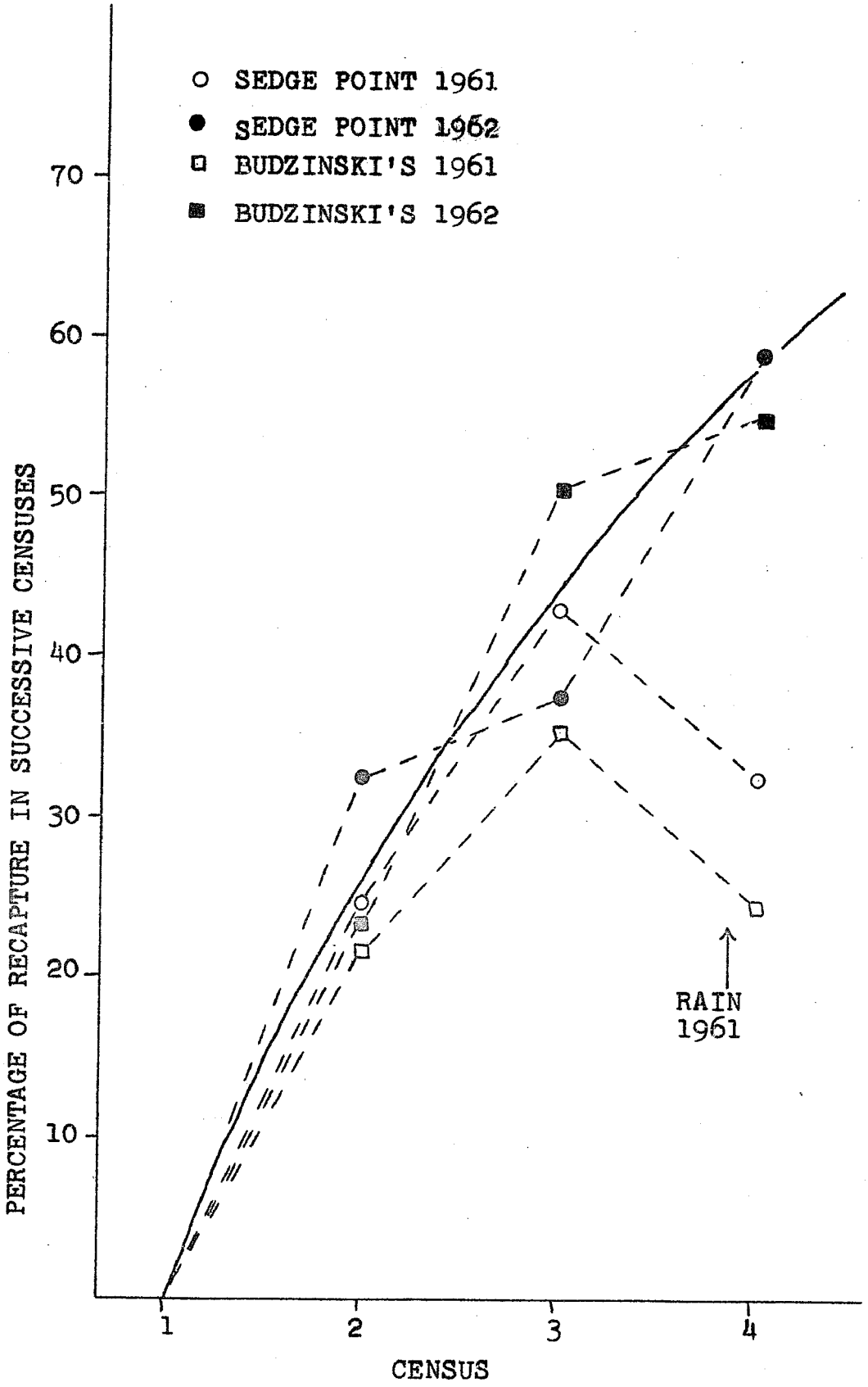

SEDGE POINT 1961
SEDGE POINT 1962
BUDZINSKI'S 1961
BUDZINSKI'S 1962
PERCENTAGE OF RECAPTURE IN SUCCESSIVE CENSUSES
70
60
50
40
30
20
10
1
2
3
4
CENSUS
RAIN
1961

FIGURE 7

census. In the third census the average percentage of recapture from the two immediately previous censuses was 41.0%, while in the fourth censuses of 1962 the average percentage of recapture from the three immediately previous censuses rose to 57.5%. The increased proportion of recaptured frogs in each successive census was due to the addition of marked frogs to the population at each previous census. When plotted, the percentages for the consecutive census periods form an asymptotic curve, the percentage of marked frogs captured increasing in each succeeding census but never reaching 100%. The points for the fourth censuses for 1961 should be considered separately since they were made following a rain in which unmarked frogs from outside the study area moved in and some marked ones moved out thereby lowering, at least temporarily, the percentage of recapture (see section on adult migrations). The theoretical percentage of recaptures to be expected in a sample if 25% of the frogs present were captured each time the areas were searched is also indicated on the graph. The empirical curve shows a good fit with the theoretical one, indicating that in each census very close to one-fourth of the frogs present were captured and that this percentage remained nearly constant in each census. The curve was not carried beyond the fourth census because rains altered the percentages.

To capture a frog the net was lowered slowly to a position immediately in front of the animal. When it was in place a sudden movement of my foot usually caused the frog to jump

directly into the net. This method proved to be less damaging to the frogs than trying to throw the net over them in a quick motion, and immeasurably easier than catching them by hand.

Most searches were made during daylight; night forays did not prove satisfactory because it was very easy for a frog to escape detection and capture among the dense vegetation. Only about one-fourth as many captures were made at night as in a comparable time during daylight. Recording notes and taking information accurately from the frog were also more difficult and time consuming. In view of these limitations night searches were made only when there was some reason to believe that information not otherwise obtainable could be gotten. Mostly they were employed only during or immediately after a rain.

Frogs were marked for individual recognition by toe clipping, following the system used by Martof (1953a). With this system a maximum of two toes of each foot was clipped. The loss of toes did not appear to influence either the activities or the survival of the marked frogs in any way.

Information about each frog was recorded at each capture. The snout-vent length was measured using a millimeter rule laid along the frog which was held flat in my palm. Pressure on the frog was usually necessary to insure that its full length was obtained, but even with this precaution small variations in length measurements occasionally occurred. The coloration, sex, exact site of capture, type and density of vegetation, character of soil and its moisture content,

abnormalities or injuries, and abnormal behavior were also routinely recorded.

The presence or absence of the thumb pad on adults was used as the primary criterion for determining sex. This, however, was not entirely satisfactory since the pad is not evident on some males during the summer. It was found that by stroking the belly of the animals lightly while holding them behind the forelimbs, males, even without thumb pads, could be induced to croak. If during the croaking the vocal sacs were enlarged the animal was recorded as a male and no further checks were felt necessary. Using a combination of the thumb pad and croaking reaction it was possible to determine the males of the population. All adults not definitely identified as males are considered for the purposes of this study to be females. Young frogs, generally those less than 60 mm long, could not be sexed externally and were simply recorded as immatures.

To facilitate indicating the exact location of capture sites, both study areas were laid out in a grid using wooden stakes to mark the intercepts. A grid with 20 meters between stakes was used except in the gravel pit at Budzinski's where stakes were at 10 meter intervals, enabling more precise designation of capture sites. This was necessitated by the taller vegetation and irregular topography. Each stake was assigned an identifying number and all captures were recorded in relation to the nearest stake.

At Budzinski's farm, the entire pasture proved too large to sample completely at regular intervals so that it became necessary to set aside a portion of it as a primary study area. The area chosen was 100 x 80 m, including the entire marsh, the western one-third of the gravel pit and the area between. This region offered a cross-section of the conditions present throughout the field, including within it the two bodies of water as well as the entire range of soil moisture along an uphill gradient from the wettest area of the marsh to the dry ridge along the rim of the gravel pit.

The primary study area at Budzinski's and the area around the east pool at Sedge Point were searched completely at weekly intervals. The remainder of the pasture at Budzinski's and the area around the west pool at Sedge Point were searched at irregular intervals as time allowed. In these outlying areas, prominent landmarks and extra stakes placed in the areas most frequented by frogs, were utilized to designate the sites of captures.

Various areas in the vicinity of both Budzinski's farm and Sedge Point, where it was believed frogs might be found, were also searched as time allowed. On all occasions when passing through an area any frog seen was captured. During 1962 several forays up to 1.5 km away from Budzinski's farm and one km from Sedge Point were made in search of marked frogs.

The two study areas were mapped in 1961 by plane table.

Trapping

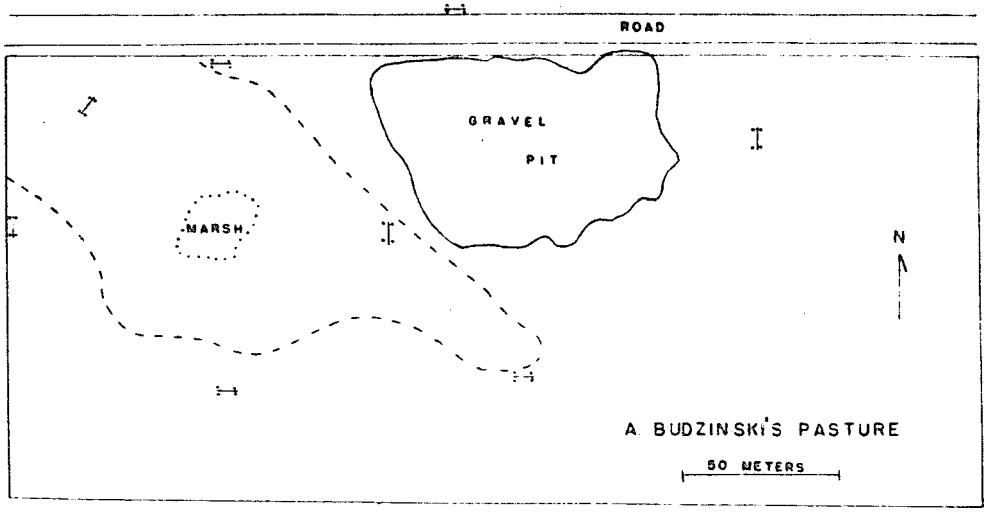
To sample population movements, frog traps were set up at strategic locations in and around both study areas. Each trap consisted of a fence, 30 cm high by 7.62 m long, of 6.3 mm mesh hardware cloth, with pits placed on both sides of the fence at each end, one foot short of the end of the wire (Fig. 8). Generally a frog encountering the fence moved along it until it fell into one of the pits on that side. In this way the direction and magnitude of population movement could be ascertained.

The pits were made of no. 10 fruit cans (15 cm diameter) with bottoms and tops removed, stacked one on top of the other and sunk into the ground. In 1960 all pits were two cans deep (34 cm). These proved effective in capturing frogs up to 40-45 mm long but larger ones could leap out. This was corrected in 1961 and 1962 by making the pits three cans deep (51 cm) and placing a trap-door midway down the pit so that frogs could fall in but could not leap out.

Not all adult frogs moving to the fence fell into the pits; twice adults were seen to leap over them. They did not appear to avoid them intentionally, however, for they did not increase the length of their hops. Apparently the longer leaps of adults enabled some to escape the pits. Of 17 young observed on various occasions moving along the wire, however, all eventually were trapped. Adults which maintained home ranges in the vicinity of a trap probably learned to avoid the pits. This seems likely because several frogs known to reside in the area

Figure 8 (Top) Frog trap south of Budzinski's marsh. Pits at the near-end of wire show as black ellipses. White object in foreground is plastic bottle with funnel for sampling rainfall. Note also the nature of the vegetation on the dry ridge (July, 1961). (Middle) Locations of traps in Budzinski's pasture. Four traps at cardinal compass points around marsh were used in 1960; others were added in 1961. (Bottom) Location of traps at Sedge Point. Three traps adjacent to swamp were used in 1960; others were added in 1961 and center trap near swamp was abandoned. The two traps on the lake shore extended 2 m into water and had pits at upper end only.




ROAD
GRAVEL
PIT
MARSH
N
A. BUDZINSKI'S PASTURE
50 METERS

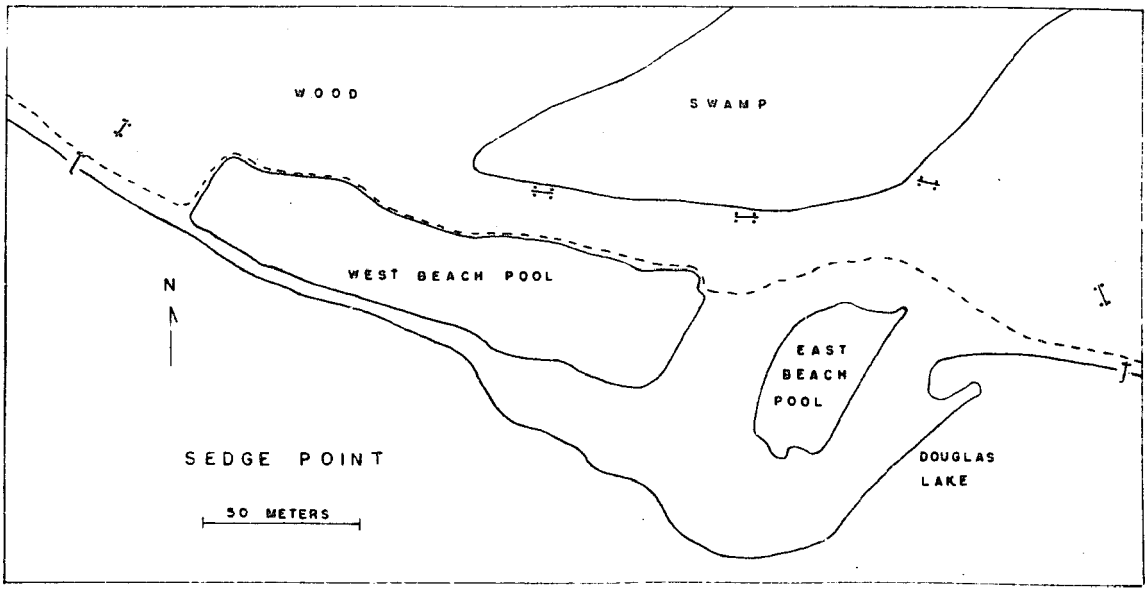

WOOD
SWAMP
WEST BEACH POOL
N
EAST
BEACH
POOL
SEDGE POINT
DOUGLAS
LAKE
50 METERS

FIGURE 8

of traps were never captured in them, and two instances of trailed frogs turning at right angles when they approached to about 50-60 cm of a trap, thus avoiding them, were noted. The evidence shows that, in general, trapped frogs are transient in the vicinity of the trap.

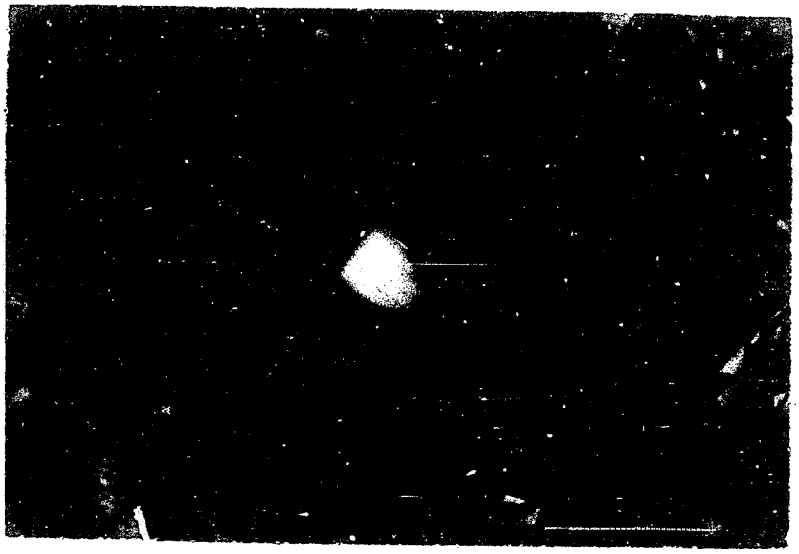
In 1960 four traps were used at Budzinski's farm, placed at the cardinal compass points around the marsh, 40 m from its edge. Three traps were placed in the woods north of the Sedge Pools, 20-30 m from the pools, at the south edge of the swamp. Their locations are shown in Fig. 8.

In 1961 and 1962 more traps were added at each place. At Sedge Point four traps were placed in the woods, but not in the same places as in 1960, and two were placed along the lake shore. At Budzinski's three were added around the gravel pit, one among the sumacs, 150 m south of the marsh, one in the northwest corner of the pasture, and two in the field west of the pasture at 200 and 400 m from the marsh.

Trailing

A device (Fig. 9) carried by individual adult frogs, which made it possible to follow their detailed movements for several days, was developed and used during 1962. The "trailers," patterned after the turtle trailers devised by Stickel (1950), consisted of a sewing machine bobbin wound with white nylon sewing thread and mounted in a holder carried on the frog's back. The holder for the bobbin was made from a section of rigid plastic tubing with a flat plastic bottom glued to one side and mounted on an elastic band, 6.3 mm wide, which was

Figure 9 (Top) Leopard Frog carrying a trailing device. Thread trail extends toward top of picture. (Bottom) Diagram of trailing device.



25 mm

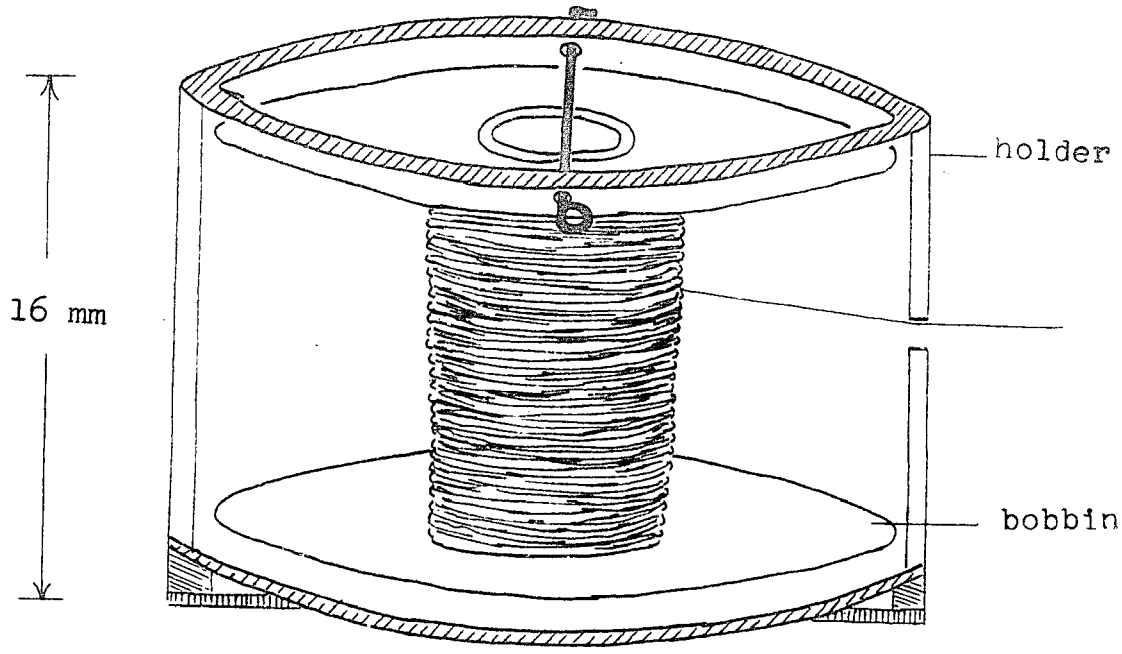


FIGURE 9

placed around the waist of the frog. The holder had a wide slot cut in its back side to permit the thread to play out behind as the animal moved. A short wire, run through two holes in the holder and across the top of the bobbin, kept the latter in place. The loose end of the thread was tied to a small stake placed close to the site of capture when the frog was released. As the frog changed locations the bobbin on its back unwound and its route was marked by a trail of thread.

A single bobbin holds about 50 m of thread, which proved to be ample for two to three days for most frogs in fair weather. For a few inactive individuals a single bobbin lasted as long as seven days. During rains at night, however, when the frogs became very active, the bobbin lasted only one or two hours, necessitating an all night vigil in the rain to replenish thread as it ran out. The end of the thread was tied to the bobbin so that frogs could not escape readily if they ran out of thread, which they occasionally did.

To change the thread the animals had to be captured. This could sometimes be done by a quick movement of the hand but more often a net was needed. The empty bobbin was then removed from the holder, after first removing the wire holding it in place, and a new, fully wound bobbin put in its place. The elastic saddle did not need to be removed from the frog. The animal with its new thread supply was then returned to its original position and released slowly enough

that the animal merely settled back into the position held before being handled. Occasionally the process of bobbin changing and releasing the animal did cause an individual to jump a few meters away from the site of capture. These animals were not disturbed further, and it was found that they commonly returned to the original capture site in a short time. Such handling had little influence on their activities even when it was done fairly frequently.

Travel routes, as shown by the thread trail, were plotted on graph paper in the field. Trailed frogs were usually checked each morning and evening to provide an adequate thread supply and to plot movements which had occurred. After the trail had been mapped the thread was removed from the field. Detailed route maps were made for 136 frogs, providing clear demonstration of the activity of individual frogs, sometimes for fairly long periods. The longest records covered 35 days from July 26 to August 29, and 33 days from June 17 to June 21 and June 27 to July 21. Five others were trailed for 20 or more days each, 12 for 10-19 days and 117 for less than 10 days.

Although the device was mounted upon the back of the frog and had to be carried by it wherever it went, it did not seem to hinder the animal's jumping ability seriously. Trailed frogs responded as quickly to the approach of danger as did untrailed frogs and were able to execute normal jumping movements. The added weight of the device (about 8.5 gm when full of thread) may, however, have shortened slightly the length of

the jump, but except possibly when escaping predators, this was probably of little consequence to the frog. No frog less than 60 mm long was trailed, though frogs as small as 50 mm were able to carry the device without its noticeably hindering their activities.

Carried, as it was, next to the skin the trailer or the belt holding it occasionally irritated the skin on the hip and thighs. This usually took the form of a small area which was rubbed raw by the belt. In all cases where any irritation was noted the frog was immediately released from the trailer and no attempt was made to trail it further until the irritated area had healed completely.

As the bands which held the trailers on the frog were elastic, frogs occasionally crawled out of them and escaped. Although this often meant the loss of a frog after being trailed several days (a rather frustrating experience), it proved useful, for whenever a frog's thread became tangled in the grass, as it sometimes did, the animal then escaped after a brief struggle. If left in the holder without being able to move they would have been easy prey for snakes or might have died of desiccation before being checked again.

The trailer did affect the swimming ability of the frogs, making their movements awkward. Three frogs were drowned as a result of the thread becoming tangled in aquatic vegetation. During the summer, when water was scarce and the animals resided in the field, this was of little consequence, however. Occasionally a frog in a woods would attempt to enter a small

crevice such as a mouse burrow or a cavity beneath a log. At this time the device sticking up on their backs presented a problem. Usually the struggling frog knocked the trailer sideways so that it was carried on its side and the frog was able to enter and leave the crevice. Carrying the trailer in this manner seemed to be no more troublesome than carrying it on their backs. Three frogs which entered crevices were lost, however, because they became tangled in the thread, cutting them severely, causing death in two and the ultimate release of the third due to injuries.

Climatic Data

In order to keep an accurate and continuous record of climatic conditions several instruments were utilized and many were left continuously in the study areas. A Freiz hygro-thermograph was placed directly on the soil among the grass under a shelter at both Budzinski's farm and Sedge Point to obtain continuous recordings of temperature and relative humidity. The shelters, painted light green, consisted of a roof supported on four legs with three sides completely open allowing free circulation of air. A Kessler dew recorder was used at Budzinski's farm in 1961 and 1962 to obtain a continuous record of the duration and amount of dew. This instrument also served to indicate the times at which rains began as well as giving a general indication of wind velocity and duration at any given time through the fluctuations of the dew pan as the wind blew. During 1962, two Piche evaporimeters were used at Budzinski's, one occupying a position near

the marsh while the other was placed outside the pasture on the south side among the sumacs. A Belfort microbarograph was used at Budzinski's to obtain a continuous record of barometric pressure. In addition to the above records, spot checks of temperature and humidity were made frequently with a small mercury thermometer and a hand aspirated psychrometer. A microanemometer (Anemotherm Air Meter, Model 60) was used to make a few spot checks and comparisons of wind velocity late in 1962. Plastic bottles fitted with funnels 75 mm in diameter were set up in both areas to sample rainfall.

Local Movements and Activity of Adults

Considerable information regarding the activities of adult leopard frogs was obtained in the summers of 1961 and 1962 by both direct observation and through the use of trailing devices attached to individuals. Observations in the field were made from a blind mounted upon a platform 1 m high, an arrangement which permitted the watching of frogs at distances of up to 10 m in areas where vegetation was sparse. The blind was placed in position, in a new locality, at least 24 hours before observations began, allowing the animals time to adjust to its presence. The vicinity of a small pond in Budzinski's gravel pit where frogs could be easily seen was the site of most observations. Attempts to watch frogs among the dense grass of the field were less successful, for only one frog could be seen at a time and if it moved was generally lost from view. Locating frogs in the grass was difficult without disturbing them. Observations reported in this chapter were all made in fair weather and were about evenly divided between daylight and dark; daytime observations were made both in morning and afternoon, but all night observations were limited to the hours preceding midnight. No difference in activities was noted between the day and night but this may have been due to the use at night of two battery-powered spot lights, covered with frosted glass to produce a diffuse, low intensity illumination, which may have modified

the frogs' usual behavior somewhat. Observation periods ranged from one hour to two hours 40 minutes.

Observations

Of 23 adults watched, 11 (48%) remained in the same location for the entire period of observation, though all made movements of some part of the body. Seven of these shifted positions so as to face a different direction, eight twitched their rear legs rapidly as if to relieve a cramped muscle, and two changed from a sitting to a lying position. Three which moved to face another direction did so in apparent response to an insect moving closeby but only one was seen to feed, lunging forward to snap the prey from the ground and then settling back to its previous position. The causes of the position shifts of the remaining four are not known but may have been prompted by a moving object which I failed to see or perhaps by a cramped position and a consequent attempt on the part of the frog to find a more comfortable one.

Of the 12 (52%) which did move from their locations during an observation period, seven did so at the approach of snakes. Four, sitting near the pond's edge, leaped directly into the water, disappearing in its depth and surfacing elsewhere. One, also sitting near the pond, was caught by the snake just as it sprang toward the pond and was eaten. Two, sitting among sedges in the gravel pit more than 10 m from water, made a rapid series of four or five leaps when approached by snakes, changing direction with each bound, and

were lost from view in the surrounding vegetation.

Six (including two later disturbed by snakes) of the 23 frogs observed left their positions to capture prey which was moving on the ground 20-30 cm away. During an afternoon, one adult changed positions four times in less than 10 minutes, feeding each time it moved, finally stopping and settling down at a new location about 1 m from its original position. Five of the frogs seen to feed were on bare wet soil, less than 1 m from the pond's edge, and of these only one returned to its former position after feeding. Another, sitting among sedges more than 10 m away from the pond returned to its former location after stalking a small beetle by "crawling" slowly after it for a distance of 25-30 cm.

Of the 23 frogs watched, only one changed locations during the period of observation without an obvious stimulus to do so; this one moved from the edge of the pond to a new position on completely bare, wet soil approximately 1 m from the water, remaining in the new spot for the remainder of the observation period.

Quiescent Leopard Frogs always sat so their thighs were in contact with the moist soil though sometimes they lay prone with bellies touching the soil as well. In areas where the soil was bare of vegetation, as arcund the ponds in the gravel pit, frogs commonly could be found sitting or lying in shallow depressions such as hoof prints where they were nearly surrounded by a low wall of mud. In such situations, the rate of water loss is probably decreased due to the more

or less enclosed nature of the cavity, reducing air circulation. In the fields, where the soil was generally covered by a mat of dead grass, frogs characteristically pushed the dead vegetation away with their hind feet clearing a patch of moist soil just large enough to accommodate themselves. These small bare patches were often surrounded on three sides by a horseshoe-shaped ridge of the dead grass, 10-15 mm high, which had been pushed aside, resulting in easily recognized "forms," which were common in fields where frogs were abundant (Fig. 10).

Detailed Movements

To present a clear picture of the usual pattern and method of movement of adult frogs the records of three animals have been selected from 40 trailed for five days or longer for detailed description and discussion. These were picked as illustrations because of the relatively long periods over which the animals were trailed and because together they illustrate a wide range in behavior, patterns of movements, and habitats occupied.

Number 2976, adult female, 73 mm (Fig. 11) -- Captured in a field of bluegrass adjacent to Budzinski's pasture, 170 m from the nearest body of water, this animal was first fitted with a trailer on June 17, but on June 18 she had escaped after moving only 6 m. Three days later, on the morning of June 21, she was found again, sitting in a form in the field 2 m from the edge of a

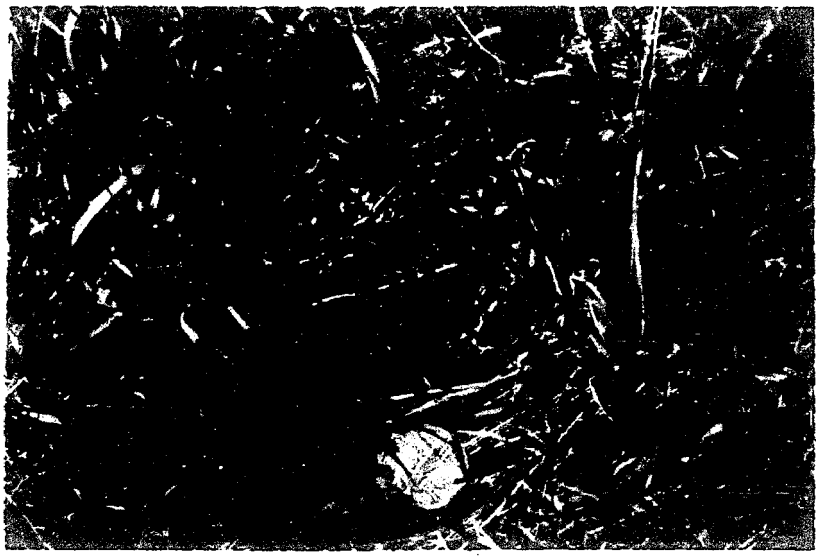


Figure 10 Small patch of moist soil cleared of dead vegetation by a Leopard Frog to produce a form. Fifty-cent piece is 30 mm in diameter.

Figure 11 Trail of adult female 2976 in bluegrass (June 17 and June 21-July 8). Circles indicate forms in which the animal was found sitting; numbers within circles show the sequence in which forms were used. Dates and times at which the animal was found in each form are indicated beside them (J = June, JY = July, A = August; time to the nearest hour follows the colon). See text for complete description.

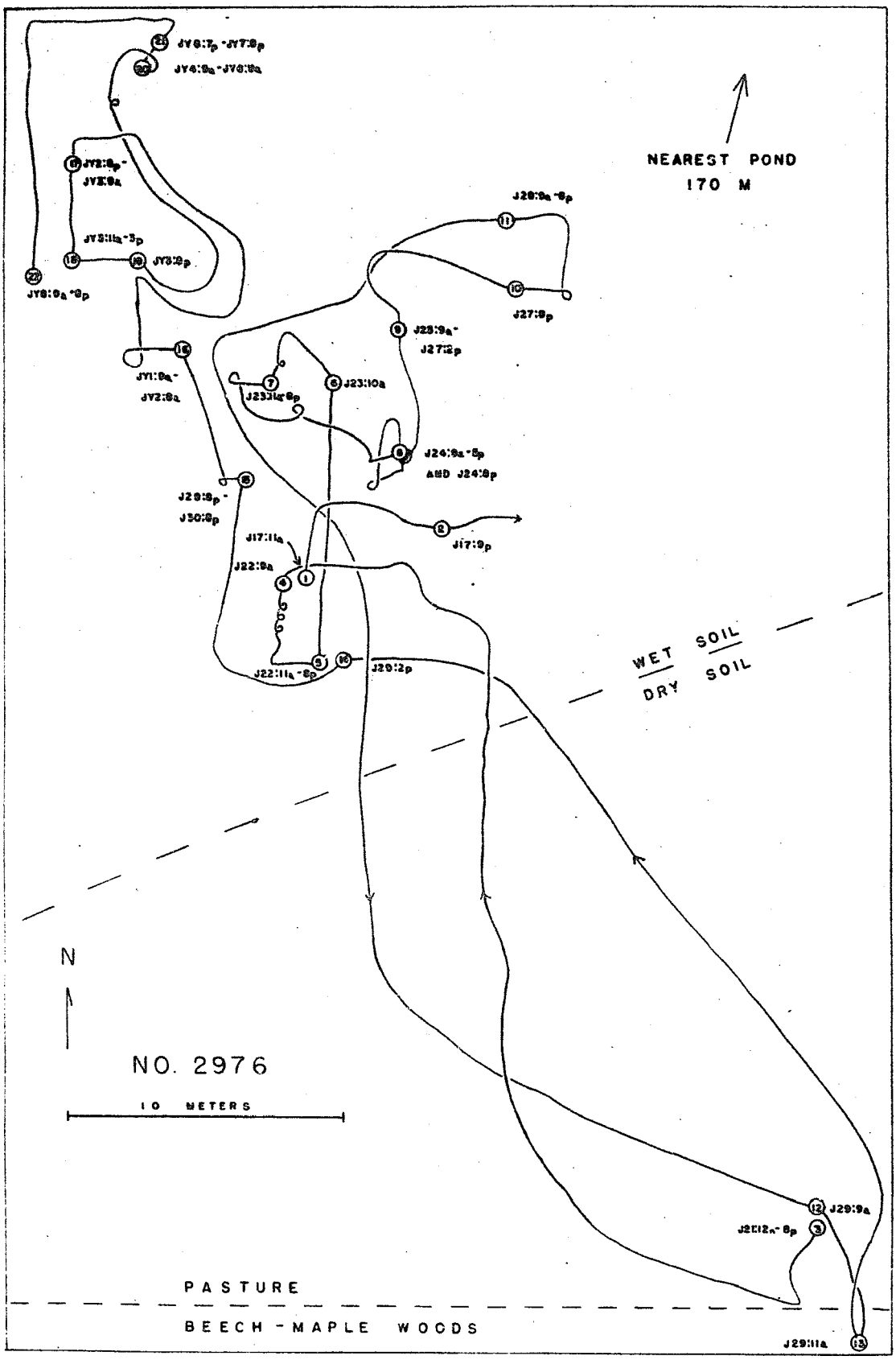

NEAREST POND
170 M
WET SOIL
DRY SOIL
N
NO. 2976
10 METERS
PASTURE
BEECH - MAPLE WOODS

FIGURE 11

beech-maple woods and 22 m from her original capture site. After being resaddled she remained in the form near the woods edge until after nightfall; sometime during the dark she returned to the area of her first capture, possibly to the same form occupied on June 17 (it was not possible to be certain) but certainly within 1 m of it. For the next seven days until June 28 she moved at irregular intervals during both day and night, after each move constructing and occupying a new form. On one occasion after leaving a form she returned to it again in less than three hours following a 3 m trip. Movements from June 22 to 27 carried her in a general northeasterly direction, but at dusk on June 28 (8 p.m.) she reversed her direction and moved in the night across a strip of dry soil 20 m to the woods edge again. Here she was found at 9 a.m., June 29 sitting in a form among loose leaves on dry soil less than 1 m from the form occupied on June 21. By 11 a.m. she had moved into the woods and was sitting on barely damp earth which she had cleared of leaf litter, but at 2 p.m. she had recrossed the dry region and was occupying a newly made form within 1 m of the one occupied on June 22.

By 8 p.m. she had moved again to a new form 6 m farther into the wet-soil region; here she remained for two days. During the night of June 20 she shifted to a new form and for the next eight days moved at irregular intervals in a general northwesterly direction. On July 8 her trail had again turned back toward the area where first captured when she was unfortunately caught and eaten by a snake.

Number 2400, adult female, 81 mm (Fig. 12) -- On June 27 this animal was recaptured in a field of bluegrass adjacent to Budzinski's pasture after having been trailed for a brief period previously. (Her earlier trail is not included here but is discussed in another section). During the next 16 days she remained in a small area of the field, more than 150 m from the nearest body of water. From June 27 until June 30 she moved at irregular intervals, never more than 3 m at a time, just inside the margin of moist soil, constructing new forms as she moved, some less than 50 cm from the previous one. Sometime in the night of June 29, however, she moved 11 m northward to an area where the soil was noticeably wetter. On the evening of June 30 she was found occupying a nearby form (8) in which she remained continuously for five days, without moving from it,

Figure 12 Partial trail of adult female 2400 in field of bluegrass. Forms are numbered in the order occupied; three forms used on more than one occasion each have more than one number. A few trails are shown as dotted or broken lines to prevent confusion. Dates and times as in Figure 11. See text for complete description and Figure 25 for earlier trail.

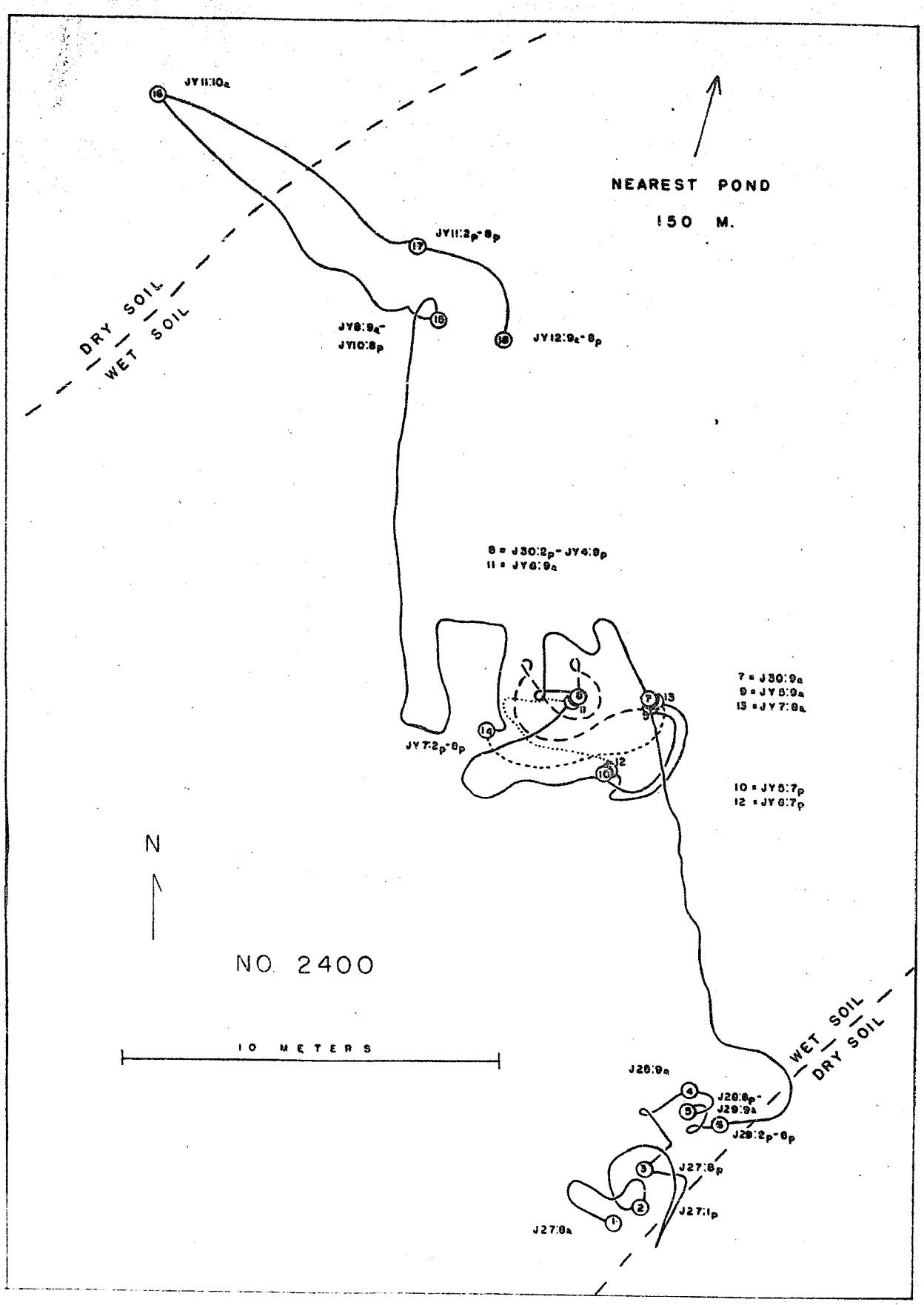

NEAREST POND
150 M.
DRY SOIL
WET SOIL
JY11:10a
JY11:2p-8p
JY8:9a-
JY10:8p
JY12:9a-8p
8 = J30:2p-JY4:8p
11 = JY6:9a
7 = J30:9a
9 = JY6:9a
13 = JY7:8a
JY7:2p-8p
10 = JY6:7p
12 = JY6:7p
N
NO. 2400
10 METERS
WET SOIL
DRY SOIL
J28:9a
J28:8p-
J29:9a
J29:2p-8p
J27:8p
J27:1p
J27:8a

FIGURE 12

though she did shift positions occasionally so as to face in different directions. During the night of July 4 she moved 8 m, changing direction three times, to reach a form previously used on June 30. By the evening of July 5 she had again shifted to a new form, and during the night returned to the one (8) occupied from June 30-July 4. On the evening of July 6 she was sitting in the previous day's form but by the following morning, July 7, had moved for the third time to the one (7) used on June 30 and July 5. During the day, however, she shifted to an entirely new spot, remained there until after nightfall, then moved 12 m northward, over a route involving seven changes of direction of 90 degrees, to another location. This form was occupied continuously for three days until the night of July 10. On the morning of July 11 she was found sitting in a dry area 8 m from her previous form, but by 2 p.m. had returned again to the wet soil, moving almost parallel to the route taken during the previous night. When removed from the field on July 12 (the field was cut for hay) she was still on the wet soil 2 m from the July 8-10 form.

Number 3523, adult female, 86 mm (Fig. 13)--Unlike the previous two animals, which resided

Figure 13 Partial trail of adult female 3523 in Picea-Alnus swamp. Circles indicate stopping places; only numbers 1, 10 (used four times) and 16 were forms where the animal cleared the soil of leaf litter. Triangles indicate occupation of cavities underneath masses of roots. Places occupied are numbered consecutively in the order used. A portion of the trail has been enlarged to show more detail. Form number 10, occupied four times, was in an indentation at base of a root hillock. Dates and times as in Figure 11. See text for description and Figure 16 for remainder of trail.

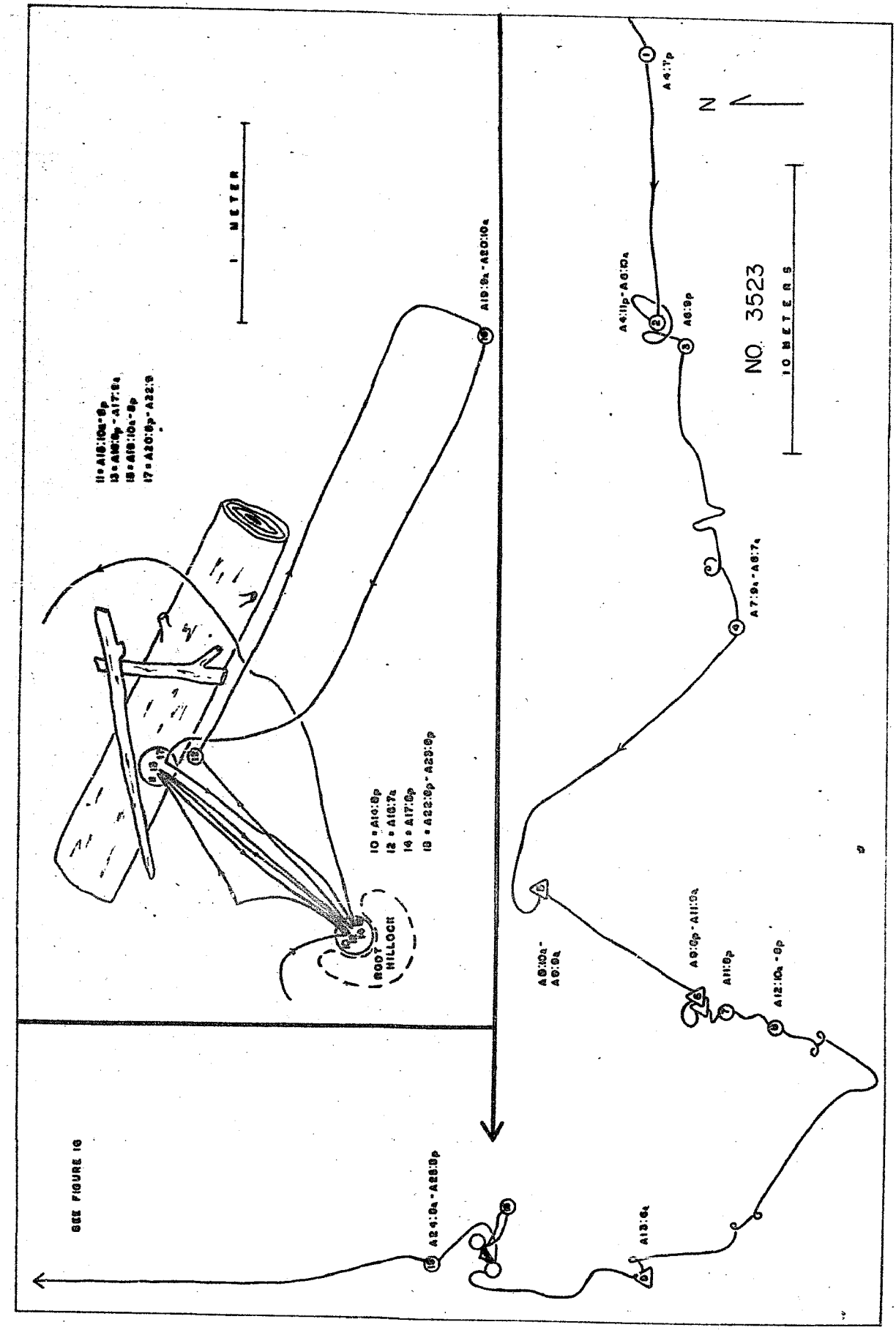


FIGURE 13

in grassy fields, this frog occupied a portion of a densely wooded swamp from August 4 until she was released on August 29 when the study was terminated. Though there was no water in the swamp after June, 1962, the soil was continually wet and the undergrowth of horsetails, sedges and other herbaceous plants luxuriant. The dominant plants were Picea mariana and Thuja occidentalis, both very abundant, with Alnus rugosa less abundantly scattered throughout the area. Cornus stolonifera and Taxus canadensis were common shrubs. Several species of Solidago, Eupatorium perfoliatum, E. maculatum and Scirpus americanus grew in dense stands up to a meter or more in height. Horsetails (Equisetum arvense) formed a very dense, grass-like cover over the floor of the swamp, intermixed in places with raspberries (Rubus sp.) in dense tangles.

First entering the swamp on August 4, this animal moved at irregular intervals, both day and night. Unlike the frogs in the field she did not construct forms, sitting instead on already bare soil, in cavities, or on wet leaf litter. On three occasions she was found in cavities under root masses, sitting on the bare soil and four times sitting on top of wet leaf litter. On August 14 she was in a

shallow indentation at the edge of a hillock of roots overgrown with dense sedges in a form she had constructed by clearing the soil of leaf litter. For the next 11 days she shifted between this spot and the top of a dry log a meter north, except for a two-day excursion of 3 m after which she returned to the log. She was found in this form four times, on top of the log three, and once on wet soil at the side of the log, just below her usual site on its surface. Once she remained on the log continuously for more than 48 hours in a period of dry weather. On August 24 she moved 4 m northwest and was found here in a form which she had constructed among the dense vegetation. Following a rain on August 25 she moved 30 m northward, remaining there until the night of August 28 when she continued about 20 m to the woods edge in a light rain. Because of the longer distances covered, the directness of the trails and their occurrence in rain, the latter two moves were not considered to be typical local movement; they are treated separately in the next section (Fig. 16).

Summary of Trailing Records

As it is impossible for lack of space to present the trails of all frogs in detail, a general summary of their

more important aspects follows.

Of the 40 frogs trailed for five days or longer, 33 (83%) moved in a winding, twisting route, their trails often doubling back upon themselves so that they returned toward the point of original capture. The greatest dimension of the area traversed by these 33 frogs was 7 m for one animal, 10-19 m for seven, 20-29 m for six, 30-39 m for nine, 40-49 m for four and 53 m for one animal. Frogs trailed less than five days also remained in small areas, but a tendency for them to return towards the site of original capture was not so clear, undoubtedly due to the brief time involved. Of the seven other frogs trailed for more than four days which did not remain within a local area, three moved to ponds, probably the result of a need for water, while four made trips of 50 m or more during nocturnal rains. Such movements are the subjects of later chapters.

Though frogs sometimes moved two, three or more times in a 24-hour period, making new forms at each location, some forms were occupied for several days. Two frogs occupied single forms for five consecutive days without moving from them. One individual utilized a form for eight consecutive days, but not continuously, for during the period she made four brief excursions varying from 1-33 m in total length but returned again to the same spot after each. Another occupied a form for two days before escaping from its trailer, but 13 days later he returned to the same spot, remaining in it for six more days, shifting each night to a depression on

top of a mat of dead grass 8 cm away and returning to the form each morning (Fig. 15). Four frogs occupied single forms continuously for four days, five for three days, six for two days, and 17 for longer than 24 hours. The average number of forms occupied per frog per day was 1.15.

Thirteen frogs utilized a single form on more than one occasion. The length of time the frogs remained away before returning varied from fewer than four hours (probably only a few minutes) for trips of less than 1 m, to 12 days for a trip involving a total movement of almost 100 m (Fig. 15). Of 22 trips made by 13 frogs from a form followed by a return to the same spot, eight involved distances of less than 1 m, 10 from 1-10 m, and four more than 10 m.

Occasionally frogs made brief excursions from their usual locales into regions of dry soil, usually returning within a few hours, but not necessarily to the same form. Six such travels, involving distances of 9-45 m (mean 17.3 m), were made by five animals. The movement of no. 2976 to the forest edge provides an example, though the distance involved was not so great in any of the others.

Six frogs were trailed for periods of five days or longer in densely wooded swamps, and seven others entered wooded areas for briefer periods. The behavior of these animals differed from that of frogs in the field, for in the woods they did not often construct forms, instead frequenting cavities under logs and root masses, cracks between logs and the surrounding soil, and sometimes resting

where they could lie against the already bare moist soil. In areas where the leaf litter was saturated, or after rains, they frequently sat on top of the moist litter, but only rarely did they clear the litter to sit on the bare soil beneath. Trailed frogs in woods were found in cavities of various sorts on 43 occasions, in cracks alongside logs on eight, sitting on top of dry logs on 10, on already bare wet soil on six, in a mouse burrow on one, on wet leaf litter on 38, on dry leaf litter on one, buried under leaf litter on seven, and on wet soil which had apparently been cleared of dead vegetation by the frog as was usual in the fields on six occasions.

Movements of frogs occurred at irregular intervals both during day and night but among all trailed frogs 64% of the distance moved in fair weather was covered between 8 p.m. and 8 a.m., presumably during the dark period, almost twice the distance moved during daylight. No differences in the nature of activity between day and night nor between the sexes could be detected.

Discussion

As both trails and observations indicate, Leopard Frogs are rather sedentary animals during summer, spending a large part of the time sitting quietly, either in forms in the fields or on wet substrate in the woods. Only infrequently do they change locations and then they seldom move more than 5-10 m to a new site. Thus, even over periods as long as 25 days they tended to remain within a small portion of the

available habitat, often sitting in the same spot for several days at a time. Observations and capture data of some other species of anurans also indicate rather sedentary habits. Heatwole (1961) stated that the "activity period" of Rana sylvatica "is characterized by their sitting motionless until some prey item comes within range or they are disturbed." Individuals of Scaphiopus holbrooki have been found to remain in their burrows for an average of 9.45 days at a time (one remained 104 days), surfacing only occasionally to feed (Pearson, 1955). Stille (1952) believed that Bufo woodhousii fowleri remains in retreats for several days at a time, leaving them only briefly to obtain moisture and then returning.

The normal travels of trailed frogs formed complicated patterns with numerous turns, doublings and criss-crossed paths. In almost all frogs there was a tendency for certain parts of the area traversed to be frequented more often than others. Usually frogs tended to return frequently to particular small regions so that movements often appeared to radiate out from a more or less central area. No. 2976 provides a good example. In the 21 days she was trailed she returned to the region of her first capture after two brief trips to the woods edge. Even as she moved in the grass, first toward the northeast, then northwestward, her trail tended to return toward the region where she was first found.

Although Leopard Frogs have no burrow or nest as do many animals to which they repeatedly return, many did show an apparent affinity for certain spots. Some frogs occupied

particular forms for several days at a time, and some which left forms returned to them, or their immediate vicinity, after absences of up to 12 days. One frog (3523, Fig. 13) in the woods alternated between a form and the top of a nearby log for a 10-day period. It is likely that certain forms, or at least relatively small regions, toward which they direct much of their activity, possess a special significance to the frogs and can be thought of as representing very simple, rather temporary homes. There is no doubt that the forms provide shelter, for their occupancy considerably reduces the rate of water loss (see next section). A certain amount of concealment is probably also afforded the frogs, for several became partially covered with dead vegetation in the process of clearing the soil.

Why frogs, as they moved about their local areas, stopped and constructed new forms where they did is not clear. It is unlikely that the locations of forms are determined by chance, as might happen if the frogs constructed one wherever they became fatigued, for the moves were seldom more than a few meters, and on much longer migrations (100 m or more) the frogs showed no evidence of tiring. It is more probable that as the animals move about they are seeking particular favorable conditions (high relative humidity, the wettest soil, etc.) and stop upon finding a suitable place.

Though, in general, tending to move only short distances from one stopping place to another, usually much less than 10 m at a time, six Leopard Frogs made trips of up to 45 m

(round trip) in only a few hours and then returned to the area they had left. All such journeys were made into dry areas where the animals could not have survived long. These trips may have been exploratory excursions into heretofore unutilized adjacent areas or they may have been attempts to occupy familiar areas which, due to dryness, were no longer suitable. No. 2976, for instance, twice moved to the woods edge where the soil was barely damp on June 21 and completely dry on June 29. Inasmuch as the early summer of 1962 was unusually dry, (only 16 mm of rain falling between June 11 and July 19, whereas in the same period of 1961 more than 100 mm fell), it is likely that the area adjacent to the woods had been wetter in previous years and may have been utilized by the animal. The fact that she moved to nearly the same spot at the woods edge on each occasion indicates a familiarity with the area; perhaps the two brief trips indicate a continued affinity for the region, the result of previous experience, even though drought prevented its permanent occupancy in 1962.

The twisting and winding nature of local movements was characteristic of all trailed Leopard Frogs. It is probably brought about, at least in part, by the nature of the habitat, the dense vegetation and variations in the microrelief often necessitating indirect routes. Trails were found on occasions which detoured around mounds or ridges of earth, dense clumps of sedges, and the mouths of woodchuck burrows. A part of the winding movements, however, is probably the result of "exploration" of the immediate area, perhaps

"searching" for more favorable moisture conditions, for the moisture of the soil plays an important role in the water economy of Leopard Frogs. It is also possible that some movement is the result of restlessness or the need for exercise from sitting for long periods in one spot, the twisting nature of the route being brought about by a tendency to remain within a relatively small region while exercising. It is unlikely that such movements represent a search for food, as Rana pipiens is generally passive in this respect, waiting for food to come to it. They probably seldom, if ever, forage.

Occasionally as frogs moved from place to place they made turns of 360° or more, sometimes several in succession, resulting in short, tight loops in their trails. As many of these turns were followed by a change in the direction of travel it is likely that they are in some way related to the orientation of the animals to their environments. Possibly they represent a temporary loss of bearing and an attempt by the frogs to reorient themselves to their surroundings. Or it is also likely that the animals follow particular "pathways" as they move about their local areas and, once learning a particular trail, are obligated to make the same moves each time they travel over it. Noble (1931) has suggested that the frequent reappearance of useless movements in successive trials as frogs run a maze may be due to a "muscle memory" which obligates them to repeat the same kind and number of movements each time, once they have learned the pathway. Some

may have been due to a chance encounter with prey resulting in brief distractions of the frogs in their travels and the consequent temporary deflection of the pathway to capture it. The movements were not due to disturbance by me as they almost always occurred in my absence. When frogs were replaced in their forms after a bobbin change they usually settled into their former positions, only rarely hopping away; movements known to have been caused by the handling of the frogs were always so noted. These single loops were also not the result of disturbance by snakes, for at the approach of one a frog characteristically made a series of several leaps, changing directions with each leap, resulting in a complex series of twists and turns which were so characteristic as to be readily recognizable.

Many of the very short excursions (1 m or less) from forms and return can probably best be explained as feeding trips, for they appear to fit well the pattern of feeding behavior observed among frogs at the pond's edge. As an insect or other prey passed within sight the frogs probably moved from their forms following the prey until it was captured or escaped, then retreated to their former positions on the wet soil.

Migrations

Although adult Leopard Frogs generally confined their activities to relatively limited areas, on rainy nights some individuals embarked on excursions from their usual places of residence. These excursions, sometimes involving distances of 100 m or more across regions not usually inhabited by Leopard Frogs, differed markedly from daily movements. In addition to involving much greater distances these nocturnal journeys were more or less continuous through the night in a single direction, often in nearly straight lines, and seldom showed the twisting and turning which characterized local activity.

Of 110 records of frogs carrying trailers through 12 rainy nights in the summer of 1962 (many of these frogs were trailed during more than one rain) 17 showed excursions beyond the bounds of the usual regions of activity. Four of the 17 made such journeys twice, providing a total of 21 such trips. Distances traveled ranged from 40-160 m (mean, 74.2 m) in a single night. The rest of the 110 frogs carrying trailing devices during rains did not deviate noticeably from their usual daily movements, moving a mean distance of only 9.5 m (range 0-32 m).

Detailed Movements

As examples of these nocturnal excursions the trails of three animals have been selected. Though none can be

designated as typical, together they illustrate all the major behavior patterns shown on the 18 other excursions. Each will be described and discussed individually.

No. 3239, adult female, 80 mm (Fig. 14) -- This animal, one of the few female residents in Budzinski's pasture, was captured five times in the northwest corner of the field between July 16 and August 11, 1962, at which time she was fitted with a trailer. During the 27-day period preceding August 11, seven nocturnal rains fell, during each of which at least one trailed frog moved out of its usual area. No. 3239, however, apparently remained in its normal place of residence during at least one of the rains, for she was captured here the day following a 19 mm rain during the night of July 19; if she left the area at any time prior to being saddled she obviously returned. After being fitted with a trailer she remained in the vicinity of her previous captures for four more days, moving about the area in typical local movements, even through a 7 mm rain on the night of August 12.

About 7 p.m. on August 15 rain began falling, lasting until 10 p.m. and depositing 0.8 mm. At 11 p.m. this animal was out of the form she had been occupying earlier in the evening, sitting on top of the grass about 5 m away, still within her usual area. Sometime between 11 p.m. and 12

Figure 14 Trail of adult female 3239 in Budzinski's pasture. Solid dots in trail indicate forms occupied. Dates and times indicate their order of occupancy (J = June, JY = July, A = August; times to the nearest hour follow colon). Arrows show timing during migration. Circled dots are sites of capture prior to trailing. Insert shows position of area diagramed in Budzinski's pasture.

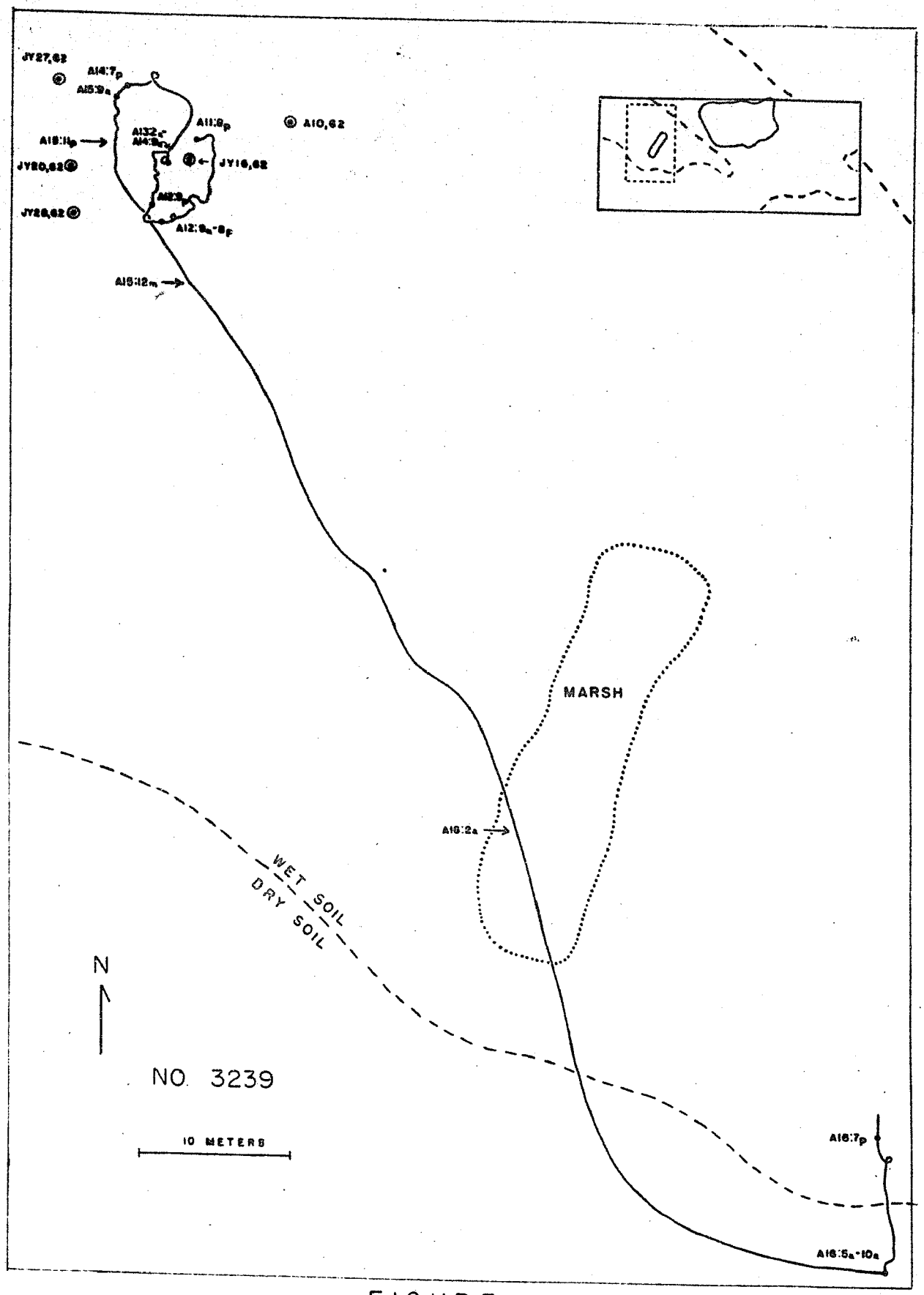

JY27,62
A14:7p
A15:9a
A11:8p
A10,62
A15:11p
A13:2a
A14:8p
JY20,62
JY16,62
A12:8p
JY28,62
A12:9a-8p
A15:12m
MARSH
A16:2a
WET SOIL
DRY SOIL
N
NO. 3239
10 METERS
A16:7p
A16:5a-10a

FIGURE 14

mid., after the cessation of rain, she began moving southeast. Passing through the marsh, which at this time contained no water, she continued 45 m beyond. At dawn (5 a.m.) she stopped on the dry ridge which the light sprinkle of rain had scarcely wetted, 110 m from her last form. She remained in a new form on the ridge, barely damp from the light rain, for at least 5 hr before moving at a right angle to her previous path, 12 m to the area of wet soil. Unfavorable moisture conditions during the hot, clear day of August 16 probably forced this last move. Unfortunately she broke the thread here and escaped; her "home" area was searched twice more but she was not captured again.

No. 2761, adult male, 71 mm (Fig. 15) -- First captured on July 14, this animal was occupying a form in the northwest corner of the pasture. Saddled, he remained in the same spot for two days, leaving it only once on a brief 1.5 m trip, then returning. He escaped on July 15, but on July 24 was recaptured 9 m from his previous site and again was fitted with a trailing device. A light rain began falling at 10:30 p.m.; lasting until 12:30 a.m. it left 4 mm. During the interval between 8 p.m. (when fitted with a saddle) and midnight, the animal moved about 30 m southeast.

Figure 15 Trail of adult male 2761 in Budzinski's pasture. Solid circles indicate forms and arrows indicate timing of movement during migration. Insert indicates position of area shown in Budzinski's pasture.

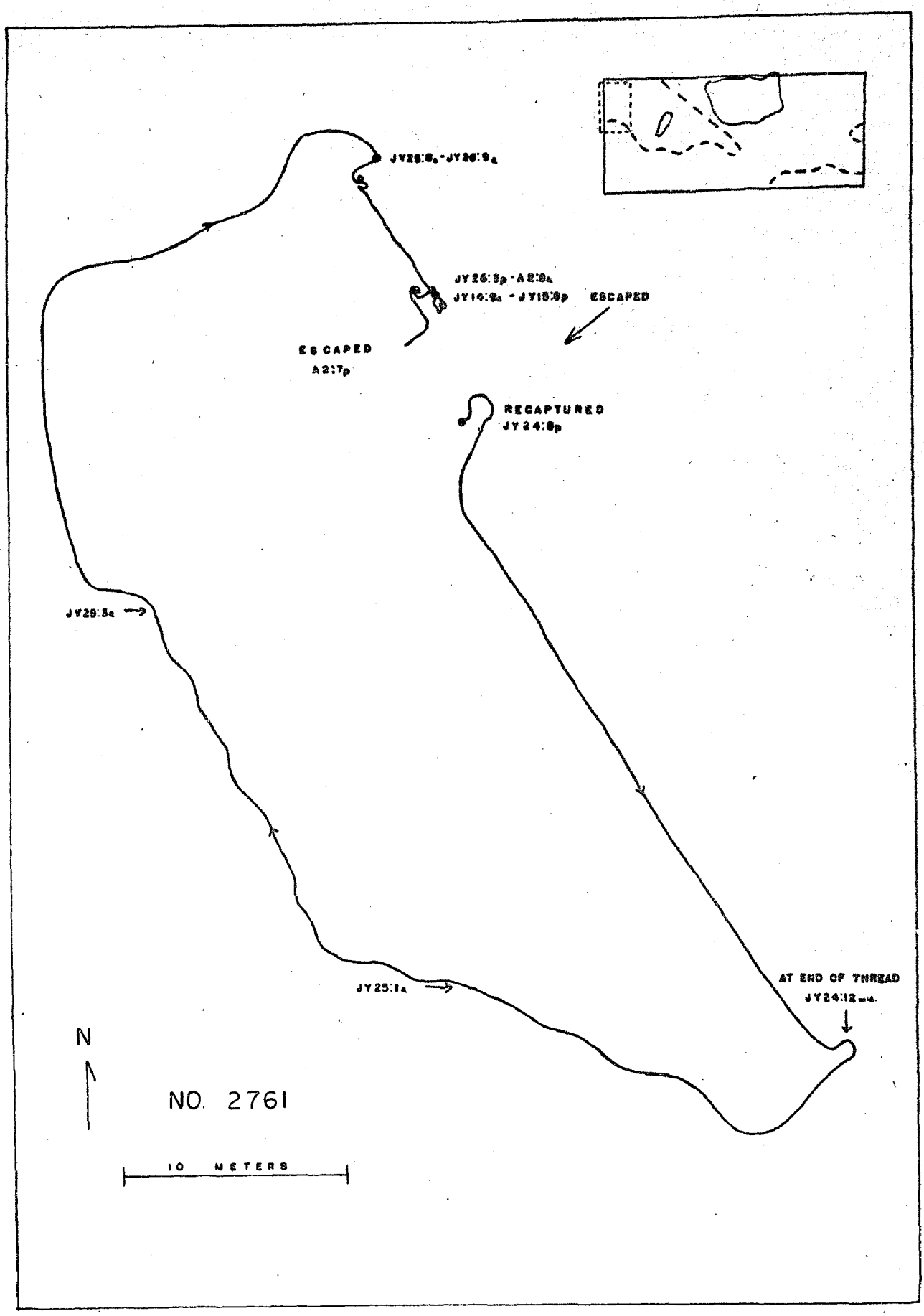

JY28:8♂-JY30:9♂
JY26:3♀-A2:8♂
JY14:9♂-JY15:9♀
ESCAPED
ESCAPED
A2:7♀
RECAPTURED
JY24:8♀
JY29:5♂
JY25:8♂
AT END OF THREAD
JY24:12 mts.
N
NO. 2761
10 METERS

FIGURE 15

At midnight the animal was found sitting on the wet grass, having reached the end of his thread. Supplied with a new bobbin about one-half hour before the rain stopped, the animal reversed his direction of travel sometime before 1 a.m., and by 8 a.m. had returned to within 7 m of the form occupied July 14-15. Here he remained throughout July 25. Sometime after 9 a.m. July 26, he moved back to the form in which he had been sitting when first found 12 days before, remaining in it until August 2 when he again escaped.

No. 3523, adult female, 86 mm (Fig. 16) -- This animal, captured for the first time on July 25 in the area north of the marsh, did not show typical local movements. Instead she moved at irregular intervals for a 9-day period across the study area, generally towards the southwest, until on August 2 she was only about 10 m inside the edge of the wet soil. Shortly after a 0.8 mm rain began falling at 10 p.m. August 3 she started moving and crossed a field of Agropyron repens and clover, normally dry and uninhabited by Leopard Frogs. Her route was in a nearly direct line, the deviations being caused by handling when changing the thread. The fact that she resumed her

Figure 16 Trail of adult female 3523. Dates and times as in previous figures. See Figure 13 for details between August 4 and 25.

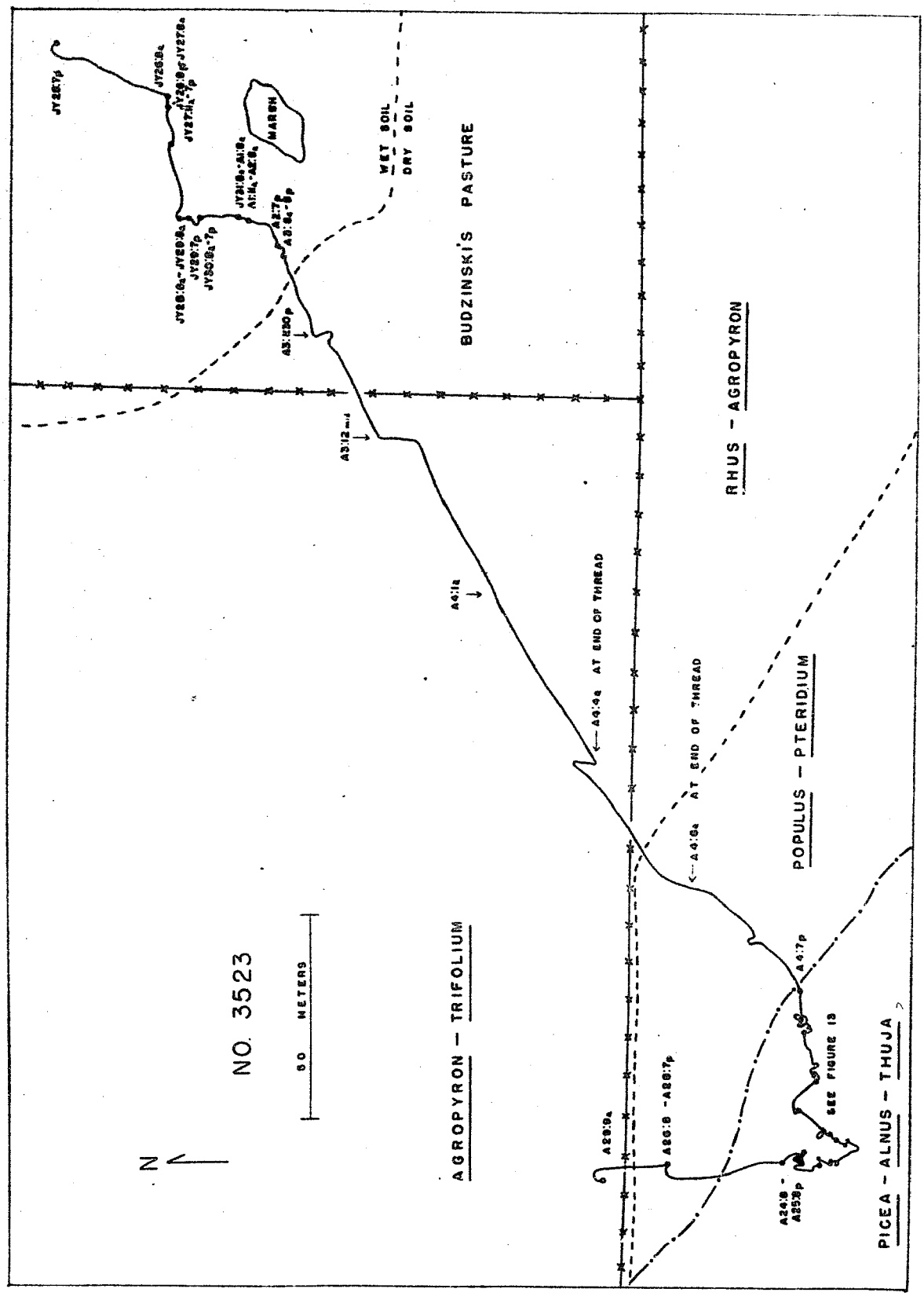

N
NO. 3523
50 METERS
AGROPYRON – TRIFOLIUM
BUDZINSKI'S PASTURE
WET SOIL
DRY SOIL
MARSH
RHUS – AGROPYRON
POPULUS – PTERIDIUM
PICEA – ALNUS – THUJA
AT END OF THREAD
AT END OF THREAD
SEE FIGURE 18

FIGURE 16

original direction of travel towards the southwest even after being handled indicates this was not random movement but that she was moving toward a particular destination. By 6 a.m. the following morning she had entered the edge of a woods adjacent to the field. Moving 35 m during the daylight, she reached the dense vegetation of a low swampy area dominated by Picea mariana, Alnus rugosa and Thuja occidentalis. Although the soil here was wet, and remained so throughout the summer, there were no ponds or other bodies of water. For the next 21 days she remained in the swamp, moving short distances at irregular intervals in an area 20 x 30 m, even though three rains fell during the period. Her activities during this latter 21 day period were considered in considerable detail in the preceding section. On August 25 she moved about 30 m toward the woods edge, remaining there until August 28 when she again moved northward 20 m. As both moves were made on nights when rains fell these probably represent excursions from the home range. She was released on August 29 so it is not known if she returned to the woods.

Summary of Trailing Records

Except for 3523, all trailed frogs which had begun

excursions during nocturnal rains stopped at daybreak even when it continued to rain, constructing a typical form wherever they found themselves, even though conditions were not suitable for permanent residence. The length of stay in the region they had reached and their subsequent behavior varied considerably. Three of the frogs which left their places of residence returned to them in the same night (e.g. 2761, Fig. 15). In two of these the time at which the animal turned back corresponded very closely with the time of cessation of the rain, although in one the return may have been brought about because he ran out of thread and was unable to proceed until about the time the rain stopped. In the third, rain continued through the night, yet the animal, after moving 50 m and crossing a gravel road, turned abruptly between 12 mid. and 1 a.m. and returned to within 10 m of the form she had left three hours before. It is possible that the reversal in direction corresponded with a temporary cessation of rain, but this is not certain. In all three of these frogs a homing ability is indicated. This was especially evident in 2761, for its return to a previously occupied form indicates both an attraction to, and ability to locate, a particular spot in the field.

On the other 20 excursions six frogs reached, and stopped at daybreak in, low areas where the soil remained permanently wet and which were usually inhabited by Leopard Frogs. Presumably they could have remained indefinitely. Of these six, one remained in its new form all day, but returned the

40 m to its former area during a light rain (0.8 mm) the following night. A second remained in its new form for two full days before moving to a pond in the gravel pit on the second night after the migration; here it was lost to a snake. Three remained in the region which they had reached until each escaped or was released, one, two and five days later. The behavior of a sixth frog (3523) which upon reaching the wet woods remained for 21 days in an area 20 x 30 m, has been described previously.

Eight excursions took animals into regions not usually inhabitable by Leopard Frogs, such as onto the dry ridge and into adjacent fields. The length of stay in these areas varied, depending on the wetness of the soil, hence on the amount of rain which had fallen. Two animals, after occupying their new forms only a few hours, retreated to wet regions during the day immediately following their excursions (e.g. 3239). The rains, each less than 0.8 mm, had barely wet the soil and the hot, sunny weather during the day dried it rapidly. Three frogs spent the entire day following their excursion sitting on the damp soil, but recommenced their journey the following night, even though no more rain fell. One of these moved an additional 20 m to a region with permanently wet soil; a second moved 60 m farther in the direction it had been traveling, reaching a wet woods; the third moved 100 m farther, after having moved 140 m during the night of the rain, until it reached a low wet area of an adjacent field. Three others remained in the outlying

regions which they had reached during their excursions for two full days, but during the second night after their migration, by which time the soil had all but dried, retreated to wet regions from which they had come.

Three frogs which made excursions in the rain escaped before their subsequent behavior could be learned.

Homing

Illustrations of excursions of frogs from their home areas are also available from capture data, which, since they cover longer periods than trailing records, provide additional information. In Figs. 17 and 18 are shown the capture sites of all frogs in their second season or older which were captured four or more times, at least once within 48 hours after a nocturnal rain at a distance of 50 m or more from their usual areas of residence. It is assumed that these frogs migrated during the rain. For the 14 whose post-rain capture was in an area normally unsuitable for frogs, such as the ridge or in some adjacent fields, this is a reasonable conclusion; for those taken in permanently wet regions there is some doubt as to when they moved there.

Of the 30 animals shown (8% of the 391 adults and subadults taken four or more times), 25 definitely returned to their former region following the rain, or were moving towards it, indicating not only a strong attachment to their home ranges, but the ability to relocate their former areas after leaving them. Only five did not show this pattern of

Figure 17

Capture sites of all adults captured four or more times, at least one of them within 48 hours after a nocturnal rain and at a distance of 50 m or more from the home range. All were males except 589. Large circles indicate post-rain captures in an area permanently suitable for Leopard Frogs (as determined by their normal presence); large dots indicate post-rain captures in an area not permanently suitable; small circles indicate first capture. Dates of captures are listed in order below:

431: Aug. 5-10-18-25 (1960) - July 22-Aug. 1-3-20-Sept. 16 (1961) - June 22-July 21 (1962)
589: July 17 (1961) - May 21-June 22-28-July 5-24 (1962)
619: July 22-24-Aug. 1-3-5-7-22-23-Sept. 16 (1961)
645: July 30-Aug. 1-7-23 (1961) - July 10-20 (1962)
672: Aug. 14-16 (1961) - June 12-28 (1962)
699: Aug. 23 (1961) - May 21-June 22-July 12-27 (1962)
814: May 21-July 5-12-Aug. 3 (1962)
1231: June 15-16-25-July 9-18-22-26 (1962)
1354: July 8-14-21-25 (1961)
1449: July 14-18-19-21-31-Aug. 2-21-22 (1961) - June 12-27-July 8 (1962)
1452: Aug. 1-16-22 (1961) - May 21-June 28 (1962)
1939: Aug. 4-5 (1961) - June 12-14-26-July 23-Aug. 10-19-29 (1962)
2032: Aug. 11 (1961) - June 10-16-July 2-9-26-Aug. 10-11 (1962)
2624: July 15 (1961) - June 27-July 4-21-Aug. 26 (1962)
2671: April 27-June 12-25-July 26 (1962)
2830: June 23-24-26-Aug. 4-18 (1962)
2857: June 5-26-July 9-20-26 (1962)
2943: June 14-21-25-July 9-17-20-Aug. 18 (1962)
2992: June 21-27-July 12-13-Aug. 20-27 (1962)

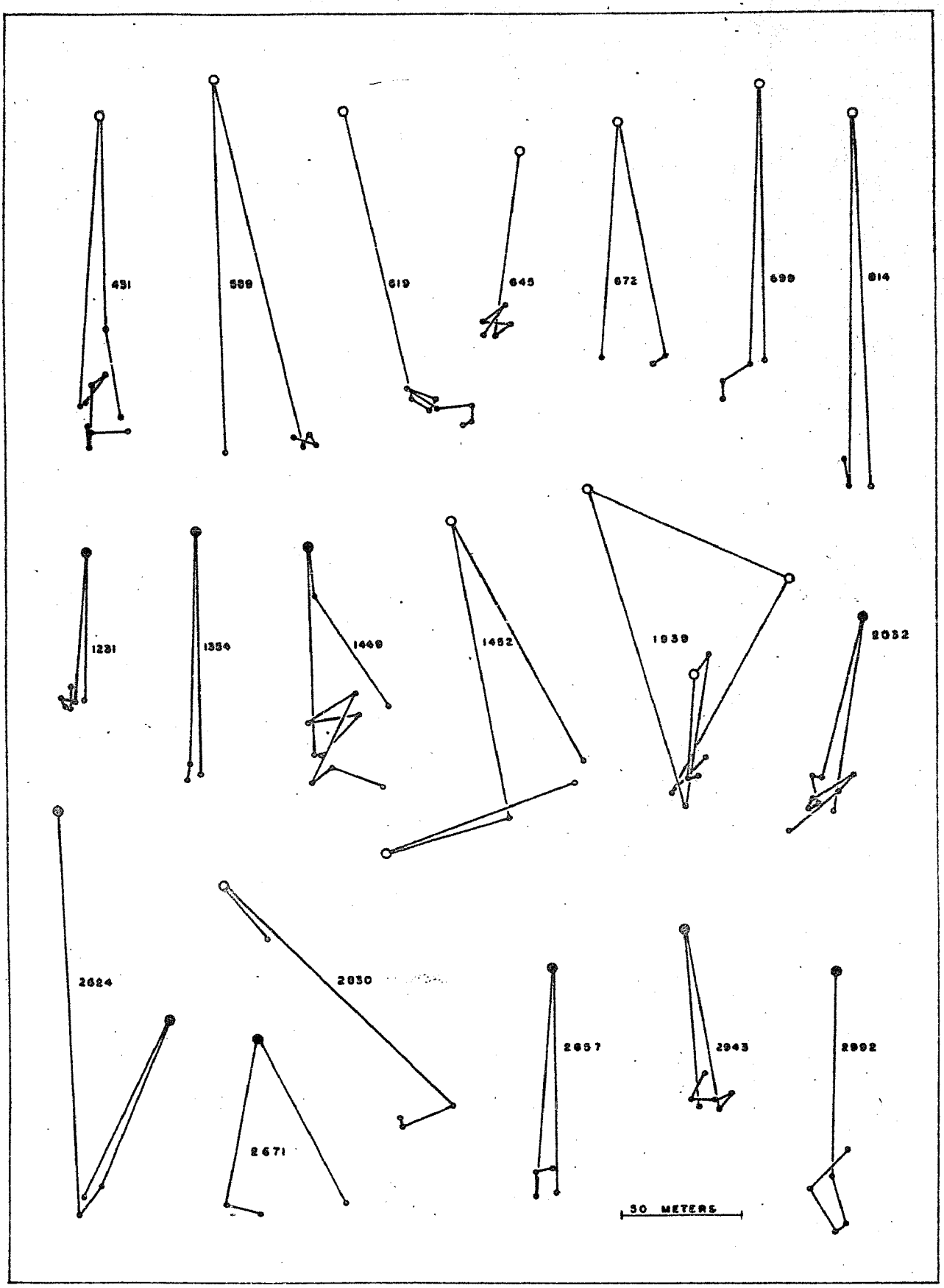

431
589
619
645
672
699
814
1231
1354
1449
1652
1939
2032
2624
2830
2671
2657
2943
2892
50 METERS

FIGURE 17

Figure 18

Capture sites of all second season frogs (sub-adults) captured four or more times, at least one of them within 48 hours after a nocturnal rain and at a distance of 50 m or more from the home range. Large circles indicate post-rain captures in an area permanently suitable for Leopard Frogs (as determined by their normal presence); large dots indicate post-rain captures in an area not permanently suitable; small circles indicate first capture. Dates of captures are listed in order below:

680: July 21-26-27-Aug. 2-8-11 (1961)

1298: July 4-5-10-14-20-21-29-Aug. 4-18-21-22 (1961)

1385: July 10-18-21-27-Aug. 10-13 (1961)

1472: July 18-26-27-Aug. 8-22 (1961)

1479: July 18-21-25-Aug. 2-7-8-11 (1961)

2750: June 30-July 7-20-Aug. 20 (1962)

2805: May 19-June 19-26-July 7-27 (1962)

2840: July 2-9-9-20-26-Aug. 10-12-14-18-20 (1962)

2854: June 25-30-July 3-7-18-27-Aug. 15 (1962)

2873: June 6-11-26-July 13-23-26-27 (1962)

2897: June 10-27-July 22-Aug. 17 (1962)

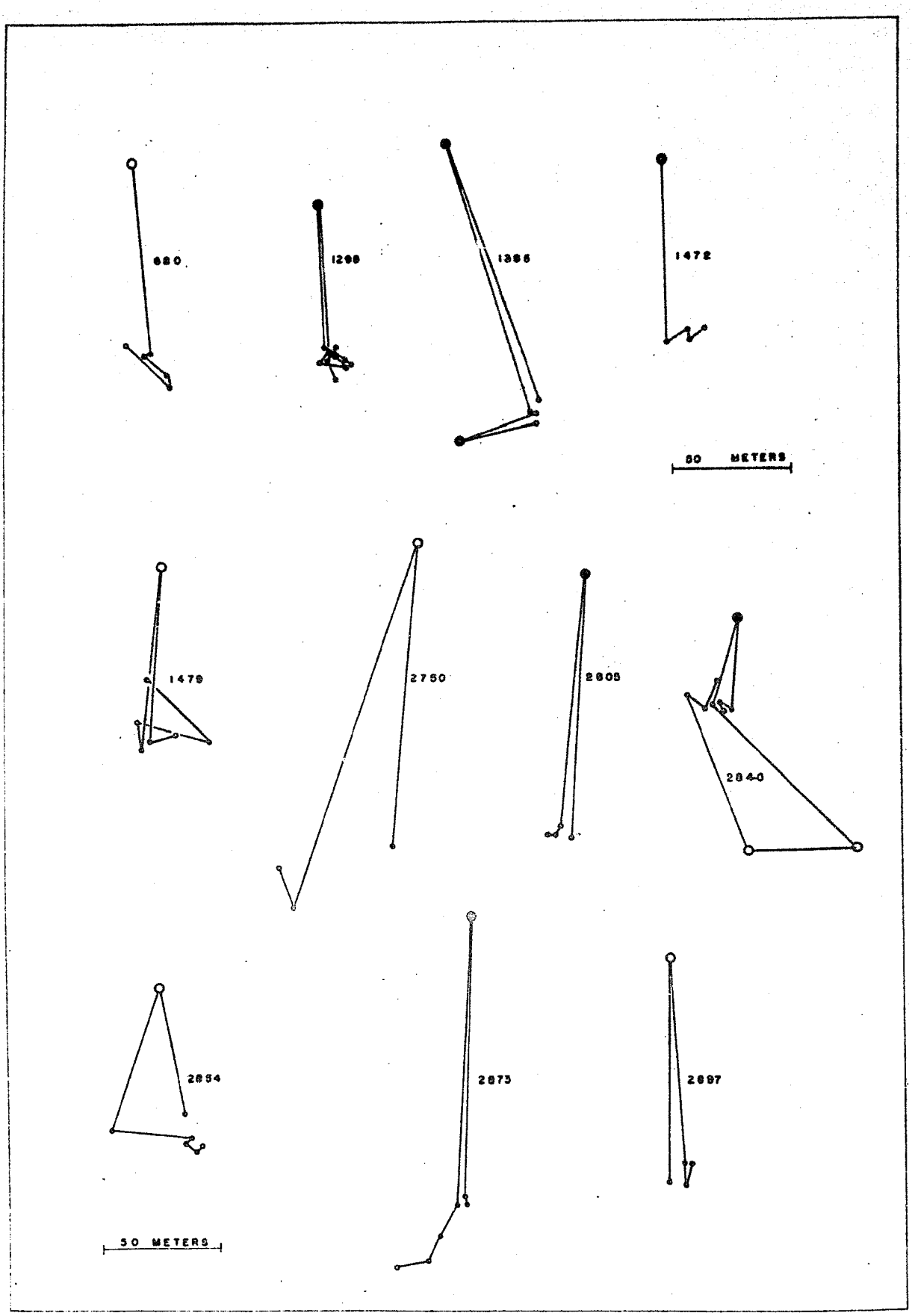

680
1298
1386
1472
50 METERS
1479
2750
2805
2840
2854
2873
2897
50 METERS

FIGURE 18

movement. One of these, adult 2992, was captured off his home range on the last census of 1962 so there was no opportunity to recapture him. Adult 619 was captured off his range on the last census of 1961 and may not have survived the winter or may have moved elsewhere in 1962. Adult 645 and subadult 680 were not found again though their ranges were searched at least twice following the rain. They may have remained in the areas to which they had moved though it is equally likely that they returned but escaped capture or were lost through death. Subadult 1472, on the other hand, was first captured following a rain and later was captured four times over a 26 day period in the study area. This animal may have just entered the region from elsewhere, thereby shifting its area of activity, or it may simply have escaped capture prior to July 18.

Fourteen of the migrating frogs were captured, following rains, in areas suitable for continued residence as indicated by the normal presence of Leopard Frogs. Eleven of these nevertheless later returned to their former areas and one had moved towards his previous home when last captured.

Five frogs were captured away from their usual regions following rains on more than one occasion. Adult 1939 and subadult 2840 apparently left their areas on three occasions while subadult 1385 and adult 1452 left theirs twice, yet all ultimately returned. Adult 2624 probably left his area twice also. The direction of travel varied each time for all of the animals which moved more than once, indicating that the direction of migration was at random.

Factors Influencing Migrations

During rainy nights trailed frogs were checked at intervals of approximately two or three hours; consequently it was not always possible to pinpoint the exact time at which an animal left its form and embarked on an excursion. Three, however, were known with certainty to have begun moving almost simultaneously with the onset of rain. Nine other excursions were known to have begun from 0.5 to 4.0 hours after it began. The remaining nine could have begun either before or after the rain started; none were definitely known to have started prior to it. Because excursions occurred only with rain and 12 of 21 (57%) were definitely known to have begun either simultaneously with, or sometime after, the onset of rain, it is probable that rain itself was the environmental factor initiating such behavior.

The proportion of frogs carrying trailers which left their home ranges during rains showed a significant positive correlation with the duration of nocturnal rain ($r = .896$ with 14 df; $P < .01$). As was indicated previously, not all became active immediately at the onset of the rain; some did not begin to emigrate for as long as four hours after rain began while others did not move at all. There was, however, no significant correlation between the duration of the rain and the mean distance moved by the migrating frogs. Such a correlation would imply that movement continued only so long as the rain fell. Although two frogs did turn back at approximately the time the rain stopped, excursions once initiated

usually continued through the night even in the absence of further rainfall, and in four instances they did not begin until after the rain had stopped.

No significant correlation could be found between the per cent of trailed frogs which became active and either the amount or the intensity (amount/duration) of rain. Thus, a light sprinkle did not apparently differ significantly from a heavy downpour in stimulating frogs to activity. On five nights excursions occurred though less than 1 mm of rain fell.

It is unlikely that the increase in atmospheric moisture accompanying rains was important in initiating emigrations or in allowing them to occur, for the relative humidity in the grass on the study areas, even over dry soil, reached saturation every night during the three summers of study.

Neither the absolute level nor the relative change (amount of change/time) of atmospheric pressure showed a significant correlation with the per cent of trailed frogs which became active.

Intensity of light was an important factor affecting migratory behavior, for excursions from the home range occurred only at night. Diurnal rains of greater intensity and longer duration than many night rains failed to initiate such activity. In addition, movement of migrating frogs almost always stopped at daybreak and usually did not resume until nightfall if it resumed at all.

A positive correlation, significant at the 5% level ($r = .605$ with 14 df), was found between the minimum temperature

during each rainy night and the distance moved by emigrating frogs. During those nights with the highest minimum temperatures frogs tended to move farthest, while nights with lower temperatures showed much less activity. The lowest temperatures of the 14 rainy nights occurred on June 17 and 18 (14.5 and 13.5 C respectively); the lowest recorded for the other twelve was 16 C. Though in general rainy nights have higher minimum temperatures than non-rainy ones, seven rainless nights in the summer of 1962 had minimum temperatures above 16 C, yet no migrations occurred. It is not surprising that activity in a poikilothermic animal shows a relation to temperature, but high temperatures in the absence of rain did not initiate migrations.

Distance and Rate of Movement

The greatest distance moved during a single night was 160 m by a 79 mm female, which began moving sometime between 10 p.m. and 1 a.m. and stopped about 6 a.m. Giving the maximum time allowance of eight hours this represents a rate of 20 m/hour. This is undoubtedly well below her actual rate because she ran out of thread on one occasion and was unable to continue moving until her bobbin was replaced. A 79 mm male traveled a greater total distance during an excursion, but over a period of two nights. He moved 140 m between 1 a.m. and 6:30 a.m. the first night, representing a rate of 25.4 m/hour, and continued the second night moving an additional 100 m between 8 p.m. and 8 a.m. The maximum rate of movement for excursions 100 m or longer was attained by an

81 mm female, moving 140 m between 2 a.m. and 5 a.m., a rate of 46.6 m/hour. Undoubtedly the rates given do not represent the maximum abilities of Leopard Frogs, due in part to the fact that the exact times at which the animals started and stopped are not known. The presence of the trailer did not alter the mode of locomotion of the frogs, but the additional weight probably did shorten the animals' leaps, hence reducing their speed. No measures were made of the effect of the trailers on speed of movement.

One trailed frog was watched for a brief time in the process of migrating. Its leaps were about 20-30 cm long, each followed by a pause of approximately 15-30 seconds while the animal remained in an upright position. As the frog was followed for only three to four minutes it is not known whether longer stops were made, or if movement continued at the same more or less regular pace throughout the night. It is very possible that the lamp used to observe the animal, even though the beam was not directed at it, caused it to react differently than usual.

Effect of Migrations on Dispersion

The nocturnal migrations often had a marked, though temporary, effect on the dispersion of the population. In Fig. 19 are plotted capture sites of all frogs in their second season and older taken during a period of fair weather on August 10, 1962, when the entire pasture was carefully searched with the aid of ten people from the Vertebrate Natural History class at the University of Michigan Biological

Figure 19 Capture sites of all subadult and adult Rana pipiens taken in a census of Budzinski's pasture in fair weather, August 10, 1962. Dots, adult males; circles, adult females; crosses, subadults.

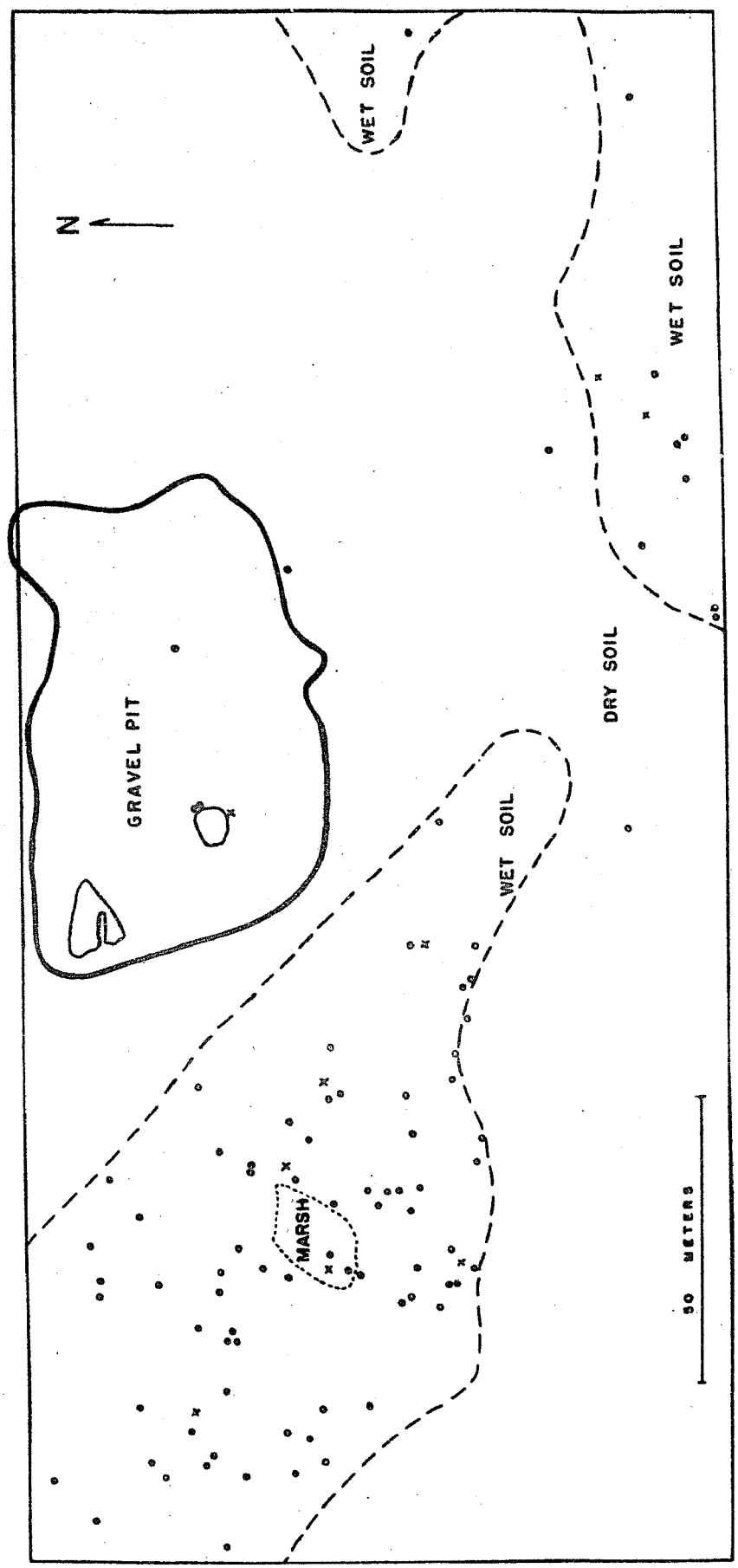

N
WET SOIL
WET SOIL
DRY SOIL
GRAVEL PIT
WET SOIL
MARSH
50 METERS
— — — LIMITS OF WET SOIL
——— STANDING WATER
---------- OUTLINE OF MARSH (NO STANDING WATER)

FIGURE 19

Station. On that day almost the entire population was confined to the low areas of the field where the soil remained permanently wet; this was the usual situation except after night rains. On July 20, during a rain (19 mm) which had continued intermittently since about 10 p.m. July 19, the entire pasture was censused by the same group. Although it was searched thoroughly, most of it being covered twice, only 41 subadult and adult frogs were found. Due to the extensive movement which had taken place during the previous night they were no longer confined to the low parts of the field but were scattered more or less at random, many of them on the normally uninhabitable ridge (Fig. 20).

Discussion

Though the fact that many species of frogs become hyperactive during rains has been reported in the literature by several workers, the nature of this activity is largely unknown, for previous studies of anuran behavior have had to depend almost entirely on recapture data and limited direct observation. In the present study, through the use of trailing devices, it was possible to obtain more complete information regarding activities at such times. The results indicate clearly that movement during rains is sometimes of a different nature than usual daily activity, for the frogs leave their home ranges and move in a direct route until daybreak, a marked contrast to the short, often winding movements from form to form on their home areas.

Figure 20 Capture sites of all subadult and adult Rana pipiens taken in a census of Budzinski's pasture on July 20, 1962, following a night with 19 mm rain. Dots, adult males; circles, adult females; crosses, subadults.

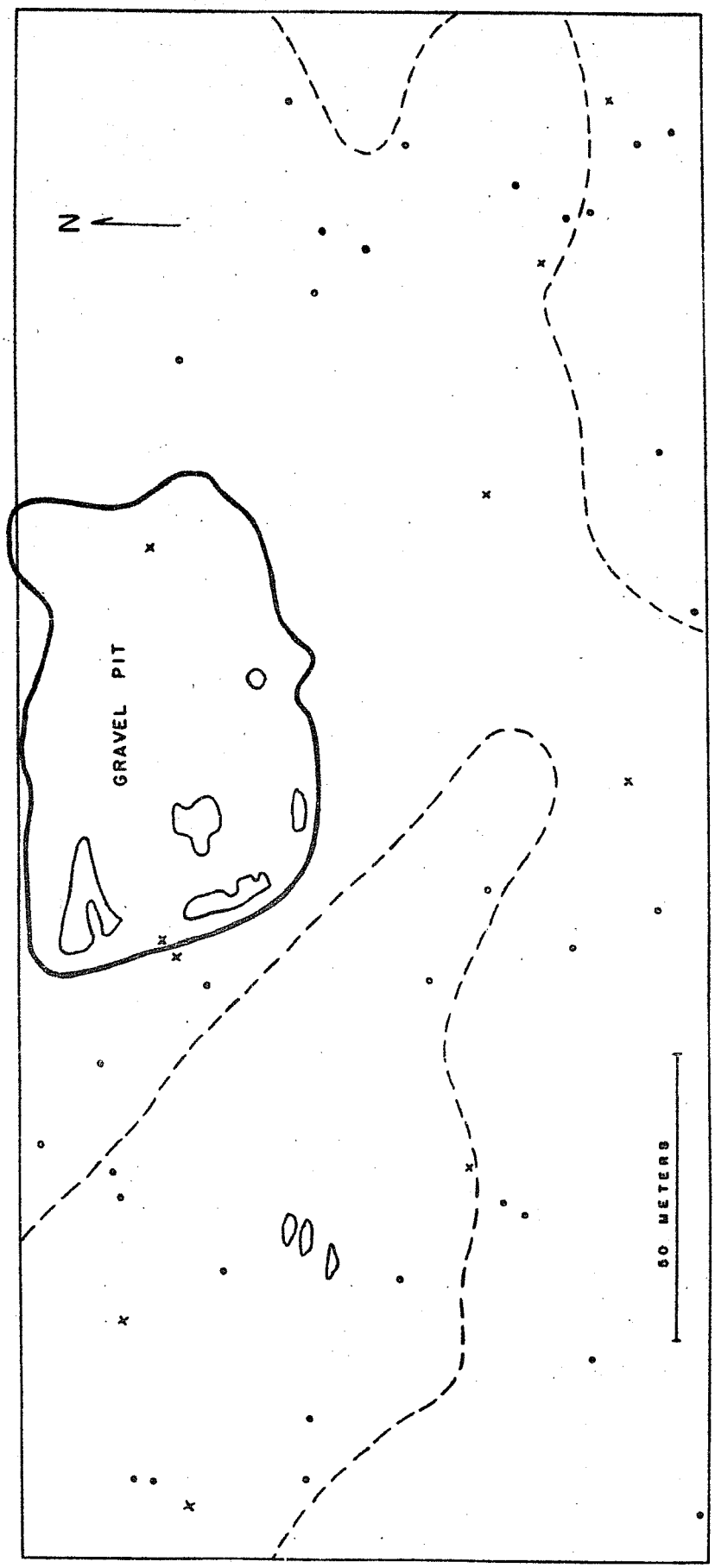

N
GRAVEL PIT
50 METERS
STANDING WATER
LIMITS OF PERMANENTLY WET SOIL

FIGURE 20

Evidence of excursions from their home ranges during rains, perhaps similar in nature to those shown by Rana pipiens, has been reported for three other species of anurans. Martof (1953b) found that Rana clamitans occurred in large numbers at greater than usual distances from their home ranges along stream banks on rainy nights. Rana nigromaculata, which during clear weather maintained small home ranges around a pond, was found to leave them during rains, moving several meters from the water (Kikuchi, 1958). Similar behavior has been reported for Acris crepitans, individuals being found to move as far as 200 feet from their usual pond-edge home ranges during rains (Pyburn, 1958).

Other animals, too, are known to make extended trips of unexplained nature from their home ranges, though not necessarily during rains. Cunningham (1960) reported brief excursions from the home range and return for Batrachoseps pacificus. Box turtles (Terrapene carolina), too, occasionally make extensive trips from their usual areas, sometimes following nearly the same path on successive occasions (Stickel, 1950). Species of Peromyscus have been reported to make migrations from their normal ranges (W. F. Blair, 1940; Storer, Evans, and Palmer, 1944; Stickel and Warbach, 1960) and Layne (1954) found occasional Tamiasciurus hudsonicus as far as 275 m from their usual areas.

No relation between the occasional nocturnal migrations and the bodily needs of the Leopard Frog was obvious; the function of the excursions was not readily apparent. They

apparently play little part in the dispersal of the species, for evidence indicates that most frogs, if not all, eventually return to their previous areas. Martof (1953b) suggested that in Rana clamitans the sallies from the home range enable frogs to learn their way around in the area and thus permit them to return more or less directly to their home sites. Similarly in Rana pipiens it is likely that the journeys increase the animals' acquaintance with a wider area.

Migrating Leopard Frogs do not always return directly to their former areas following a rain. Some may continue moving a second night if conditions are favorable. Though most frogs which stop migrating in regions which dry quickly following the rain retreat to more suitable areas in two or three days, some frogs which reach permanently wet soil may remain in these new localities for longer periods. Some, perhaps, are prevented from returning until another rain because of the drying of intervening regions which they must cross. It is also possible that, except when forced to retreat by unfavorable moisture conditions, Leopard Frogs do not normally return to their former areas except when it rains. In any case, frogs entering the study area from outlying areas during rains probably account for a large part of the transients which were captured once or twice in a short period and never seen again.

As all excursions of trailed frogs occurred on nights when rain fell, and as more than half of these began simultaneously with or sometime after the onset of rain, there can be little doubt that rain is at least a necessary climatic

condition for such movements. In all probability it is the stimulus initiating the excursions rather than one which simply allows them to take place. This is supported by the fact that in five rains of less than 1 mm excursions onto the dry ridge and outlying fields occurred, despite the fact that the small amount of rain had barely wetted these regions, so that they were scarcely more suitable for habitation than on most nights when there was a heavy dew. In addition, if migrations occur simply because the region surrounding the home range is habitable, at least temporarily, it is reasonable to expect that frogs would make excursions throughout the wet soil region on almost every night, for this area is suitable for continuous occupancy all summer. In fact, however, each Leopard Frog limited its activities to a small part of the habitable area, leaving it only during rains.

The behavior of 3523 (Fig. 16) deserves special note, for her movements differed in several respects from the usual pattern. Only one other frog, also a large female (81 mm), showed similar behavior, her trail closely resembling that of 3523 in all respects including the same destination. In fact, after moving into the woods, both entered the same cavity under a root, though not on the same occasion, and occupied the same region of the swamp. These two animals were probably not residents of the study area but of the woods. Several factors point to this conclusion: (1) Although the study area had been repeatedly searched for three months prior to their capture, neither had been captured;

(2) the movements of the two animals within the study area were not typical local movements but, in general, tended to take them almost directly across the region to the western limits of the wet soil; (3) in the first rain which fell after the frogs had been saddled both moved in a nearly direct line toward the southwest, the same direction which their trails across the study area had taken; (4) though each was disturbed several times to change the thread supply during its migration across the adjacent field, the disturbances causing deviations in their paths, both invariably reoriented themselves in their former direction of travel, indicating their journey was not in a random direction but directed toward a particular goal; (5) when arriving in the woods both adopted typical local movements, 3523 remaining in an area 20 x 30 m, through three subsequent rains, until released while the second frog remained in an area 15 x 20 m for 12 days until she died of injuries incurred when she became tangled in her thread. There is little doubt that the home ranges of these animals were in the woods. It is probable that their presence in the study area resulted from excursions during rains prior to their capture. After being saddled each apparently continued moving towards her home range but, due to the dry field intervening, was forced to stop at the western edge of the study area until a rain allowed her to continue home.

Water Relations

Perhaps the most essential requirement for terrestrial existence of organisms is the ability to avoid excessive loss of water. Amphibians as a group have not developed integumentary modifications to conserve body water as have the other terrestrial vertebrates, yet despite this failure to meet the problem of water conservation effectively some amphibians are essentially terrestrial, though usually confined to moist places. This is true of Rana pipiens, for during the summer adults occupy moist fields or wet woods, often continuously for several weeks at a time, rarely returning to ponds.

Though Rana pipiens has been shown by Thorson and Svihla (1943) and Thorson (1955) to be able to survive a loss of nearly 50% of its body water, it is unlikely that this tolerance alone is responsible for its ability to remain almost continually away from ponds. Since evaporation goes on continually from the surface of these animals, even in a saturated atmosphere, at rates nearly proportional to the relative humidity (Adolph, 1932), water loss from frogs living in the fields I studied must have occurred at fairly rapid rates, for the humidity in the grass regularly fell to 40-50% for 8-10 hours in each rainless day. With such continual loss, body moisture would surely have reached the lethal level in a few days if water had not been obtained from some source

to make up the loss. In addition to food, rain, dew and soil moisture are possible sources of water in a terrestrial environment.

There is little doubt that Leopard Frogs can and do utilize moisture from rains, obtained either by droplets falling directly on them, from brushing wet objects or from sitting on wet surfaces and in temporary puddles. They are not, however, dependent on the temporary wetting from rains, for during a 30-day period of drought, June 19 to July 19, 1962, in which only 8.3 mm of rain fell, Leopard Frogs with trailers showed no indication of leaving the fields for the ponds, faring quite well despite the lack of rainfall. While rains occurred at irregular intervals and did not provide a regularly dependable moisture supply, dew and moist soil were almost always regularly available, and seemed particularly likely to be important sources of water. Consequently the ability of Leopard Frogs to obtain water from these two sources and their importance in water economy were investigated briefly in the present study.

Use of Soil Moisture

To determine if frogs could obtain moisture from the soil, samples of earth were collected at four localities along the soil moisture gradient in the northwest section of Budzinski's pasture in August, 1962, following a week of rainless weather. These samples, one from the marsh which at the time contained no standing water, a second from a point midway between the marsh and the periphery of the

wet area, a third from 1 m inside the outer margin of the wet soil and a fourth from the dry ridge, were obtained by cutting rectangles of earth and placing the entire blocks intact into terraria. By removing the soil in one piece, including about the top 10 cm of earth, which would just fit the containers, the characteristics of the soil surface upon which the frogs sat were essentially unchanged. The water content of each sample, expressed as per cent of dry weight of the soil, were 375% in the soil from the marsh, 54% midway along the moisture gradient, 37% at the margin of the wet area and 2% on the ridge. Adult male frogs (59-74 mm) captured from various localities in the vicinity of The University of Michigan Biological Station were placed in an inch of water in enameled pans and forced to remain for 24 hours. Each was then gently dried with a soft towel and weighed to the nearest 0.1 g to determine its fully hydrated weight. The contents of the bladder were then forcibly expelled by pressing on the lower abdomen and the animals allowed to dehydrate slowly in an open container for another 24 hours, after which they were reweighed. The frogs were divided randomly into four groups of eight and each group placed into one of the four terraria and the containers covered with plate glass. Humidity in the three containers with moist soil was between 95-100%; a container of water, unavailable to the frogs, kept the humidity at the same level in the terrarium with the dry soil. No attempt was made to maintain a constant temperature but all terraria were kept under identical conditions so that

the temperature of all varied together. After sitting for 24 hours on the soil each frog was gently wiped with a soft towel to remove any clinging dirt and reweighed to determine if it had regained any of the weight lost during the dehydration period. As the handling of the animals in cleaning off the soil particles generally caused them to expell the contents of their bladder, weights obtained did not include the urine. Since no food was provided throughout the experiment and Leopard Frogs cannot obtain water from the atmosphere (Adolph, 1932) gains in weight can be attributed to the uptake of water from the soil.

All frogs on wet soil gained back at least a part of the weight lost during the dehydration period, but the amount of weight regained differed among the three groups. (Table 1). In 24 hours those on the wettest soil (375% soil moisture) regained a mean of 87.3% of the weight lost during dehydration; the frogs on the soil with 54% moisture regained 78.4%; those on the soil from the margin of the wet area (34% soil moisture) regained only 56.1% of their lost weight. All frogs placed on the dry soil from the ridge (2% soil moisture) continued to lose weight. It is evident that Leopard Frogs are able to extract moisture from wet soil, the rate of uptake increasing with the wetness of the substrate.

Because of the exclusion of the contents of the bladder from the weights of the rehydrated frogs the final weighings do not accurately represent the state of body moisture in the animals. Since the production of urine ceases during

Table 1

Changes in weights among partially dehydrated frogs placed on soil of various degrees of wetness

	Group I	Group II	Group III	Group IV
Moisture content of soil (% of dry weight)	375	54	37	2
Mean hydrated weight (grams)	26.87	25.05	26.97	25.39
Mean dehydrated weight (grams)	23.65	21.76	24.35	22.76
Mean weight after 24 hours on soil	26.46	24.34	25.82	22.43
Mean % of body weight lost during dehydration	11.9	13.1	9.7	10.4
Mean % of lost weight regained in 24 hours on soil	87.26	78.41	56.1	----

periods of dehydration and water is resorbed from the bladder (Nussbaum, 1878; Adolph, 1927; Steen, 1929) the presence of urine indicates that a frog is obtaining an adequate supply of water. Seven of the eight frogs rehydrated on the wettest soil produced a copious amount of urine as did six of those on the 54% soil. Only three rehydrated on the 36% soil urinated and each barely a trace. None on the dry soil urinated. Had it been possible to include the contents of their bladders in the final weighing the mean weights of the two groups on the wettest soil would have been considerably higher and the mean percentage of weight regained would probably have approached or surpassed 100%.

An indication of the wetness of the soil upon which Leopard Frogs can normally survive under natural conditions was obtained by taking surface soil samples in the latter part of June and early July, 1962, from the vicinity (15 cm or less) of 16 forms occupied by trailed frogs for periods of 24 hours or longer. The moisture percentages of these samples ranged from 25-65% with a mean of 47.1%. The least wet sample was taken from near a form which had been occupied by an 81 mm female (No. 2400, Fig. 12) for five consecutive hot, rainless days. The animal showed no signs of dehydration, indicating that she was able to maintain her water balance adequately under the prevailing conditions. As all frogs trailed were quite large (60 mm or more) no significant correlation between size and moisture content of the forms could be found.

Use of Dew

To determine the importance of dew in the water economy of Leopard Frogs, several animals were deprived of it and their behavior and ability to obtain sufficient moisture to survive compared with a comparable group living under more normal conditions. This was done in the following manner. In the northwest section of Budzinski's pasture where the soil was permanently moist and where Leopard Frogs were common, two enclosures 1.8 m square and 0.9 m high of 6.3 mm mesh hardware cloth were erected side by side. At the top of each, 6 cm of wire were bent inward at right angles so that frogs could not leap out; the bottom edges were sealed with earth to prevent escape via that route. Though small insects entered the enclosures through the wire and larger ones flew in through the open top, snakes large enough to harm the frogs were unable to enter the cages. The conditions within each enclosure were those normally encountered in the field; no ponds were included so that the only sources of water exclusive of food were rain, soil moisture and, in one cage, dew. Over one enclosure a sheet of thin, transparent vinyl plastic was erected on a wooden frame so that it stood 0.6 m above the top of the wire cage. This effectively prevented dew from forming in the enclosure below, yet permitted light to pass through. Daily checks of temperature and relative humidity revealed no differences between the two cages. Measurements of light intensity on a bright sunny afternoon gave readings of 4160 and 4240 ft candles for the

covered and uncovered cages respectively, a difference of slightly less than 2%.

On July 28 ten adult male Leopard Frogs (60-76 mm) were placed in each enclosure and allowed to remain until August 29. At that time, all 20 frogs were in good health, and no differences could be detected between those which had been deprived of dew for 33 days and those which had not. It is obvious that dew was not a necessary source of moisture though it may have been an important supplement. Several pieces of evidence indicate that it was, in fact, utilized by Leopard Frogs when available. These will be discussed below.

For a period of seven days, beginning the morning of July 30, each of the 20 caged frogs was weighed twice daily, morning and evening, and the mean weight of the frogs in each cage determined for each weighing. As it was necessary to capture the animals with a net and they often urinated upon being removed from it, the weights did not include the contents of the bladder. Attempts after each weighing to force the frogs to further expel urine were unsuccessful, indicating that all had empty bladders when weighed. Records were kept of the occurrence of urination before weighing, and estimates of quantity (trace, average, copious) were noted. The mean weights at each weighing of the frogs in the two cages are shown in Fig. 21, plotted as a percentage of the mean of all weighings of all frogs in the group.

The groups of frogs with and without dew both showed fairly regular fluctuations in weight, the mean weight of

Figure 21 Mean weights of frogs in "dew" and "dew-less" cages each morning and evening plotted as percentage of the mean of all weighings of each group. Dots indicate mean weights of 10 frogs with access to dew; circles indicate mean weights of 10 frogs without access to dew.

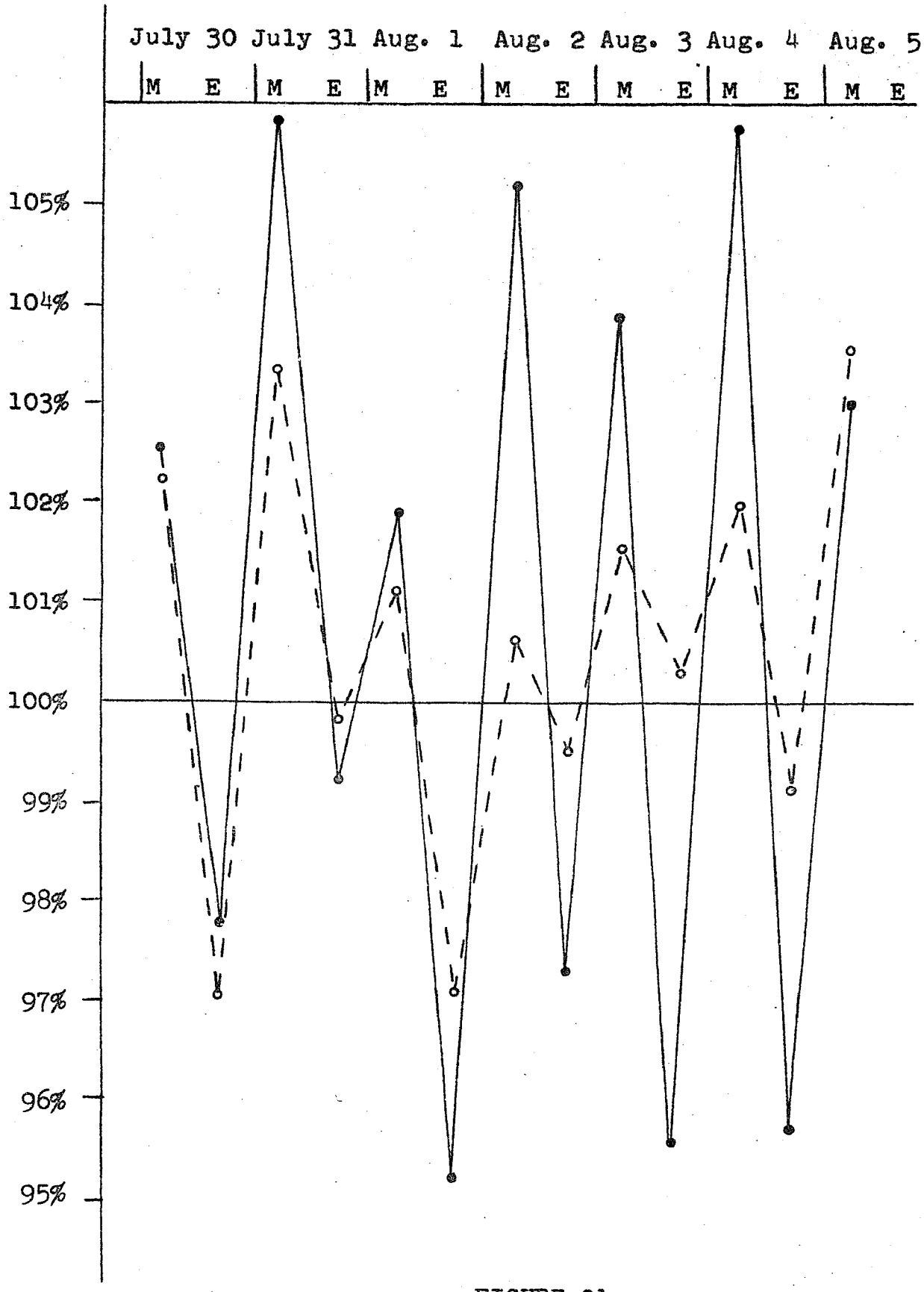

July 30
July 31
Aug. 1
Aug. 2
Aug. 3
Aug. 4
Aug. 5
M E M E M E M E M E M E M E
105%
104%
103%
102%
101%
100%
99%
98%
97%
96%
95%

FIGURE 21

both groups being greatest in the morning and least in the evening. Part of the change in weight was undoubtedly due to intake of food, for the animals were free to eat, but, as feeding occurred at any time of the day or night whenever the opportunity presented itself (Kilby, 1945), the regular fluctuation of the group as a whole was most likely the result of the uptake and loss of water. This is supported by the fact that in the morning the bodies of frogs were always sleek and glistening with moisture and they commonly urinated when handled, whereas in the evening their skin usually appeared dry and urination occurred only occasionally (Table 2). Thus, frogs in the field undergo a net loss of water during the daytime, the amount lost by evaporation exceeding uptake from the soil, but at night, when uptake exceeds loss, they are able to replace the water lost during the preceeding day. In this way they are able to survive in regions where moisture conditions are not always favorable, so long as their body water does not fall below the critical level before they are able to make up the loss.

Daily fluctuation in weight, however, was considerably greater among the frogs with access to dew than among those without it. Since the mean weights of the two groups were very close (28.9 and 30.4 g) it is unlikely that the difference was due to more rapid gain or loss of water associated with size. Though the reason for this difference is not readily apparent, records of urination indicate that, in general, the frogs with dew possessed an abundance of body

Table 2

The number of times frogs in cages with and without dew urinated when handled in morning and evening.

	Morning		Evening	
	Dew Cage	Dewless Cage	Dew Cage	Dewless Cage
No urine or a trace	8	29	56	60
Urine average or copious	62	41	4	0

water more commonly than did those without dew. In Table 2 the number of times frogs in each group expelled urine when handled is shown, those which expelled only a bare trace being grouped with those which produced none, as both probably indicate a lack of a surplus of body water. Urination rarely occurred in the evening; only four frogs, all in the dew cage, produced more than a trace of urine. In the mornings, however, frogs in both enclosures commonly had urine in their bladders, but those in the dew cage urinated more than a trace significantly more often than did those without access to dew ($\chi^2 = 14.6$ with 1 df; $P < .001$). Since in Leopard Frogs urine secretion stops and the bladder contents are resorbed when moisture is available in insufficient quantities to offset that lost (Nussbaum, 1878; Adolph, 1927; Steen, 1929) the difference between the groups may indicate that frogs with access to dew had an excess of body water more commonly than those in the dewless cage. Thus, the greater degree of fluctuation in weight among the frogs in the dew cage was probably the result of more rapid uptake of water during the night, presumably because absorption of moisture from dew is more rapid than from soil, and a greater loss of water during the day, probably because of more frequent urination.

The locations of the frogs within the two enclosures before the dew had dissipated in the morning provide additional evidence that it may have been regularly utilized as a source of moisture. Before disturbing the animals for

their morning weighings, a visual check was made of each cage and the positions of all frogs seen were noted. In the dew cage, frogs were found 26 times sitting beside their forms on top of mats of dead grass, moist with dew. In the dewless cage frogs were seen out of their forms only eight times. Though not all frogs were seen each morning, some being out of sight among the dense grass, those not observed were most likely sitting in forms, as this was the usual behavior; frogs on top of the grass were readily visible, so probably few were missed. Assuming that those not seen were in their forms, the proportion of frogs found on top of vegetation in the morning was significantly greater among the frogs in the dew cage than among those in the dewless one ($\chi^2 = 11.22$ with 1 df; $P < .001$). Thus, it appears that when dew is available Leopard Frogs often leave their forms during the night and sit on top of the wet vegetation, presumably to absorb the dew through the groin.

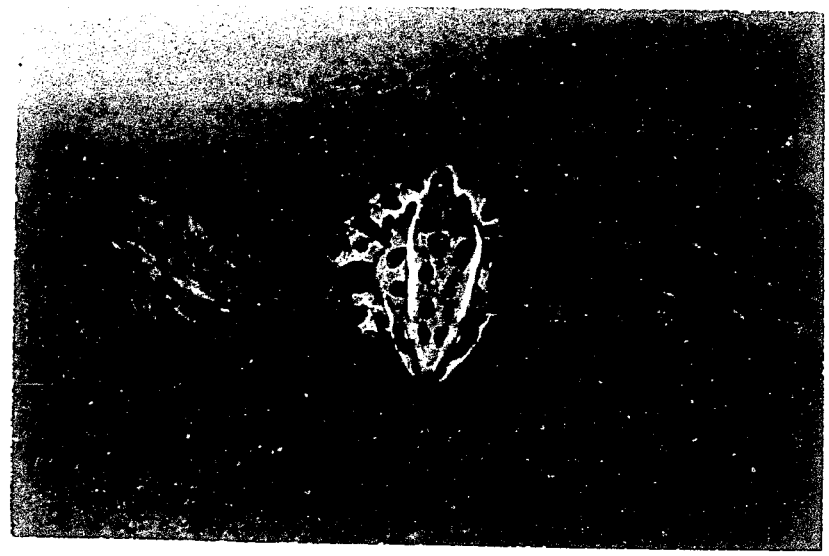
Six frogs fitted with trailing devices also are known to have left their forms during the night to sit on dew-covered vegetation, retreating to the wet soil again after the dew dissipated. A male which occupied a form in Budzinski's pasture for six consecutive days was found each morning at 8 a.m. sitting 8 cm away in a shallow depression on a mat of dead grass, wet from dew. By 10 a.m. each day he had returned to his form. Since the dew disappeared each morning between 8 and 9 a.m. it is likely that the retreat to wet soil was associated with the drying of the dew. Each evening at

7-8 p.m. the frog was still in his form, but he moved to the grassy site again sometime before morning. Of the five other frogs which similarly moved between forms and mats of dead vegetation, one alternated daily between two such sites 20 cm apart for a five day period, two shifted regularly less than 10 cm for three days, and two moved similar distances for two day periods. It is very probable that many of the other frogs which shifted from one form to another during the night also stopped on the dew covered grass.

Burying Behavior

Another behavior pattern undoubtedly related to the maintenance of water balance was noted among three adult Rana pipiens kept in a terrarium in a laboratory. The animals were placed in the container November 16, 1961, on wet soil containing water equal to 50% dry weight of the soil and the terrarium covered with loose fitting plate glass. The frogs had no access to moisture except from the soil which was allowed to dry gradually; they were not fed. For 17 days the three frogs simply sat on the wet substrate, occasionally moving about the chamber. On the eighteenth day, when the moisture content of the soil had reached 25.4%, one was found sitting in a hole 2.5 cm deep, just fitted to its body, which it had dug during the night (Fig. 22). On the nineteenth day the animal was nearly completely buried, only its head and part of its back visible. In addition, a second frog had begun digging a similar hole and was sitting in it. On the 21st day the remaining frog, too, had constructed a

Figure 22 (Top) Three Rana pipiens in terrarium occupying shallow holes which they dug as soil gradually dried. (Bottom) One of above frogs almost completely buried. Animal is facing lower right corner.



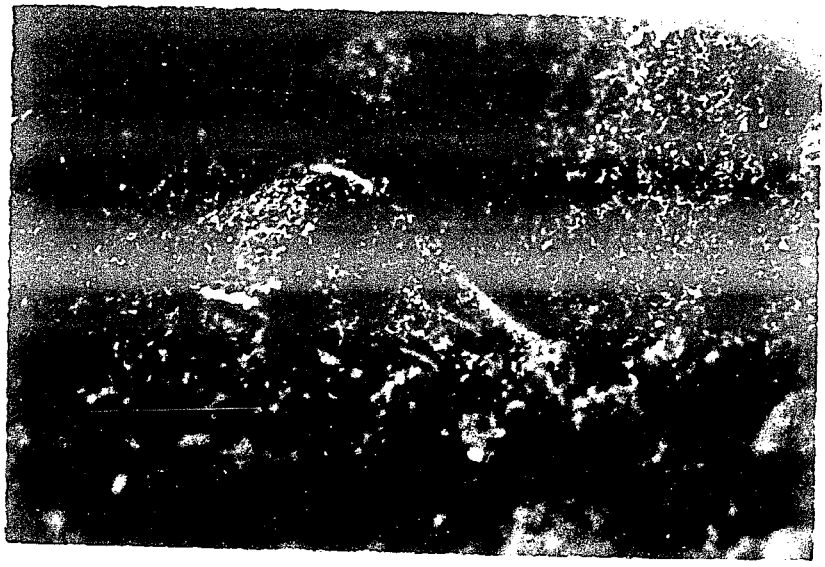


FIGURE 22

hole in the soil and was occupying it. At this time all three frogs, plump when first placed in the terrarium, were noticeably dehydrated, their skin surface dry, and none expelled urine when handled; soil moisture was 20.7%. All three remained in their holes until the twenty-fifth day when the soil was wet down; within 24 hours all had regained their normal appearance, body rotund, skin glistening with moisture and all urinated when handled.

Undoubtedly the burying reaction was brought about by a reduction in body water. Surrounding themselves with soil would tend to reduce the rate of water loss and in nature such behavior might possibly bring them into contact with moist soil below the surface. It is doubtful that such behavior is common among Leopard Frogs in their natural environment, for they probably usually return to ponds when unable to obtain sufficient moisture from the soil or dew. On one occasion, however, an adult male was found at Sedge Point buried in loose dry sand with only the tip of its snout protruding above the surface. Why it buried itself is not clear, for it was less than 10 m from the lake.

Movement to Ponds

Although adults of Rana pipiens were generally quite independent of ponds as a source of water in the summer, a few were apparently unable to maintain a favorable water balance under prevailing conditions by usual means and were forced to move to ponds. On the night of July 8, 1962, such activity was strikingly evident, for six of the 10 frogs with

trailers moved directly to water. This unusual behavior was undoubtedly caused by strong winds which blew all night causing the evaporation of 1.4 cc of water from evaporimeters in the grass, the only measurable amount of water loss from these instruments during any night in the summer. Though no other such mass movements to water occurred, six other frogs moved toward the ponds on different days, probably also prompted by an inability to maintain a favorable water balance in their usual manner (Fig. 23). Two of these moved in daylight.

Discussion

Because of their independence of standing water during the summer and their ability to absorb water from the ground, there can be little doubt of the importance of soil moisture in maintaining water balance in Leopard Frogs. The typical behavior of clearing the dead vegetation and debris from the soil, creating a form, is no doubt brought about by the need to remain in close contact with the wet soil beneath, thus allowing continued absorption. Probably many of the shifts from one form to another result from a need to find more favorable conditions as the soil in one spot becomes unfavorable for maintaining an adequate water supply.

Despite the fact that the ability to obtain moisture from soil may have been an important factor in the invasion of terrestrial habitats by amphibians, its importance has been largely overlooked. Except for Stille (1952), who found that Bufo woodhousii fowleri regularly frequented wet beaches where they sat and absorbed moisture through the groin, no

Figure 23 Routes of 12 trailed frogs moving to water. Solid lines indicate six frogs which returned to ponds on windy night of July 8, 1962. Dashed lines indicate six which returned at other times. Two trails from east side of field were made in daylight: A was found dead of dehydration at the end of the thread at next check less than four hours later; B escaped upon reaching end of thread and was found later the same afternoon in pond in the gravel pit; dotted portion of line is hypothetical route after escaping.

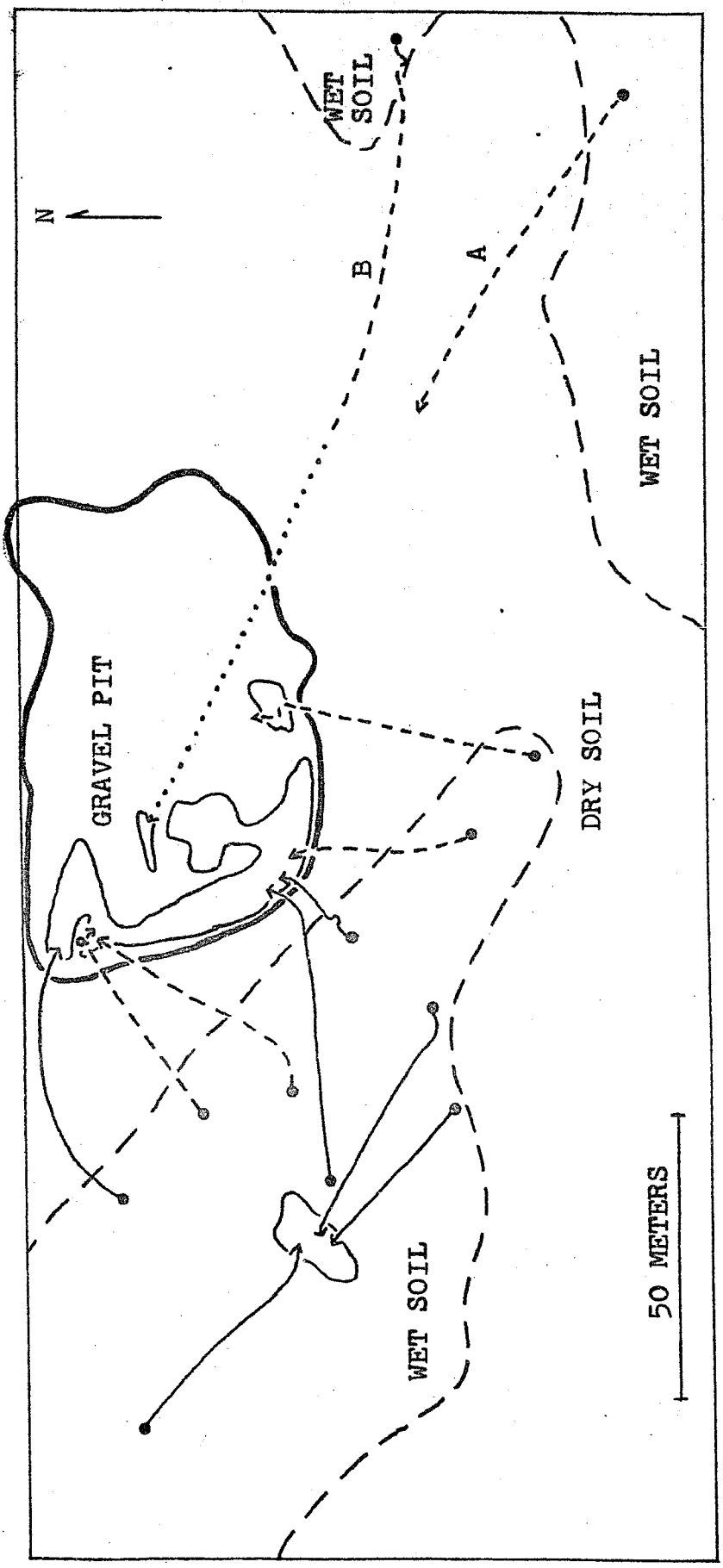

N
WET SOIL
B
A
WET SOIL
GRAVEL PIT
DRY SOIL
WET SOIL
50 METERS
— — — LIMIT OF WET SOIL
——— STANDING WATER

FIGURE 23

one has demonstrated the use of this source of water by anurans under natural conditions. Stille (1958), also showed that several species of frogs, among them Rana pipiens, could absorb moisture from a wet substrate (sand, sponge, cloth, glass, plant leaves, stone). The utilization of soil moisture may be more common than is generally realized and, if differences in this ability are found between various species, may in part account for the diverse habitats occupied.

Behavior of adult Leopard Frogs indicates that, when available, dew is also used as a source of water. As with soil moisture, absorption of dew apparently takes place largely or entirely through the skin of the groin, the animals sitting on dew-covered surfaces much as they would in forms. Stille (1958) in his laboratory observations of frogs observed a "wiping behavior" whereby the animals sitting on moist substrates such as plant leaves continually shifted positions over the surface, thus removing much of the moisture. Such behavior was not seen in this study but may well have occurred among the frogs found sitting on dew-covered mats of dead grass.

The directness of the trails of the frogs when forced to return to ponds indicates that the animals either knew where water was or were able to detect it from a distance. Since adult frogs occupied ponds during the spring (see later section) and many, perhaps all, made occasional excursions from their home ranges, it is not unlikely that they were indeed familiar with the area and knew the whereabouts of

ponds from former experience. Evidence was obtained, however, that newly metamorphosed young were also able to move directly to water (see section on dispersal). Since these animals could not have learned the location of ponds from previous experience it is very probable that Leopard Frogs can detect bodies of water from a distance. The clues which might be used in orienting to water warrant consideration.

The possibility that amphibians follow a gradient in atmospheric moisture in moving to water has been considered by several authors (Savage, 1961; Chapman and Chapman, 1958; Breder, Breder and Redmond, 1927; and others). That frogs can detect such changes is without doubt, but it is difficult to see how this would have enabled the frogs to locate water in the present situation. During the night in which six trailed frogs moved to water the relative humidity in the grass, even over the dry soil, was 100%. Under such conditions no gradient exists. In addition, two of the other frogs which returned toward water did so during daylight, moving from a wet corner of the field across the dry ridge where the relative humidity must have been less. It is obvious that they were not guided by a moisture gradient.

Sound could play no part for the frogs do not sing in the summer. Positive geotaxis was certainly not involved, for all frogs moving tc the gravel pit went uphill to reach it.

The possibility that vision plays a part in detection of water has been suggested by Muntz (1962a, b) who reported

that frogs show a strong affinity for blue light and respond differently to it than to other colors. In Rana pipiens he found that the optic nerve fibers passing to the diencephalon responded much more strongly to blue than any other color. Using Rana temporaria he found that the frogs jumped toward blue light significantly more often than toward any other color or combination of colors. He suggested that this response may play a part in guiding the movements of these animals towards water, which reflects blue light. This explanation was earlier put forth by Hooker (1911) to explain the biological significance of similar results in young Loggerhead Turtles, suggesting that they find their way to the sea by moving towards the blue light. However, since the ponds to which many of the frogs in this study moved were in the bottom of the gravel pit so that the animals could not have seen the water directly, it is difficult to see how they could have detected light reflecting from it.

Savage (1961) believed that Rana temporaria locates ponds in spring by moving toward the source of odors produced by algae in the pools. Pimentel (1960) reported that odors also guide the movements of the Rough-skinned Newt (Taricha torosa granulosa) to water and Twitty (1959) has shown that odor is of primary importance in guiding movements of Taricha rivularis. Martof (1962) found that Pseudacris triseriata tends to move toward odors from ponds, indicating that smells may guide the movements in that species. The possibility that Leopard Frogs, too, can find water by means of particular

smells associated with it can neither be proved nor disproved from data obtained in this study. However, the movements of trailed adults on the night of July 8, 1962, when six moved to ponds, were probably not guided by odors, for a strong wind blew from the west all night, yet four of the six frogs moved downwind; odors from the ponds to which they moved would not have reached these frogs. These animals most likely were familiar with the region and knew the location of the ponds. This does not, however, rule out the possibility that Leopard Frogs can detect water by smell. Perhaps those not familiar with an area are guided to water in this manner.

Emergence From Hibernation and Spring Activity

With the approach of spring, Leopard Frogs leave their hibernating quarters for the breeding ponds. Those which hibernated in these ponds presumably remain until breeding is completed, but others, which hibernated in ponds or streams unsuitable for breeding or in terrestrial situations move to the breeding sites. Though no effort was made to study activity in the spring so thoroughly as in the summer, three thorough searches of each study area on April 26-29, May 5-7 and May 19-21, 1962, provided considerable information concerning spring activity. The dates of emergence and the beginning of breeding are not known exactly but approximate dates were determined from changes in behavior and egg development, and from information furnished by residents of the area.

Time of Breeding

A chorus of frogs, probably including Rana pipiens, was first heard at Budzinski's by local residents on the evening of April 20. Air temperatures, which had reached 14 C during the afternoon, fell to -2 by midnight, causing a cessation of singing. The following evening chorusing was resumed, but only for two to three hours despite a rain which began falling about 10 p.m. No calling was heard on April 22 or 23, due to the low temperature (1-10 C) but it resumed on the night of the 24th when air temperature reached nearly 21 C.

On the evening of April 26, the first time I visited the area, mating activity of Rana pipiens was in progress as evident from the vociferous calling of males, the capture of four pairs in amplexus, and the fact that three of five single females taken had not spawned. On the following day a thorough search of the ponds revealed 74 egg masses in the marsh, 40 of these in an area of less than 1 sq m, and nine in the gravel pit. Fifty-seven of the 74 were in cleavage stages and none of the others had developed beyond the yolk plug stage, indicating they had all been deposited within the preceding 48-60 hours, as the water temperature varied from 14.5-18 C (Rugh, 1961). On the evening of April 27 only three males were calling between 7 and 10 p.m. and no other breeding activity was seen despite the mild temperature (14.5 C at 10 p.m.) and rain in early morning hours. On April 28 and 29 temperatures did not rise above 6.5 and 5.5 C respectively; no calling was heard or other mating activity seen. When Budzinski's was visited again on May 5 three egg masses were in the process of hatching and the rest were in late stages of development. None was found which had been laid in the previous week. Thus, it appears that oviposition was completed in the three-day period preceding April 27.

It is not known when calling first started at Sedge Point, but presumably frogs emerged at about the same time as those at Budzinski's, or possibly a few days later as Sedge Point was more exposed to the wind off Douglas Lake and was usually somewhat cooler. When first visited on the morning of

April 28 four pair were found in amplexus, probably having paired the preceding night, but no other breeding activity was seen. There was no calling. Though 55 egg bunches were found, all in pre-blastula stages, breeding was obviously not completed, for of 19 females captured 15 had not spawned. During the cool weather from April 28 to May 3 (maximum daytime temperature = 8, 5.5, 15.5, 9, 9, 16.5 C respectively) apparently very little egg laying occurred, for on May 6, 54 egg bunches were in early cleavage stages, indicating oviposition in the two days of relatively warm weather since May 3, while all but two of the rest were hatching or in late stages of development, indicating deposition at least a week previous. Only two bunches were found which were probably laid in the intervening week of cool weather, both in the tail bud stage. Thus, it appears that Sedge Point breeding was interrupted by a four- to five-day period of cool weather. Occasional calling males could still be heard on May 7, but as only one female (spent) was captured between May 5 and 7, oviposition had probably terminated.

Spring Emergence and Migration

An eight hour search (8 a.m. - 1 p.m., 7 - 10 p.m.) of Budzinski's entire pasture on April 27 revealed 37 adults (28 males, nine females); no immatures were found. On May 5, when the pasture was searched between 9 a.m. and 4 p.m., however, along with 27 adult males and 20 females, 20 immature frogs, young of the previous year, were captured in the shallowest parts of the two ponds (Fig. 24). Surface

Figure 24 Locations of all frogs captured at Budzinski's on three spring censuses in 1962 (April 27, May 5, May 19). Dots, adult males; circles, adult females; crosses, second season young. Arrows indicate direction of movement of five migrating frogs. Note small puddles in southeast part of field and frogs near them.

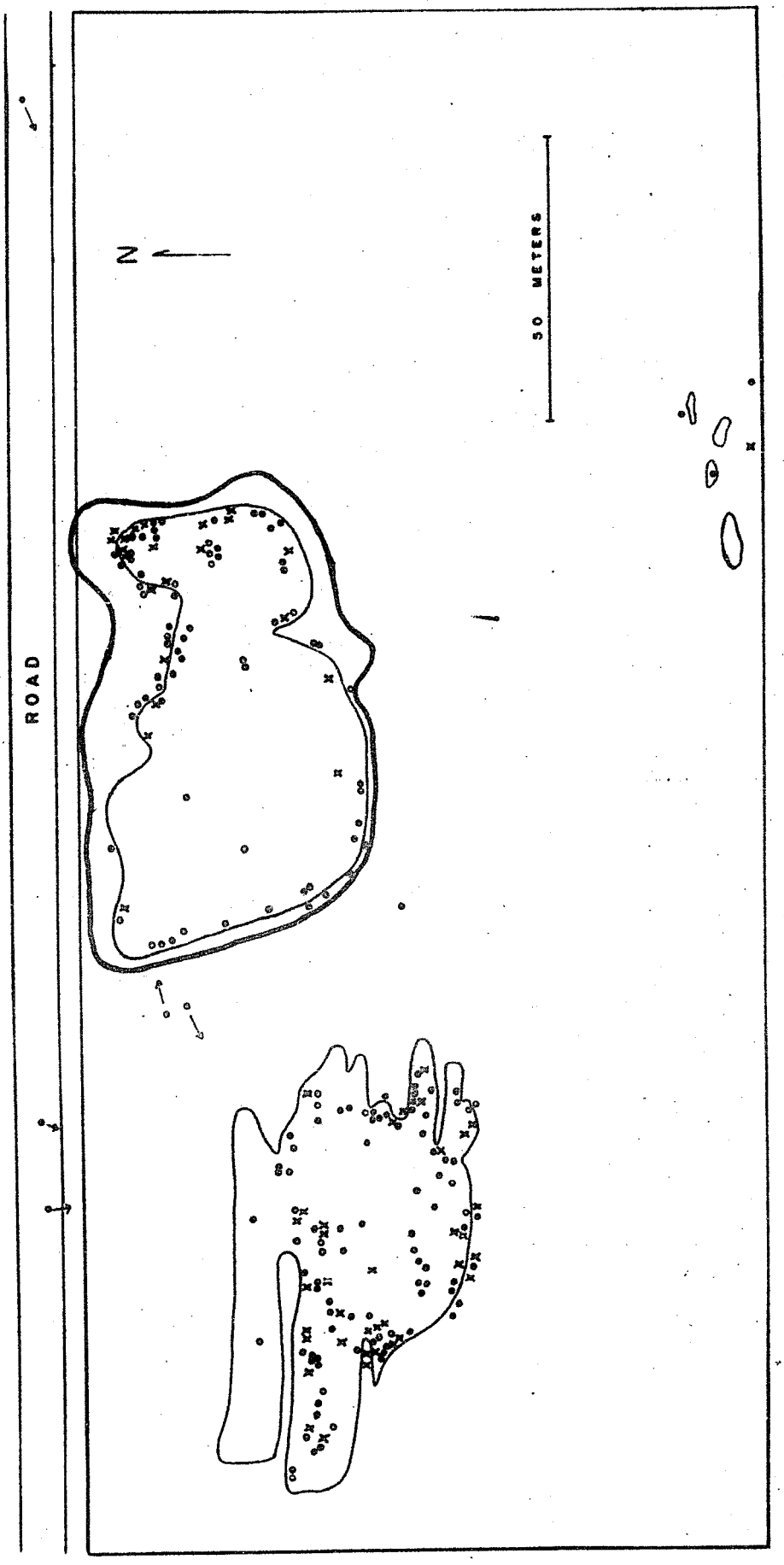


FIGURE 24

temperatures at the east end of the gravel pit where the immature frogs were congregated were 2 and 2.5 C. warmer than at the deeper west end on May 5 and 19 respectively, perhaps indicating an affinity for the warmer water. At Sedge Point no young were found since none metamorphosed in 1961, and all 1960 young had reached adult size.

Though most migration to the ponds probably occurred before my first visit to the study area, three adult males were taken on the evening of April 27 moving across a dry gravel road toward Budzinski's marsh and gravel pit from which loud choruses (Rana pipiens, Hyla crucifer, Bufo terrestris, Pseudacris triseriata) were emanating (Fig. 24). Two had not been captured previously and were never seen again, but the third had been netted on August 4, 1961, near the marsh and was captured three more times in the summer of 1962 in the same area in which it had first been found a year previous. It is likely that he had hibernated elsewhere and was returning to the marsh to breed.

Dispersion of Population in Spring

The capture sites of all frogs collected in the three spring censuses are also shown in Fig. 24. Though the entire field was searched on each occasion only 10 frogs (4% of 231 taken in April and May), three of them migrating to the marsh, and two moving between marsh and gravel pit, were found more than two meters from the two ponds. One of the frogs not captured in the larger bodies of water was sitting in a small puddle and three others in the same area were less than 10 m

from other puddles. Similarly at Sedge Point, frogs were confined almost entirely to bodies of water during the spring except when migrating. This distribution is in marked contrast to that later in the summer when most adult Leopard Frogs occupied the fields (Fig. 19).

Spring Movements

Of 231 frogs captured at Budzinski's prior to June, only one, a male, was taken in all three censuses, on April 27 at the north edge of the marsh pond and again on May 5 and 19 in the southeast corner, 40 and 45 m from the first site. Of nine males taken in two spring censuses, six were captured both times in the same pond, having moved a mean distance of 37 m (range, 15-52 m) in the intervening period. The three others had moved 50, 70 and 120 m from the gravel pit to the marsh. Four of the eight females taken twice on the April and May censuses were in the same pool on the second capture, having moved a mean of 25 m (range, 10-52 m); three others had moved from the gravel pit to the marsh (50, 80 and 95 m) while a fourth had moved 100 m from marsh to gravel pit between 10 a.m. May 19 and 9 a.m. May 20. Of these eight, four had spawned before their first capture on May 5 and one before it was first taken May 19; two were gravid when first taken on April 27 but were spent on May 5 and May 19; one was gravid on May 5 but spent on May 19. All four which shifted to a new pond were spent on their second capture. Six immature frogs taken on May 5 and again on May 19 were recaptured in the pool where first found, having moved a mean of 19 m (range,

5-55 m) in the intervening 14 days.

Of the 88 adults taken during the spring at Sedge Point, only three, all males, were captured twice, One was found the second time in the same pond, 18 m from its previous site; a second had moved from the west to the east pool (65 m); the third had moved from the east pond into the swamp (160 m).

At Sedge Point there was a general exodus from the breeding ponds following breeding in 1962, for the number of captures in the study area declined from 45 on April 28 to only four on May 21, though each of the searches was comparable in time and thoroughness. In an attempt to locate the missing frogs, the swamp north of the pool area was searched on May 7 and May 21. None was found on the first date, when only an hour was spent in the southern half of the swamp; on May 21, however, a four-hour search among the dense brushy vegetation of the swamp's northeast corner, its farthest point from the beach pools, revealed 49 adults sitting on islets of moss and leaves. Twenty-three (seven females, 16 males) were netted while 26 escaped capture. Only one male was found in the more open part of the swamp which had been searched briefly on May 7 where no islands upon which the animals could rest were found. No calling, mating activity, egg masses, tadpoles or other evidence that the Leopard Frogs had mated in the swamp was found. All females taken were spent.

At Budzinski's, exodus from the breeding ponds and return was not so noticeable though the movements of seven frogs between the marsh and gravel pit indicate that all frogs did

not remain in a single pond. Also indicative is the fact that of 47 adults taken on May 5 only three (6.3%) had also been captured in the census one week earlier when 37 had been caught. By contrast, of 76 adults found on May 19, 17 (22.3%) were recaptures from the preceding census two weeks before. Inasmuch as during the summer approximately 25% of the frogs taken in a census are recaptured in the next (see section on methods) the population appears to have remained fairly stable between May 5 and 19; the 22.3% recapture does not differ significantly from the expected 25%. The low percentage of recapture on May 5 may indicate a turnover in the population members, due to a large proportion of the frogs present on April 27 leaving the area, and immigration into the area from other ponds in the week following. It is likely that the rains (48 mm on three nights) between the first and second censuses stimulated migratory activity both at Sedge Point and Budzinski's. In the next two weeks no rains fell at night, probably accounting for the stable population in this period.

Discussion

The appearance of adult Leopard Frogs in the spring prior to the smaller ones has been previously reported by Cummins (1920). This contrasts with the situation found by Martof (1956) for Rana clamitans, in which the smallest frogs preceded the adults out of hibernation. Martof suggested that the larger amount of surface area per unit volume of the smaller frogs permits them to warm faster than the larger

ones, accounting for their earlier appearance in the spring. It is likely that, at least in Rana pipiens, other factors than rate of warming are involved. Perhaps, due to hormonal differences associated with sexual development, adults, which breed very shortly after emergence from hibernation, have a different temperature threshhold, becoming active at lower temperatures than smaller frogs. Rana clamitans, on the other hand, breeds much later in the spring and summer, the later development of physiological changes associated with breeding perhaps accounting for the later emergence of the adults. It is not likely that the small Rana pipiens were simply missed in the first census, for both marsh and gravel pit were searched thoroughly twice on April 27.

Because Leopard Frogs are residents of fields during summer, their almost total confinement to the vicinity of ponds in the spring is of interest. Among the adults the affinity for bodies of water is undoubtedly related, at least in part, to mating behavior, for they normally lay their eggs in shallow quiet water, usually with flooded vegetation, remaining in, or moving to, the ponds for breeding. Sexual behavior is probably controlled largely by hormonal changes, which may continue to influence the animals' behavior for some time after breeding has occurred, for the changes in hormonal concentrations are undoubtedly gradual, extending perhaps over several days or weeks. The fact that males still called occasionally at Budzinski's on May 20, more than two weeks after breeding had terminated,

attests to this gradual decline, though these may have been unmated males in which hormonal changes were more extended.

The affinity of immature frogs for water during the spring cannot be tied so readily to hormonal changes. It is likely that other factors are involved in keeping the frogs, immatures and adults, in the vicinity of water during the spring. One possible explanation is suggested by the finding of Donaldson and Schoemaker (1900) that Rana virescens (= Rana pipiens) collected from Minnesota and Illinois in May and placed in tanks containing stones surrounded by shallow water lost weight rapidly, as much as 18% of their body weight in 12 days, presumably due to water loss. Frogs of the same size captured in summer and fall and placed in the tank under the same conditions either gained weight, or lost only small amounts (1-2.6% in 12 days). They concluded that the large and progressive loss observed in May is a peculiarity of spring frogs. The cause of the weight loss was not determined but it may be in some way related to the changes in physiology occurring in connection with breeding, or simply to the change from torpidity to activity. If frogs in nature lose water more rapidly in the spring than summer, and the findings are not simply a result of a greater temperature change from field to laboratory in the spring (temperatures were not given in their paper), this would explain the dependence of these animals on water during the few weeks after emergence.

Other possible explanations for the confinement of spring frogs to water are: (1) an intolerance to the extreme

temperature changes which occasionally occur in spring, the tendency to remain near ponds having perhaps evolved because of the quick refuge provided by water, a medium where changes are slower and less extreme than in air; (2) a greater availability of food around the water in the spring; or (3) the lack of cover in the fields. During the early part of May Budzinski's field was covered only with a mat of dead grass laid flat by the winter snows, presenting an almost uniform brown surface upon which frogs were surprisingly obvious. Vegetation samples taken over the field on May 19, when grass shoots had just begun to give the field an appearance of green, gave an average height of grass of 15 cm, and an average of 0.16 blades per sq cm, largely rolled up and providing very little cover. By June 5, at which time the adult frogs were occupying the fields, the average height of grass was 40 cm with 0.35 unrolled blades per sq cm providing considerable concealment for the frogs.

Despite the attachment to water in the spring, considerable movement between ponds occurred, probably stimulated by nocturnal rains. This was strikingly evident at Sedge Point where the decline in population size resulting from the exodus of the post-breeding frogs was conspicuous. Here no frogs moved into the area to take the place of those which left, for there were no other large populations of Leopard Frogs within at least 1.5 km. At Budzinski's there was also apparently a general exodus immediately following breeding, but it was not so obvious, as immigration from nearby ponds tended to mask any diminution of the population.

This spring turnover appears to have involved largely, or entirely, post-breeding animals, for none of the females which moved to another pond during the spring was gravid when captured the second time. It was not possible to know if the males had mated but as no calling or mating activity was noted in the swamp at Sedge Point and oviposition apparently terminated in both areas by early May, all frogs probably had completed breeding activity before leaving the ponds. If only frogs which had already mated were involved, the movement contributed nothing to genetic exchanges between populations, at least for that year.

Although the migration of frogs to the breeding ponds from their winter hibernacula was not observed by me, such movements of Rana pipiens have been reported in the literature. Cummins (1920) trapped adult Leopard Frogs moving in the spring to a breeding pond from outlying areas; he trapped 37 females and 21 males between March 26 and April 1, the greater number of females perhaps indicating that they more commonly hibernate away from the breeding ponds than do males. Ballou (1887) described mass movements of frogs, probably Rana pipiens, from hibernation sites at the bottom of a river to prairie sloughs where they bred.

Shift From Spring to Summer Habitat

In late spring and early summer Leopard Frogs abandoned the ponds and moved to their home ranges in outlying areas. Neither the nature of the initial exodus from the ponds nor the exact time at which the shift began is known for 1962 (the only year in which the frogs were extensively studied in the spring) because the study areas were not visited between May 21, at which time frogs were still confined to water, and June 4, when they were found throughout the grass.

Movements at Budzinski's

Evidence gathered after June 4 indicates that the shift was not accomplished by all frogs in one great movement in the spring; rather, individual frogs moved to their home ranges over a period of several weeks in late May, June, and early July. Of 68 frogs captured at Budzinski's between June 5 and 17, and again in July or August or both, 24 (35%) were not yet occupying, on the earlier date, the regions in which they spent the latter part of the summer. Of the 24, 15 were still in ponds in early June, apparently having occupied them since emerging from hibernation in April, while nine were captured in the fields, but not in the areas occupied later, indicating that they were in the process of moving to their summer ranges. Twenty-three (52%) of the 44 frogs already on their home ranges in early June, had not moved to new localities, but occupied the same region

in summer that they had in spring. Nevertheless, all occupied the ponds in spring and the fields in summer. This was possible, because, as the water in the marsh receded, grass and sedges grew up where it had been, providing a grassland habitat for the frogs in those areas.

By contrast, only 10 (19%) of 53 frogs captured in late June (June 18-30), and again in July or August or both, were not in the regions which they occupied later in summer. Of these, five still remained in ponds; the other five were in the process of moving to their home ranges. Of the 10, eight were captured on their home ranges before July 9. One male was still in a pond on July 7 but was taken on his home range in the field 20 days later; a subadult remained in the marsh until after July 9 but had arrived on its home range by July 20. Both, of course, may have moved several days prior to being captured on their home ranges, for they were not trailed at this time.

Movements at Sedge Point

At Sedge Point the process of shifting between the ponds and home ranges in 1962 was complicated by the fact that almost the total population emigrated from the study area soon after breeding. The frogs gradually returned in June, as indicated by the increase in the number captured in the study area in each succeeding census (Table 3), and the fact that the number found in the swamp declined from six on June 9 to one on June 22 and none in four searches thereafter. In addition, four adult males and four females were trapped while moving

Table 3

Number of frogs captured in Sedge Point study area in consecutive censuses from April 27 to July 5, 1962. All censuses are comparable in area searched except for June 28 when only the area around the east beach pool was covered.

	No. of adult males captured	No. of adult females captured	Total	No. of hours spent searching
April 28	26	19	45	5
May 6	15	1	15	4
May 21	4	--	4	4
June 4	8	2	10	4
June 9	13	3	16	3.5
June 13	9	7	16	4
June 22	24	13	37	4.5
June 28	27	8	35	4
July 5	33	11	44	5

toward the ponds from the woods between June 7 and 30. None was trapped as they moved in the opposite direction. The return was not forced by a need for moisture, for the swamp contained water until July 7, yet they vacated the area several weeks before.

The mass exodus in May probably did not bring about the shift to the home range, at least for most frogs. In fact, nine (39%) of 23 frogs captured in the study area in April or May and again in July or August were occupying their home ranges when taken in the spring. This was possible largely because of the extensive flooding of the low areas in the spring which became grassland as the water receded, and the fact that over 90% of the resident frogs had home ranges immediately adjoining bodies of water. Thus, the spring exodus actually took many frogs off their home ranges.

Four males and two females found in the swamp on May 21 were captured later in the summer in the beach pool area. Two males had returned by June 5, two females and a male by June 22, and a male by June 28. All, of course, may have returned sooner. Three of these had been captured the preceding summer: two males returned to within 5 m of the sites of their 1961 captures; a female was captured 40 m from the location of her previous year's capture, but was not seen again.

It thus appears that the animals, after having made temporary excursions from the ponds subsequent to breeding, moved back to the regions where they habitually spent the

summer. Thus, the spring movement was not unlike the migrations from the home ranges which occurred during summer. It is possible that some frogs which had home ranges outside the study area shifted to them in the spring movement, but this is not known.

Detailed Movements

Two frogs trailed at Budzinski's in mid-June appeared to be in the process of moving from the breeding ponds to their home ranges. Their movements will be described in detail.

No. 2400, adult female, 81 mm (Fig. 25) -- When first captured on April 26, 1962, in the gravel pit pond this animal was being embraced by a male but had not yet spawned. On May 5 when recaptured in the same body of water 12 m from her first site, she was spent. Following a light rain which fell early in the morning of June 9 she was again captured, this time in the pasture about 20 m from the pit, presumably having left the water in the rain. Eight days later she was retaken in a field of blue-grass more than 150 m from the pit and across a gravel road from Budzinski's pasture. Fitted with a trailing device, her movements for the next four days are known. During the night of June 17 she moved about 20 m, perhaps stimulated by a 7 mm rain which fell in the early morning hours. On the night of June 18 she traveled 30mm

Figure 25 Sites of capture and trail of adult female 2400 (81 mm) as she moved from breeding site to home range in 1962. Solid line within gravel pit indicates water level on May 5, 1962. For details of trail between June 27 and July 12 see Figure 12. Dots on trail indicate forms; frog was moving at 8 p.m. June 20.

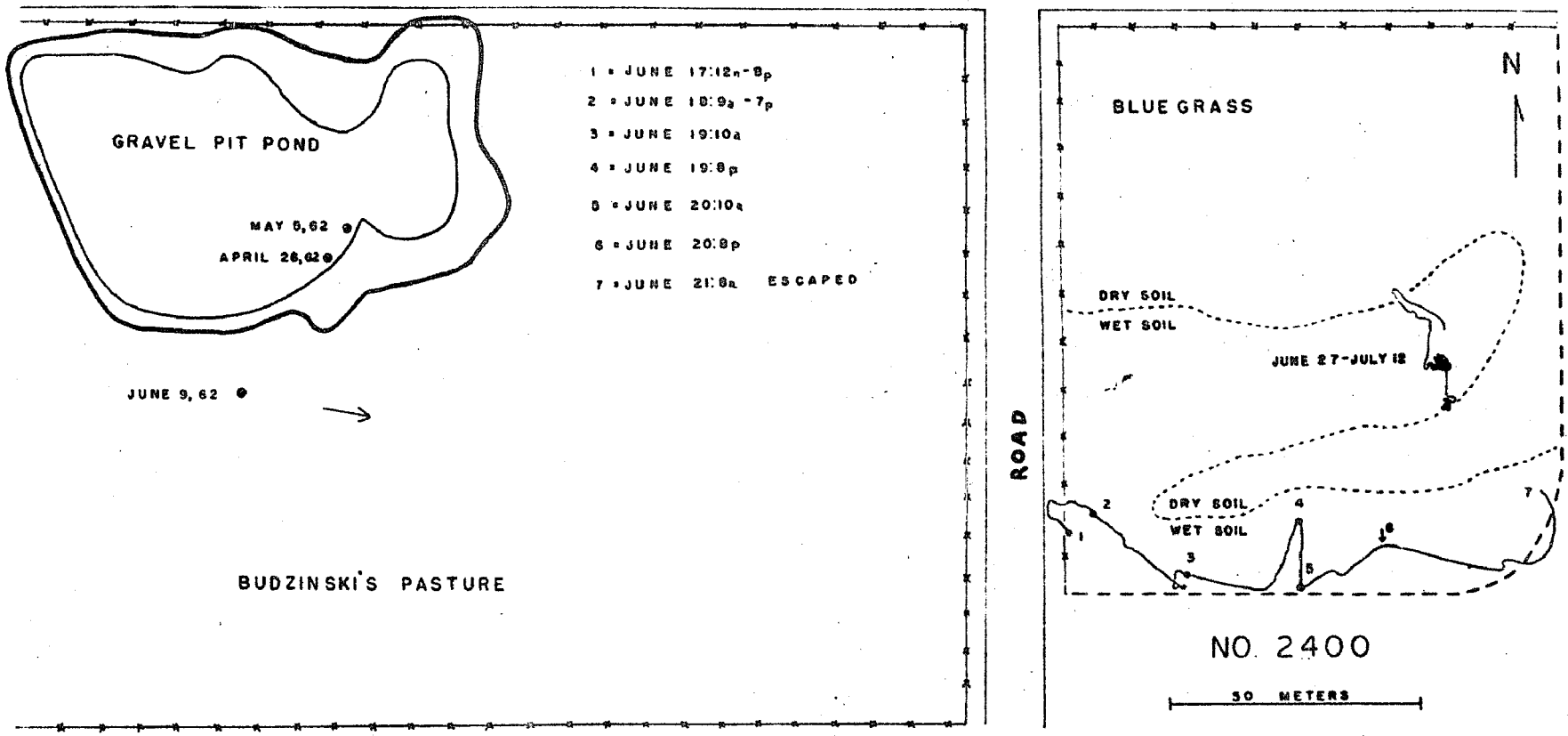

GRAVEL PIT POND
MAY 5,62
APRIL 26,62
JUNE 9, 62
1 = JUNE 17:12p - 8p
2 = JUNE 18:9a - 7p
3 = JUNE 19:10a
4 = JUNE 19:8p
5 = JUNE 20:10a
6 = JUNE 20:8p
7 = JUNE 21:8a ESCAPED
BUDZINSKI'S PASTURE
ROAD
BLUE GRASS
N
DRY SOIL
WET SOIL
JUNE 27-JULY 12
DRY SOIL
WET SOIL
1
2
3
4
5
6
7
NO. 2400
50 METERS

FIGURE 25

to the woods edge, possibly again stimulated by rain, a trace of which fell shortly after midnight. During the daylight hours of June 19 she moved 40 m more, this time into the field away from the forest, but the following night retreated again to the woods edge. Before 8 p.m. on June 20, without the accompaniment of rain, she again began moving; during the night she entered the edge of the woods but broke her thread and escaped. A thorough search of the woods and field within a 30-40 m radius of the end of the trail in the morning of June 21 did not reveal her, but on June 27 she was captured again in the field and trailed for 16 more days during which time she exhibited typical home range behavior (Fig. 12), moving back and forth in an area 20x30 m. On July 12 she was removed from the field before it was mowed for hay.

No. 2977, adult female, 85 mm (Fig. 26) -- First captured and saddled on June 17 in the same field as the previous frog, she, too, moved a short distance (15 m) into the grass during the light rain which fell in the early morning of June 18; at 9:30 a.m. she was sitting in a form on the wet soil. Within the next half hour, however, she left her place and began moving toward the woods, entering it at approximately 10 a.m. As she was not disturbed, her activity could not have been

Figure 26 Trail of adult female, 2977 (85 mm) in 1962 as she moved from breeding site to home range. Dots are forms or stopping places; arrows indicate animal actively moving or a forced halt.

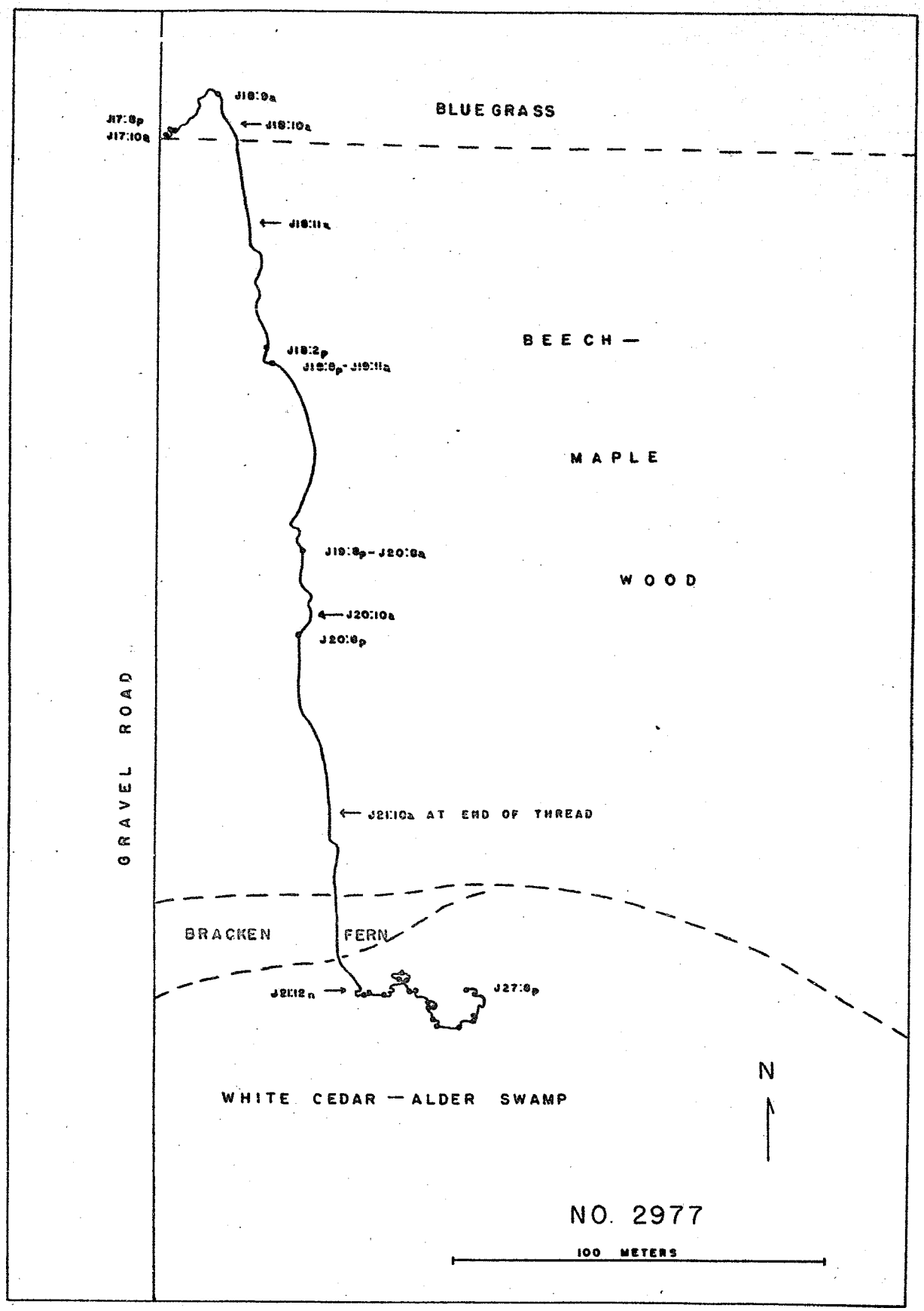

BLUE GRASS
BEECH —
MAPLE
WOOD
GRAVEL ROAD
BRACKEN FERN
WHITE CEDAR — ALDER SWAMP
J17:8p
J17:10a
J18:9a
J18:10a
J18:11a
J18:2p
J18:8p - J19:11a
J19:8p - J20:9a
J20:10a
J20:8p
J21:10a AT END OF THREAD
J21:12a
J27:8p
N
NO. 2977
100 METERS

FIGURE 26

caused by me. She continued moving through the woods until sometime before 2 p.m. when she was found sitting in a cavity under a log. By evening she had left this retreat and moved 8 m farther where she sat on top of the damp leaf litter all night, still sitting in the same place at 11 a.m. on June 19 even though a trace of rain fell during the night. The relatively cool weather (minimum temperature 12 C) may have inhibited her movement. During the following day she moved 45 m deeper into the woods, stopping again on the leaf litter for the night, but on the morning of June 20 moved about 15 m to where she was found sitting at 8 p.m. Sometime during the night or morning of June 21 she moved another 50 m to the end of her thread, where she was found at 10 a.m. After being supplied with a new bobbin she continued another 40 m during daylight, passing through an opening in the woods with a dense growth of bracken fern (Pteridium aquilinum) and moving into a Thuja-Alnus swamp where she sat for two hours or more in a small puddle, the only water left in the swamp though the soil was moist. For the next six days her trail showed typical local movements as she moved over a winding, twisting route, crawled into crevices, cavities under logs, a mouse burrow, and under leaf litter,

until on June 27 she crawled under a mat of dry leaf litter, apparently to reach the moist soil beneath. That evening she was found in the same spot, dead and badly dehydrated.

Discussion

As shown by recaptures, the shift from the spring habitat of the ponds to the home ranges in outlying areas took place in 1962 from late May to early July. Most of the shifting occurred before mid-June with only a few stragglers remaining in the ponds in late June and July. Due to the scarcity of rain in June, it is likely that the time of moving to the summer regions was more extended than is usual. Though shifts over short distances where the soil was moist could have been made without accompanying rain, it is unlikely that frogs often crossed the extensive dry areas of the field except during or immediately after precipitation. Perhaps in wetter years all frogs are on their home ranges by early June.

Although it is not possible to be absolutely certain of the age of Leopard Frogs after they reach sexual maturity, because of the large size (81 and 85 mm) of the two frogs trailed moving to their home ranges it is most probable that they were at least in their fourth season, possibly older. As evidence from recaptures shows that adult frogs generally reoccupy the same home range year after year (see next section), both were probably returning to previous years' ranges. Also, the directness of the trail of 2977,

and of 2400 as she neared her home range, indicates that these animals were not moving at random but toward particular places.

No. 2400 in moving to her home range did not follow a direct route, but rather her trail tended to show a zig-zag pattern, which may represent a "searching" for a particular area. It is equally probable that she was following a particular set of clues learned when she first established her home range in some previous year, and thus was obliged to follow the same indirect route and make the same false turns. No. 2977 may also have been following a previously learned pathway. Her trail, though undoubtedly more direct, probably does not show each small deviation in movement, for the ground vegetation in the forest upon which the thread could catch was sparse. Nevertheless trees, twigs, logs and the upturned edges of leaves tended to snag the thread and gave a reasonably close approximation of the travel route.

As each of these animals neared her home range, movements seemed to become more rapid, deliberate and direct. Had she not run out of thread, 2977 might have covered the last 100 m or more in only 3-4 hours. Certainly her trail over the last 100 m was remarkably straight even when she passed through a dense growth of bracken fern where there was ample vegetation for the thread to snag on. During the night of June 21, 2400 moved over 50 m and probably reached her home range, after breaking loose, a total distance of at least 90 m. The fact that she managed to break her

thread, taking the trailing device with her, indicates that she was intent on continuing her travel, for of all the frogs trailed, only two broke the strong nylon thread; all others which reached the end of their thread either escaped by crawling from the elastic band holding the trailing device on them or sat and waited until a new bobbin was supplied. The apparent "hurrying" as they approached their home ranges may have been the result of a need for moisture, for 2977, who was forced to sit in an unprotected site when she reached the end of her thread, was sitting in a puddle only two hours after receiving a new thread supply. It is also likely that as the animals neared their home ranges they were stimulated to more intense activity by a positive attraction to these familiar regions.

Movements of these two frogs differed in at least two aspects from summer migrations from the home range, discussed earlier. Though brief rains fell shortly after they were first fitted with trailing devices, their movements were not dependent upon precipitation, for each moved most of the distance in fair weather. In addition, both frogs moved in daylight, whereas summer migrations took place only at night, stopping at dawn. Perhaps the more subdued light in the forest was a factor allowing 2977 to remain active in daylight, but this could not have affected 2400 which was in an open field. The travel of these animals, particularly 2400, also differed from summer migrations from the home range in that movement was not continuous in one direction.

It thus appears that travel to the home range in early summer was dependent neither on rain nor darkness as were migrations of Leopard Frogs from their home ranges. Movement apparently occurred at any time, day or night, rain or shine, until the animals reached their home areas. It is unlikely, however, that frogs crossed large dry areas except in wet weather. Fitch (1956) reported that Gastrophryne olivacea also moved from the breeding ponds to their home ranges under considerably drier conditions than occurred in the migration to the pond which usually took place in downpours. He concluded that "probably the return travel is slower, more leisurely and with more tendency to keep to sheltered situations."

The cause of death of 2977 is not known; no evidence of injury, external or internal, could be found. The stomach, though not full, contained the remains of several insects, so starvation was not likely the cause. Her dehydrated condition suggests that death may have resulted from a lack of sufficient moisture. Since the importance of soil moisture to Leopard Frogs was not known at the time she was trailed, the moisture content of the soil upon which she was resting was not determined; in my notes the substrate beneath the frog was recorded as "scarcely damp." At the time of her death even the last two puddles in the swamp, in which she had previously sat, were gone. It is probable that her home range, which in former years had been much wetter, was not sufficiently moist in 1962, the result of insufficient rainfall, to permit her survival. Why she did not attempt to

return to a pond as others did is not known; the nearest body of water, however, was more than 400 m away. It is also possible that she died of "old age" since she was near the upper size limit of females (only 31 of more than 6000 frogs marked in the three years were larger than 85 mm).

Spatial Relations

Trailing records for periods as long as 25 days showed clearly that adult Leopard Frogs tended to remain in limited areas during the summer. Though some left for brief periods they showed a strong tendency to return, indicating an affinity for their home regions. Captures of second-season frogs showed that they, too, confined their normal daily activities to relatively small parts of the available habitat and returned to them after brief trips away. Most young-of-the-year, however, showed little tendency to remain in one region for long. In this chapter the spatial relations of frogs in their second season and beyond will be discussed. The distribution of young within the population will be considered briefly; a complete discussion of their movements is relegated to the sections on dispersal.

Home Range

Before pursuing the subject of limited activity areas it seems desireable to discuss briefly the choice of terms used in this paper.

As first proposed by Burt (1943) the term "home range" indicated "the area, usually around the home site, over which the animal normally travels in search of food," but excluding "occasional sallies outside the area, perhaps exploratory in nature." Carpenter (1952) introduced the term "activity range" to distinguish the region of activity of snakes, which

were not known to have a definite "home," from the concept of home range. He defined activity range as "the area covered by an animal in the course of its day to day existence," differing from a home range mainly "in the lack of a definite home site or other center of activity." Though Leopard Frogs have no nest, burrow or other "home" in the usual sense of the word, they often show strong tendencies to return again and again to particular parts of their areas, often to certain forms, which appear to have a special significance to them, and perhaps represent simple, rather temporary "homes." The forms also provided shelter, since their utilization reduced evaporation and, in a few cases at least, provided a certain amount of concealment, for frogs sometimes became partly covered with dead grass in the process of clearing their forms. For these reasons, home range seems a better descriptive term than activity range to apply to Rana pipiens and will be employed in this paper to refer to the limited region occupied by a Leopard Frog in the summer months.

Distribution of Ranges: It is difficult to distinguish on the basis of available data, between resident frogs and those which have entered the study area only temporarily, for sometimes transients are forced by unfavorable weather conditions to remain for several days or even weeks. In general, however, residents will be collected more times and over longer periods than transients so that the number of collections per individual, as well as the length of time over which collections were made, serve as an aid in

distinguishing resident frogs. For purposes of analysis a conservative practice was adopted; only those frogs captured in the study area at least three times over a period of 30 days or more within a single season were considered to reside there. The home ranges of these animals were determined by connecting the outside points of capture with straight lines and the resulting ranges for 1962 at Budzinski's plotted in Fig. 27; data from 1961 (not shown) are in substantial agreement in their distribution. Capture sites which probably were associated with brief absences from the usual area, such as captures in normally unsuitable areas or at more than 50 m from the other captures immediately following rains, were not included as part of the animals' home ranges.

Among the resident frogs the difference in the portion of the study area occupied by the two sexes of adults and the subadults is readily apparent from the figure. The subadult (second-season) frogs (mean length 40.0 - 50.3 mm) occupied the very wet regions close around the marsh and the gravel pit in the vicinity of ponds. Adult males, ranging in length from 63 to 77 mm, inhabited almost the entire moist area of the field, including the region utilized by subadults, but extending farther toward its periphery. Four also occupied the gravel pit, at least in part. The home ranges of females, by far the largest individuals in both bulk and length (68 - 85 mm long), were almost entirely confined to the peripheral areas of the permanently moist region; none was resident in the gravel pit. Thus, there is a general correlation between

Figure 27 Home ranges of all frogs resident in Budzinski's study area in summer of 1962. Heavy line indicates gravel pit; dashed line, region of field where soil remained moist all summer; dotted line, periphery of Carex-Eleocaris zone of marsh.

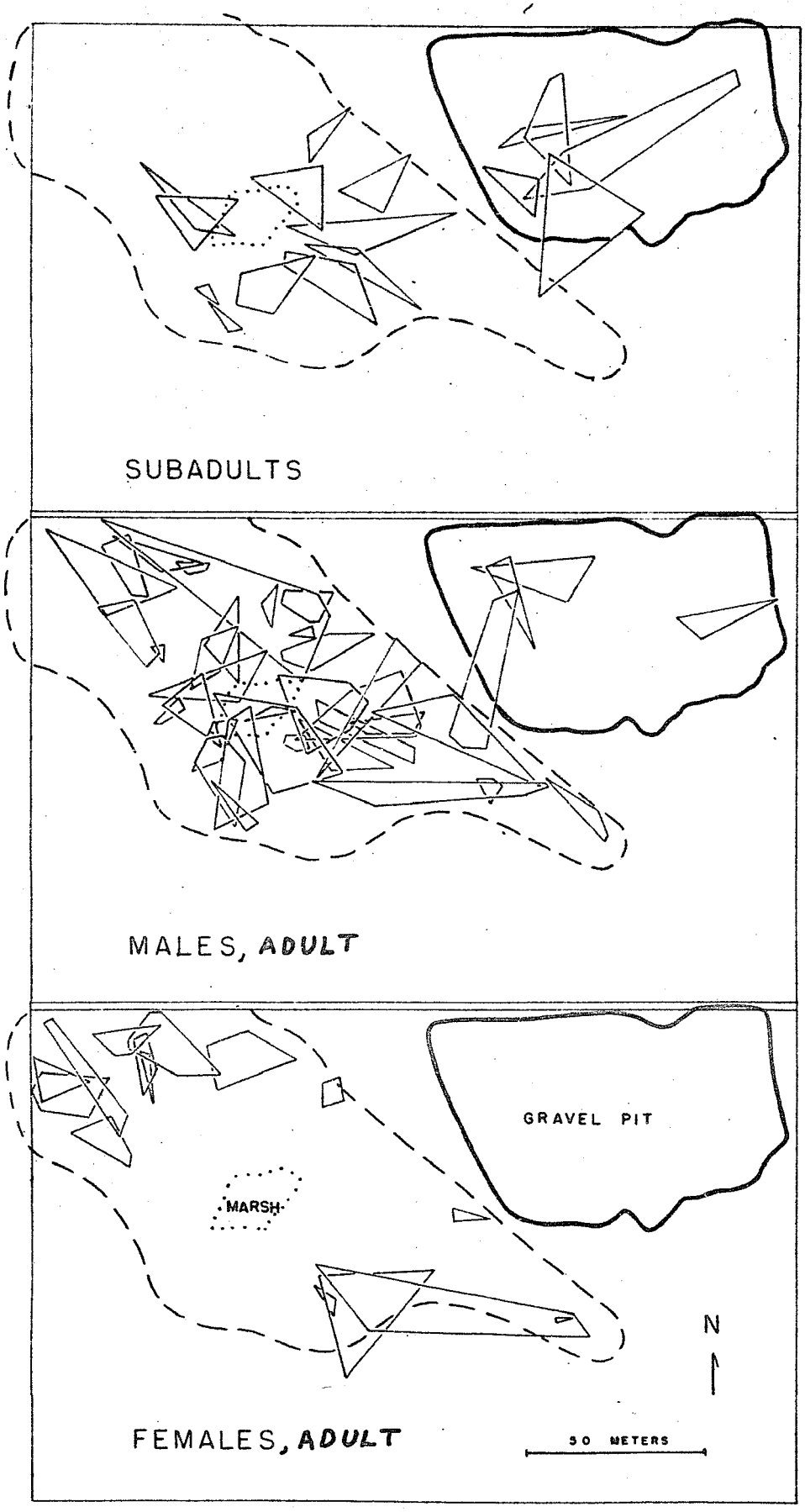

SUBADULTS
MALES, ADULT
GRAVEL PIT
MARSH
N
FEMALES, ADULT
50 METERS

FIGURE 27

the size of the frog and the wetness of the region occupied, the smallest individuals having home ranges in the wettest areas and the larger ones inhabiting the less wet regions. The water content of the soil, expressed as per cent of dry weight of the soil, ranged from 375% in the marsh to 37% 1 m inside the periphery of the moist region.

Permanence of home range: Since the regions occupied by subadult frogs and adult females were almost mutually exclusive at Budzinski's, it is reasonable to assume that as adults, females do not usually occupy the same home ranges which they used in their second season. The area occupied by adult males, on the other hand, coincided to a large extent with that utilized by subadults so that it would be possible for them to continue to occupy their subadult range as adults. Additional evidence that females, in general, utilize different home ranges in their second and third seasons, whereas males may or may not reoccupy the same range, is provided from an analysis of capture data as follows.

Of the four females captured at Budzinski's at least twice in their second season and again as mature adults, three had shifted to new home ranges in their third season. One moved 112 m from her subadult range in the gravel pit to a new one near the periphery of the moist region of the field; another left her second-season range near the marsh and moved 300 m to a new locale in a low wet area of an adjacent field; the third moved about 10 m from near the marsh to the eastern edge of the moist area. The fourth, although reoccupying her

subadult range in her third season, enlarged it, extending it more than 20 m toward the periphery of the moist soil.

Among eight males at Budzinski's captured two or more times as subadults and again as adults, five occupied the same area both years, four of these immediately adjoining the marsh and one in the gravel pit. One other moved from the marsh 34 m to a point near the edge of the moist soil; another shifted from the gravel pit 88 m to the moist northwest corner of the field; and a third moved 110 m from the gravel pit to the low area in the southeast corner of the field.

At Sedge Point the tendency for adult frogs to reoccupy their subadult range was much greater than at Budzinski's. Of six males and a female taken both in their second and third seasons, all were in the same area both years.

Once their adult home range was established, the frogs at both Budzinski's and Sedge Point showed a strong tendency to reoccupy it year after year. Of three adult females and 14 adult males captured at least twice in each of two consecutive years at Budzinski's, all were retaken in the same locality both years, the home range occupied in each year being either nearly identical or broadly overlapping. At Sedge Point the situation was similar. All of 29 adult males taken in two consecutive summers and three taken in all three summers of the study were captured each year on the same home range. Eleven of 12 adult females also reoccupied their former home range the second summer. Only a single

female (Fig. 28) shifted to a new range, occupying the area between the beach pools in the summer of 1960, but inhabiting a sedge-choked slough in 1961 and 1962. The extremely dense vegetation in the slough made it difficult to search effectively, probably accounting for the relatively few captures in the last two years. Two captures in early July, 1961, are not included as a part of the home range because the animal was not recaptured in that area again; they probably occurred as the animal was moving to her new home range.

One male taken three times at Sedge Point in 1960 in an area about 10 x 15 m was not captured at all in 1961 though his home range was repeatedly searched. In 1962, however, he was again recaptured in the same region as in 1960. It is possible that he simply evaded capture in 1961, but it is more likely that he was absent from his home range. His ultimate return, if he was absent, implies a strong affinity for that area, even after a full season's absence.

Size of home ranges: Determinations of the sizes of home ranges were based on captures during a single season to prevent slight shifts between years from increasing the apparent size of home ranges. To determine the area of the home range the capture sites of each individual were plotted on a scale map and the outside points connected by straight lines to form an irregular polygon, the minimum-home-range method of Mohr (1947). Those captures which could reasonably be assumed on the basis of available evidence to have been away from the animal's home range were excluded. The area within

Figure 28 Captures of adult female 73, the only frog known to have shifted home ranges after reaching adulthood.

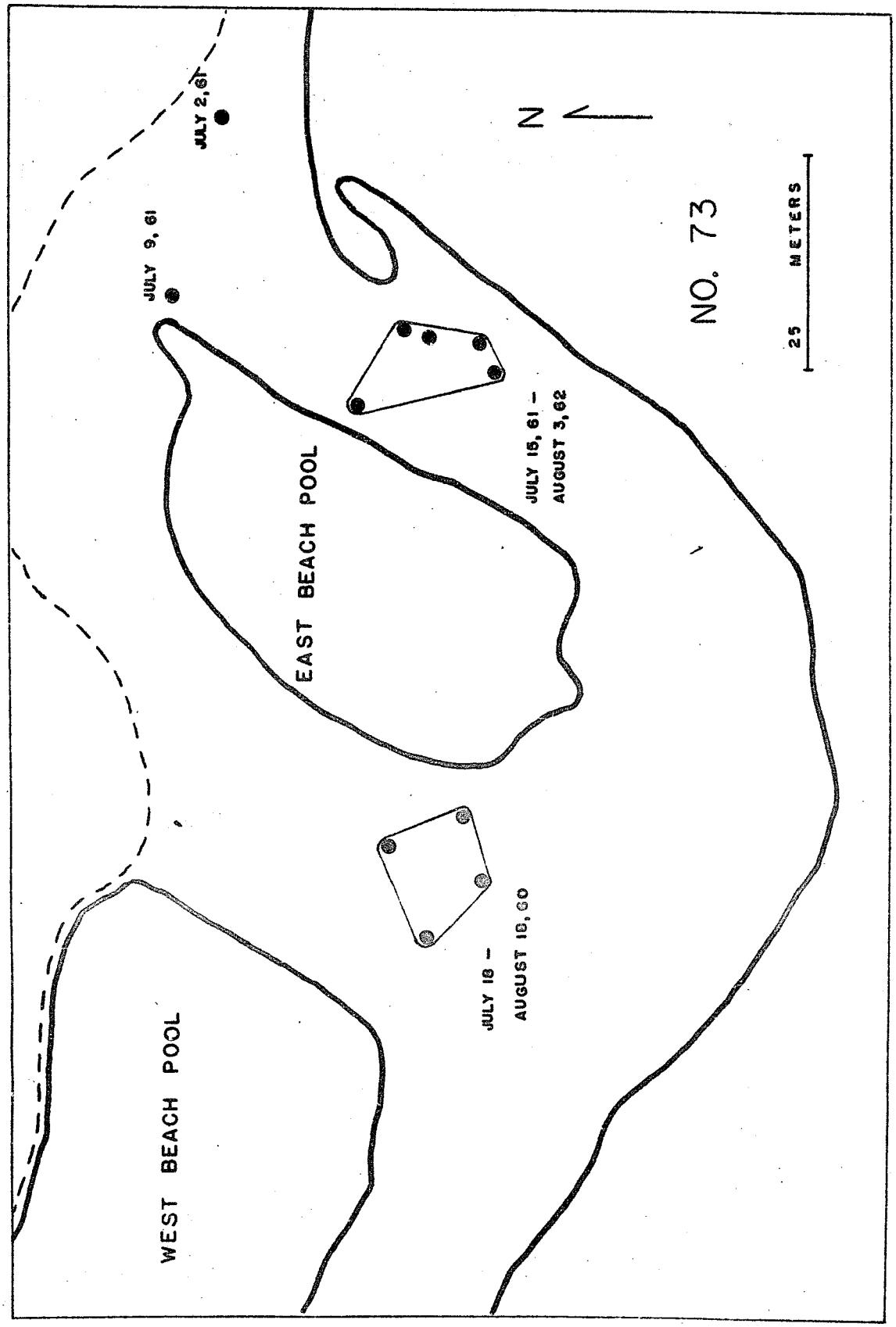

JULY 2, 61
JULY 9, 61
EAST BEACH POOL
JULY 15, 61 –
AUGUST 3, 62
N
NO. 73
25 METERS
WEST BEACH POOL
JULY 18 –
AUGUST 18, 60

FIGURE 28

each polygon was calculated by weighing to the nearest .0001 gram a piece of paper cut to the exact dimensions as plotted on the scale map. The weights were then converted to area by establishing a standard conversion graph based on weights of paper representing known areas. To minimize the influence of variation in weights of the paper, all polygons were cut from the same sheet, and paper (Nekoosa duplicator) with a low coefficient of variation was used; variation in weight between pieces of the same size cut from the same sheet was less than 0.2%.

In general, the estimated size of a home range tends to increase as the number of captures increases, approaching a maximum value asymptotically. To determine the minimum number of captures necessary to make a reasonable estimate, the mean area and standard deviation from the mean were determined separately for all home ranges based on four, five, six, seven and eight captures. Though the size of home ranges based on only four captures was much smaller than the rest, the mean size based on five did not differ significantly from those based on six or more. However, since the variance among the five-capture group was nearly twice as great as that among the groups with greater numbers of captures, a conservative procedure was adopted and only data from frogs captured six or more times in a single season were utilized in determining home range size.

It should be noted that the home ranges shown in Figure 27, showing distribution, were determined on the basis of

different criteria than were those from which range size data were obtained. Hence the ranges shown in the figure do not necessarily reflect accurately the sizes of ranges as presented here.

Among the frogs at Budzinski's, the sizes of the home ranges were as follows: subadult ranges, ranging from 85 to 515 sq m, had a mean of 283 ± 146 sq m ($N = 17$); adult male ranges, ranging from 15 to 996 sq m, had a mean of 361 ± 277 ($N = 26$); the two adult females captured six or more times had ranges of 390 and 615 sq m (mean 503 ± 159 sq m). The differences among the three groups were not statistically significant ($P > .30$) as tested by the Kruskal-Wallis One-way Analysis of Variance (Siegel, 1956). A statistically significant positive correlation ($P < .01$) between the length of the frog and the area of its home range was found, however ($r = .484$, $N = 45$).

At Sedge Point home ranges of subadults averaged 68 ± 77 sq m (range, 23-182; $N = 4$); ranges of adult males had a mean of 78 ± 45 sq m, and ranged from 15 to 165 ($N = 13$); adult females had a mean range size of 113 ± 97 sq m, and ranged from 20 to 270 ($N = 5$). The differences among the groups were not statistically significant ($P > .50$) when analyzed by the Kruskal-Wallis Test. No statistically significant correlation between body length and home range size could be found.

The home ranges at Sedge Point were significantly smaller than those at Budzinski's. As analyzed by the Mann-Whitney U Test (Siegel, 1956) the probability that the home range

sizes in the two areas are the same is less than .0003 (all home ranges in each study area were lumped).

Factors influencing range size: Density has been suggested as a factor influencing the size of home area in animals, a greater density usually being thought to cause a decrease in range size due to crowding (Burt, 1943; Stickel, 1950). Pearson (1955), in fact, has shown that range size in Scaphiopus holbrooki was smallest in dense populations. Kendeigh (1947) showed clearly that the area utilized by Bay-breasted Warblers (Dendroica castanea) was smaller in dense populations than in sparse ones. To discover whether differences in the degree of crowding of Leopard Frogs might have been responsible for the difference in range size in the two study areas, estimates of population size, and from these, density, were obtained for the two areas in 1962. Because Leopard Frogs entered and left the study areas during rains, thus altering the percentage of recapture, reliable estimates using the proportional method (Lincoln, 1930) could only be obtained from captures made during a period of no precipitation. Therefore, population estimates for both Budzinski's and Sedge Point were based upon two censuses, one week apart, during a dry period in early July, 1962.

At Sedge Point a thorough five hour search of the area around the east beach pool on July 5 disclosed 44 frogs. A comparable search on July 12 revealed 49, of which 15 were recaptures. From these data an estimate of 144 frogs present on the earlier date is derived ($\frac{44}{x} = \frac{15}{49}$, $x = 144$). The area

searched, exclusive of the open water of the pool and the bare sandy beach where Leopard Frogs rarely were found, contained approximately 3500 sq m. Thus, a density of 4.1 frogs per 100 sq m is obtained.

At Budzinski's the eastern half of the wet area in the northwestern corner of the field and the gravel pit were searched on July 3 and 70 frogs found. A comparable search on July 10 turned up 90, of which 20 were recaptures. From these figures an estimate of 280 frogs is obtained and, as the searched area contained roughly 9000 sq m, a density of 3.11 frogs per 100 sq m was determined. Thus, the frogs at Budzinski's were somewhat less crowded than those at Sedge Point.

As a check, density was also determined for the two areas using only frogs known to be resident rather than the total populations. At Budzinski's, 68 frogs were resident in the gravel pit and the whole northwest corner of the field (approximately 12,500 sq m) in the summer of 1962, while at Sedge Point there were 40 resident frogs, the criterion for residency being that used previously, three captures in the study area over a period of at least 30 days. From these figures density estimates of 0.54 and 1.14 resident frogs per 100 sq m were obtained for Budzinski's and Sedge Point respectively, the resident frogs at Sedge Point being more than twice as crowded as those at Budzinski's. It is, therefore, possible that the more crowded conditions at Sedge Point were responsible, at least in part, for the generally smaller home ranges.

The availability of water in the two study areas may also have affected range size. At Sedge Point, water was abundant throughout the summer in both of the two large beach pools and the lake surrounding the point. It is not surprising, therefore, that of 40 frogs resident in the study area in 1962, 37 (92.5%) had home ranges adjoining a body of water. The remaining three occupied areas less than 10 m from ponds. At Budzinski's, however, after mid-July when the marsh dried, the only bodies of water were two small ponds in the gravel pit. None of the home ranges of 13 adult females adjoined a body of water, and only three of 37 adult males and five of 16 subadults had ranges adjacent to ponds throughout the summer. Thus, the frogs at Budzinski's were almost entirely dependent upon other sources of water, largely soil moisture and dew, after the marsh dried, whereas the Sedge Point frogs had only to move to a pond a few meters away. It does not seem unreasonable to expect that frogs dependent upon soil moisture would move over a greater area seeking proper conditions than would those with a body of water close at hand.

The availability of suitable cover may also have been important in determining home range size in the two areas, but it is difficult to separate this from a density effect. Whereas at Budzinski's almost the total area considered, except for small parts of the gravel pit, had ample vegetation, much of Sedge Point (perhaps 25-30%) was bare sand usually not utilized by Leopard Frogs. The animals at Sedge

Point were thus forced to occupy the vegetated regions between and immediately surrounding the beach pools. Had the beaches supported suitable vegetation the animals would probably have spread out onto them and perhaps, due to reduced density, occupied larger home ranges.

It is not likely that the relative abundance of food played a significant part in regulating range size. Though no quantitative measures were made, ground-dwelling insects such as grasshoppers, crickets, leaf hoppers, beetles, etc. which contribute a large part of the food of Rana pipiens (Kilby, 1945) appeared to be much more abundant at Budzinski's. If food had been a major factor it seems logical that the frogs at Sedge Point, where food was probably less abundant, should have ranged over the larger areas in search of prey.

Territoriality

A territory is generally considered to be an area which is actively defended, either by physical contact or threat display or both, against other individuals of the same species. In the three years of this study no evidence of aggressive action between individuals or of the exclusive use of an area by one frog was seen. Home ranges overlapped to a great extent and a few were completely enclosed by others.

However, if density is, as comparisons of Budzinski's and Sedge Point suggest, an important factor regulating home range size, some sort of aggressive action or spacing regulation between individuals is implied. If the animals did not so

interact and were completely tolerant of one another there is no apparent reason for the home range size to vary with density; even in a dense population each frog could still theoretically move over as large an area as it would in a sparse population, if no interaction between the animals exists. In fact, it is reasonable to expect that in a dense population of socially tolerant individuals, the animals would move over greater areas in search of prey, for food is often less abundant where competition is high.

Although aggressive action and threat displays are easily seen in some animals, especially birds, it is possible that these same phenomena actually exist in the Leopard Frog but in a form too subtle to be discerned; or they may occur only infrequently under conditions where they could seldom be expected to be observed. Only a few frogs were watched in the fields because of the difficulty in seeing them; most observations were made in the vicinity of the ponds in Budzinski's gravel pit. Since very few older frogs maintained residence around the pond it is likely that most of those observed were temporarily off their home ranges. One would not expect to observe defense reactions among such frogs even though they might defend a part or all of their home areas in the field.

The strong tendency of some frogs to return repeatedly to particular parts of their ranges, even to certain forms, indicates a strong attachment to these areas. It is not unlikely that Leopard Frogs defend small parts of their home

ranges, or particular forms, but not their total areas. As no detailed observations of frogs definitely on their home range were made, their behavior in such situations toward other Rana pipiens is not known.

Thus, though no positive evidence of aggressive action or defense of an area was found in this study, the possibility that Rana pipiens does have some degree of territoriality is not ruled out. Martof (1953a) presented evidence of territoriality existing in a closely related species, Rana clamitans, even though he saw no aggressive behavior. He found that males maintained their relative positions in a population for long periods, apparently recognizing their neighbors, and concluded that this represented a weak form of territoriality.

Habitat of Young

Whereas frogs in their second season or older commonly occupied the fields wherever the soil was sufficiently moist, young-of-the-year were seldom seen in such environments except during migrations in the rain, instead being found generally within a few meters of ponds. The difference between the habitats of young-of-the-year and older frogs is illustrated in Figure 29 where all frogs captured in August, 1962, in the field, marsh and gravel pit at Budzinski's have been grouped by size; captures on eight rainy days have been excluded. Although 31 recently metamorphosed frogs were captured in the field, none was taken there more than once, indicating they were transients in that habitat. These 31 young in the field represented only 11% of all frogs taken

Figure 29 Size frequencies of frogs captured in August, 1962 in Budzinski's field, marsh and gravel pit.

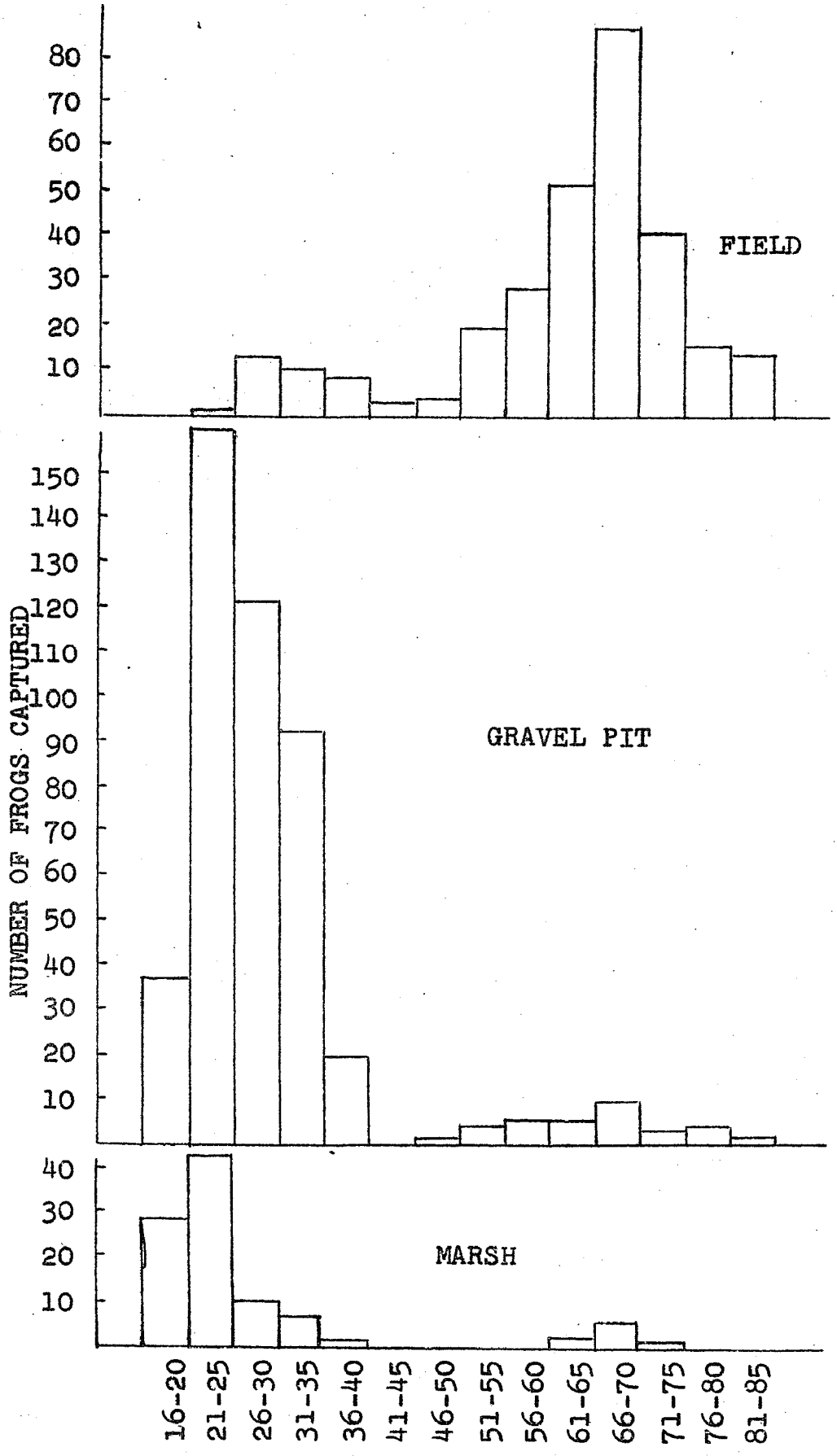

FIELD
GRAVEL PIT
MARSH
NUMBER OF FROGS CAPTURED
SNOUT-ANUS LENGTH IN MM
16-20
21-25
26-30
31-35
36-40
41-45
46-50
51-55
56-60
61-65
66-70
71-75
76-80
81-85

FIGURE 29

in the field, and only 6% of the young-of-the-year taken in all three habitats.

The occurrence of young in the vicinity of water was not due simply to the fact that they metamorphosed there; during rains they dispersed over the countryside but after a few days of rainless weather again clustered around water (see section on dispersal).

In an effort to determine if the small frogs were capable of existing in the habitat of the adults a brief experiment was made. Ten recently metamorphosed frogs, 22-26 mm long, were confined in a 30 x 30 cm hardware cloth cage in a moist portion (soil moisture, 50-60%) of Budzinski's field, in dense grass approximately 40 m northwest of the marsh, where adult frogs were abundant but no young lived. In the 15 days of confinement (August 14-29) four of the frogs disappeared. As no evidence of their remains could be found it was assumed that they had either escaped or had been eaten by small snakes which wriggled through the wire. At the end of the confinement period the six remaining frogs were all in good health, having grown an average of 2.1 mm in length during the interval.

Because of the brief period of time involved, the loss of four frogs, and the heavy rains during the period of confinement (a total of 136 mm. in three rains, August 15, 24-25 and August 28) it is not possible to make any definite conclusions as to the ability of the young to survive indefinitely in such an environment. It is clear, however, that at

least 60% of them were able to survive and grow in the habitat of the adults, even over a 10 day rainless period. Thorson (1955), however, has presented ample evidence that small individuals are more dependent on water than larger ones. It is likely that a greater need for moisture is the primary cause of their confinement to ponds, and that under more adverse conditions, through which a large frog might easily survive, the young would succumb.

The possibility that the young are excluded from the grassy areas occupied by adults for other reasons than inability to maintain a proper water balance cannot be ignored. Perhaps they do not remain long in these areas because of aggressive action by resident adults forcing them to move to other regions. Possibly those young which do remain in the fields are subject to a greater degree of predation, both by resident frogs and snakes, than are those near the water. This is not unlikely, for cannibalism in Rana pipiens has been noted by Kilby (1945) and Donaldson and Schoemaker (1900) and has been seen by me. Snakes probably are able to capture young frogs in the field more easily than they can capture adults, for the small ones take shorter leaps; young frogs around ponds generally elude snakes by diving into the water, but in the field they would be entirely dependent upon their hopping ability to escape.

Spacing of Individuals

As I depended upon the movements of frogs in locating them in dense vegetation, it was not possible to determine

the exact spot in which frogs taken in censuses had been sitting before being disturbed, hence no information on the exact distances between individuals in the field was obtained. Around the ponds in the gravel pit at Budzinski's, however, Leopard Frogs could be easily seen and their relationships to each other were noted on several occasions.

In late summer large numbers of recently metamorphosed young could be observed in fair weather sitting on aquatic vegetation in the ponds or within 2-3 m of the water on the bare mud. These young appeared to be completely tolerant of each other, for in these dense populations distances of less than 10 cm separating individuals were the rule. It was not at all uncommon to find three or four young sitting together less than 1 cm apart, sometimes their bodies actually touching. No evidence of aggressive action between young was seen and there was no indication that individuals occupied particular spots. Young taken on one side of the pond on one day frequently were taken on the opposite side when next captured.

Although in the vicinity of the ponds subadult and adult frogs were not nearly so numerous as young, at almost any time a few could be found there. Though the ponds probably were not within the home ranges of most adults observed, some subadults may have been on their ranges. The presence of these older frogs apparently affected the spacing of young only slightly, for the young commonly sat within only a few centimeters of them. Although slow movements of adults,

such as when stalking prey, did not apparently affect the young, sudden movement of a large adult sometimes caused the smaller animals nearby to scatter slightly. This was probably an avoidance response similar to that manifest when a snake or other large object moved nearby. Since the typical behavior of adults was to sit quietly for long periods, their presence did not usually disturb the young.

Also, so far as could be determined, there was complete social tolerance among subadult and adult frogs. On several occasions subadults were found sitting within 10 cm of each other, and two instances were noted of subadults sitting so that their bodies touched. The closest recorded distance between two adults (both females) was 40 cm. All other adults observed were at least 60-70 cm apart, usually several meters. It is possible that the failure to find adults closer together was the result of an intolerance of one another, but it is more likely that it was simply because there were seldom more than four to five adults in the vicinity of the ponds at any given time, hence the chances of two being together were slight. In any case, the possibility of aggressive behavior toward other Leopard Frogs among adults on their home ranges is not ruled out.

Discussion

In most species of anurans which have been carefully studied individuals have been found to restrict their activities

to relatively small regions of the available habitat, their home ranges. The tendency to remain in a small area for long periods, sometimes up to several months, has been described for Rana clamitans (Martof, 1953b), Rana nigromaculata (Kikuchi, 1958), Rana pretiosa (Turner, 1960), Scaphiopus holbrooki (Pearson, 1955), Syrrhophus marnocki (Jameson, 1955), Acris crepitans (Pyburn, 1958), Hyla regilla (Jameson, 1957), Gastrophryne olivacea (Fitch, 1956), Prostherapis trinitatis (Sexton, 1960), Bufo boreas (Carpenter, 1954) and Bufo woodhousii (Stille, 1952). In addition, many species including Rana clamitans (Breder, Breder and Redmond, 1927; Martof, 1953b), Rana catesbeiana (McAtee, 1921; Ingram and Raney, 1943), Bufo terrestris (Bogert, 1947), Bufo regularis (Chapman and Chapman, 1958), Scaphiopus holbrooki (Pearson, 1955) and Hyla regilla (Jameson, 1957), have been demonstrated to have a homing ability, indicating a strong attachment for their home ranges.

Fitch (1958) has stated that individuals of Rana pipiens which he studied on the University of Kansas Natural History Reservation, in contrast to most other anurans, tended to wander over the entire habitable area. Evidence from the present study, both from trailing records described previously and capture data, demonstrates that, in northern Michigan at least, individual Rana pipiens limit their activities during the summer to relatively small areas. Though they sometimes leave their ranges during nocturnal rains or when forced by unfavorable conditions, they generally return. In addition,

once an adult frog establishes a home range it tends to return to the same region each summer.

Among Budzinski's frogs there was a general correlation between the size of the animal and the wetness of the habitat occupied, the smallest frogs living in the wettest regions and the largest in the least wet. This is as would be expected, for Thorson (1955) demonstrated that small Rana pipiens are more dependent on moisture than larger ones. He showed that even though the smallest frogs (5-14 g) contained proportionately more water they reached their limits of tolerance to water loss in less than half the time taken by the largest ones (60-74 g) because they lost water at a much more rapid rate. He found, for example, that in 10 hours under comparable conditions the largest frogs lost about 14% of their body weight as compared with 46% by the smallest. The larger frogs, which lose water more slowly, are no doubt able to maintain an adequate water balance on soil with fairly low moisture content upon which a smaller frog cannot survive.

There is, however, no obvious reason why adult females should not be able to have home ranges in the wettest parts of the field occupied by subadults and males, yet none resided there. It is probable that these larger frogs occupied the peripheral regions not solely because they were able to do so, but because crowding and competition were less in these areas. Since the relatively small frogs, subadults and small males, tended to cluster in the wettest areas the density there was much greater than in the peripheral regions. It

is likely that Leopard Frogs tend to reside in areas where competition is least but where there is sufficient moisture for them to survive. Thus, the shift to new home ranges made by most females and many males as they reached adulthood may have resulted from a tendency among these animals to occupy regions where crowding is least. The shift and enlargement of home ranges by two females, one moving from near the marsh as a subadult to the periphery of the moist region in her third season, and the other extending her range into a less wet area (both described earlier) support this view, for both shifted to regions where fewer frogs resided. Martof (1953b) reported that the home ranges of subadults in Rana clamitans also were not so permanent as adult ranges, for the subadults commonly moved to new regions as they matured. He found that the small frogs occupied shallow water almost exclusively whereas adults had home ranges near deep water. I believe, this shift to deep water, where young did not occur, may have been the result, among other factors, of less crowded conditions in the habitat of the adults.

At Budzinski's a statistically significant positive correlation between the body length of the frogs and the area of their home ranges was found. Although the same correlation among Sedge Point frogs lacked statistical significance, the fact that the mean size of home range was least among the smallest frogs (subadults) and greatest among the largest (adult females) probably indicates that the same tendency

existed there as well. Had more home range estimates been available for the subadult frogs at Sedge Point, the correlation might have been significant.

The greater size of the area occupied by the largest animals at Budzinski's might have been due to decreased density, for they tended to occupy the outlying regions where there were fewer frogs. Or perhaps the near-minimal moisture conditions in these peripheral areas, and an accentuation of the dearth of water in long rainless periods, caused the large animals in these regions to move over greater areas, especially toward the marsh, in search of suitable moisture conditions. It is unlikely that the availability of food affected home range size, for prey was probably most abundant in the peripheral regions where there were fewer frogs. In any case, Leopard Frogs seldom forage for food, rather tending to wait passively for it.

Sex Ratio

In both study areas in all three summers adult males were collected more commonly than adult females. The ratio among adult resident frogs in 1962 was 2.20:1 at Sedge Point and 2.47:1 at Budzinski's, both favoring males. In 1960 and 1961 the ratio at Budzinski's appeared to be even more in favor of the males (7:1) but this was undoubtedly due to sampling bias since most collecting was concentrated in the area around the marsh and in the gravel pit, neglecting the peripheral areas of the moist region where females were later found to reside; this was corrected in 1962. The ratio of adult resident frogs at Sedge Point was closely similar in the three summers.

The deviation of the ratios among resident adults in both study areas from the expected 1:1 was statistically significant at the 1% level. The difference is not due to an inability to determine the sex accurately, since all animals counted as males were definitely identified as such by the presence of thumb pads or vocal sacs or both. Those adults not so identified as males were considered to be females. Although the actual ratio may be slightly more in favor of males, due to the possible inclusion of some males with the females, I believe the sexes of most adults were accurately determined. The sex of many females was verified by the presence of eggs in the body cavity in late summer or in the

spring, and that of many males by the swollen thumb pad, calling, or amplexate position in the spring of 1962. Of 26 adults breeding in spring of 1962 whose sex had been determined in the summer of 1961 by the presence or absence of thumb pads or vocal sacs, all were found to have been sexed correctly.

Any of four factors could have been responsible for the abundance of males in the population: (1) males may be more commonly produced through some peculiarity in the sex-determining mechanism of the species; (2) sex reversal may occur, some "females" becoming males; (3) there may be a differential elimination of the sexes so that more males survive than females; (4) or there may be behavioral differences between the sexes such that males are more commonly captured.

To check the possibility that the preponderance of males was due to some peculiar genetic sex-determining mechanism 125 newly metamorphosed frogs were collected from a large breeding pond near Budzinski's. When the sex of these individuals was determined by examining the gonads, 61 were found to be males and 64 females. This difference does not deviate significantly from the expected 1:1 ratio. Thus, the excess of males must be the result of one or more of the remaining factors. Evidence of the possible influence of each will be presented.

As Leopard Frogs of all ages are almost totally confined to water during the spring, proportions of the sexes of mature frogs at the breeding ponds before they invade the fields probably closely approximate the actual ratio in the adult

population. Three censuses of the ponds at Budzinski's during the spring of 1962 yielded ratios of 3.11:1, 1.35:1 and 1.97:1 on April 27, May 5 and May 19 respectively, all favoring males. At Sedge Point a ratio of 1.37:1 was obtained on April 28, but on May 6 it was 15:1, due to the post-breeding emigration from the area. On May 21 only four males, no females were taken. The ratios obtained on April 28 at Sedge Point (1.37:1) and May 5 at Budzinski's (1.35:1) did not differ significantly from 1:1. However, the fact that all spring samples favored the males probably indicates that the adult females are actually outnumbered. The slight surplus of males may be due to some females becoming males, but as there is no evidence that sex reversal occurs naturally in Rana pipiens, it is more likely due to a greater mortality among the females. This would not be surprising since they tend to occupy less favorable habitats at greater distances from water than do males; also, their heavier bodies, especially when full of eggs, may make them less agile than the smaller males and therefore more prone to predation.

In the summer, after the frogs had left the ponds, the proportion of males in most census samples was nearly double the lowest proportion in the spring. It appears likely, therefore, that even though males probably outnumbered females slightly in the population, the difference in the proportions of each sex taken in the study area in summer was accentuated by another factor.

As has been pointed out in a previous chapter, adult females tended to occupy less wet areas than males due to

their lesser dependency on moisture. It is probable that the fewer females in the study areas in the summer is, to a large extent, the result of their leaving the vicinity of the ponds for more distant regions. Evidence that this is actually the case is provided by the finding that in a field adjoining Budzinski's pasture, more than 150 m from the nearest pond, the ratio among resident frogs was 1.2:1, still favoring males slightly, but indicating that at this greater distance from the water females were relatively more abundant than in the study areas.

The changes in proportions which occurred in samples taken in censuses following rains provide further evidence that the scarcity of females in the study areas was the result of their tendency to occupy regions more distant from ponds. While the ratio in most censuses in the summer of 1962 at Budzinski's ranged from 2.14:1 to 3.53:1, in two censuses (June 10 and July 20) which immediately followed nocturnal rains, it was 0.85:1 and 1.61:1 respectively. Similarly at Sedge Point where proportions in most censuses in summer ranged from 3.00:1 to 4.33:1, on two censuses made closely following rains the proportions fell to 1.28:1 and 1.84:1. These shifts towards more equal division of the sexes were most likely the result of many animals migrating from their home ranges, and moving over the countryside. Thus, males which usually predominated in the study areas tended to leave, while females from outside entered, producing a more equal ratio.

Discussion

Reports of unequal sex ratios among adult anurans are not uncommon. Males have been reported to be more abundant than females in breeding populations of *Rana catesbeiana* and *Rana clamitans* (Raney, 1940), *Bufo woodhousii* (Bragg, 1940), and *Bufo americanus* (A.P. Blair, 1943), while in *Rana temporaria* (Pelseneer, 1926) and *Rana esculenta* (Balli, 1938) and in summer populations of *Rana pretiosa* (Turner, 1960) females were more common. Turner found, however, that in *R. pretiosa* the sexes were present in nearly equal numbers until the fifth year of age when females predominated, possibly indicating a greater mortality among older males.

Though the males apparently predominate slightly in adult *Rana pipiens*, the deviation from the 1:1 ratio in the region of ponds is accentuated in summer by behavioral differences between the sexes. In general, the larger females tended to reside in less wet places at greater distances from water than did the smaller males, hence were less often taken in the study areas in the vicinity of ponds. Behavioral differences have been reported to account for deviations in the sex ratios found in other anurans as well. Pyburn (1958) found an apparent deviation from a 1:1 ratio in the breeding ponds favoring the male in *Acris crepitans*, but he later demonstrated that this was due to the fact that the males, conspicious by their calling, were more likely to be captured, while females tended to move away from the ponds into the vegetation where they were overlooked. Martof (1956) found that, considering all adult

R. clamitans taken on their home ranges outside the breeding season, the females were more common, though the deviation from a 1:1 ratio was not statistically significant. He stated that males returning from breeding may have had to move to locations farther from the ponds because the niches closer at hand were already occupied. Thus "if an area located farther from the breeding ponds was considered, perhaps the males would be found in greater abundance in the nonbreeding season than the females. Or if a larger area had been studied, a one to one ratio might have been obtained." Jameson (1957) found that in the semi-aquatic Hyla regilla males were dominant in the area of the breeding ponds; females were obtained only following hard, warm rains. Thus, the lack of females in the ponds was the result of differences in behavior, each sex occupying a different habitat.

Dispersal of Young

Every species has some means for dispersal at some stage of its life cycle, permitting the extension of its range into other favorable habitats and increasing its chances of continued survival as local conditions gradually change. In the majority of vertebrates the dispersing phase occurs early in the life of individuals, the young usually maintaining no "home," but instead moving considerable distances. The distance the dispersing animals travel influences the amount of inbreeding and the rate of spread of genetic factors, thus controlling in part the direction and rate of evolution in local populations.

In the present study considerable effort was devoted to an analysis of dispersal of newly transformed young Rana pipiens. In the three summers of field work more than 3500 young were marked and 971 recaptures made. In this section the pattern of dispersal in the two populations studied will be considered. Environmental conditions affecting dispersal movements are discussed in the following chapter.

Budzinski's Farm

On August 1, 1960, four traps were placed at the cardinal compass points around Budzinski's marsh, each 40 m from the water (Fig. 8). Supplemented by additional traps in 1961 and 1962, they provided information on the direction, intensity and times of emigrations. Captures of individuals

by hand provided additional information.

Occurrence and Pattern of Dispersal: The year 1960 was particularly good for Leopard Frog young due to excessive rain which kept the ponds at Budzinski's full all summer, allowing large numbers of tadpoles to survive to metamorphosis. Several large emigrations occurred from the marsh in August, the only period when the population was studied. In 1961 and 1962 the number of young emerging from the marsh was much smaller because of early drying of the ponds before the bulk of the tadpoles had transformed. Though dispersal took place, no spectacular emigrations such as those in 1960 were observed.

As shown by the emigrations in 1960, the number of young dispersing was not evenly distributed in time. Large numbers left the marsh on certain favorable nights, August 1, 6, 11-13, and 16-19, while only a few (usually less than 10) were trapped while emigrating on the other nights (Fig. 30). The young dispersing on the nine nights mentioned above constituted approximately 80% of the total number dispersing in August.

Throughout the dispersal period in August, 1960, some young were also trapped as they entered the region of the marsh, the largest numbers being taken on nights following mass emigrations. Evidence indicates that a large part of these came from other ponds. Since the length of the four traps, considered as arcs of a hypothetical circle with a 50 m radius around the marsh, constituted 9.2% of the circumference of the circle, the trap samples should represent approximately 9.2%

Figure 30 Numbers of young trapped while entering (circles) and leaving (dots) the region of Budzinski's marsh in August, 1960. Irregular solid line above shows barometric pressure; minimum temperature during each night is indicated by short horizontal bars; rainfall in millimeters is shown by arrows (T = trace). Barometric pressure data were obtained from United States Weather Bureau, Pellston, Michigan, approximately 16 km WNW of study area.

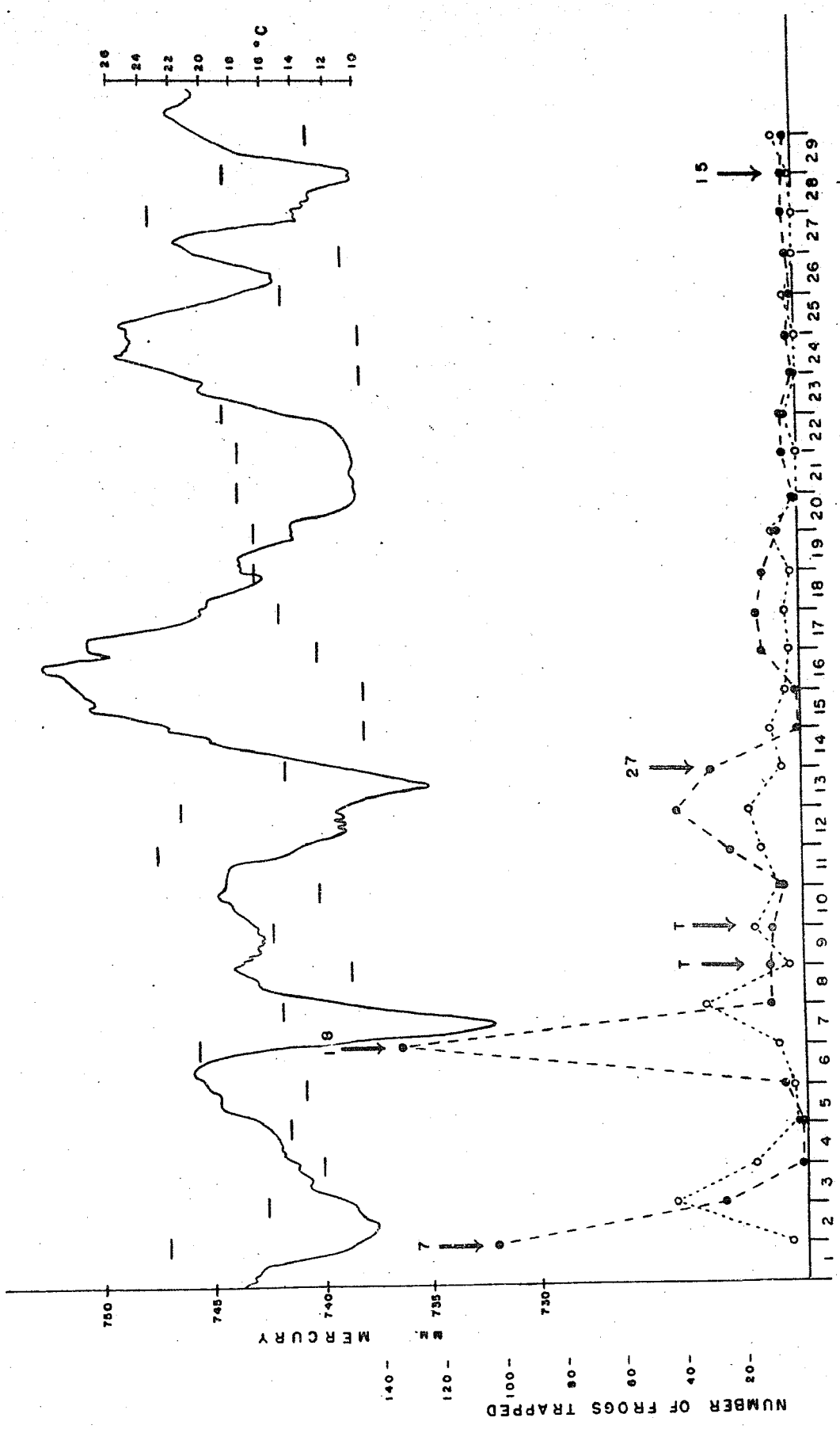


FIGURE 30

of the total number of frogs entering or leaving the area. Thus, if all frogs trapped while entering the marsh region were local animals returning after dispersing, roughly 9.2% of them should have been recaptures. However, only 11 (4.7%) of the 232 trapped while entering the marsh area had been trapped earlier (one to three days) as they emigrated from the region. This proportion differed significantly from the expected ($\chi^2 = 5.03$ with 1 df; $P < .05$), indicating that a large part of those entering the marsh came from other regions. In fact, it is very probable that the vast majority came from other ponds, for the emigrating frogs trapped and marked were more likely to return to the marsh, and of being retrapped if they did so, than were those which dispersed freely. This was in part because the trapped frogs were not released until morning, hence did not move so far. Also, they were released on the opposite side of the trap, so that if forced to return to the marsh by unfavorable conditions, the likelihood of trapping them again was great. Thus the percentage of marked young retrapped while returning to the marsh was probably greater than among the emigrated group as a whole.

In Table 4 are shown the total numbers of young frogs trapped while emigrating from the marsh in 1960 and 1961. Though in 1960 the largest number of trapped young were moving eastward toward the gravel pit, the differences in the proportions dispersing in each of the four directions did not differ significantly from that expected if dispersal were random in all directions.

Table 4

Young trapped while dispersing from Budzinski's marsh in each direction. None was trapped in 1962.

Traps	1960	1961
North	102	0
East	136	39
South	109	0
West	125	0

In 1961, however, all 39 young which were trapped at various times while leaving the marsh, were moving eastward toward the gravel pit; one, in fact, was later captured by hand in the gravel pit pond. Such non-random movement implies that some factor not operating in 1960, or operating to a smaller degree, influenced the direction of emigration. As the marsh, full in 1960, was without water after August 2 in 1961, the movement of the young frogs may have been in response to a need for moisture. Their orientation towards the pit may have been the result of their moving toward water, for it contained the only ponds in the immediate vicinity. If the movement to the gravel pit was, in fact, prompted by a need for moisture, a means of detecting water from a distance is implied, for the newly metamorphosed young could not have known of the ponds from prior experience. Neither could they have seen the water directly, for it was in the bottom of the pit, separated from the marsh by a ridge. The mechanisms which might be involved in distant detection of water have been discussed in an earlier section.

In 1962, because only a handful (probably less than 100) of young metamorphosed in the marsh before it dried in mid-July, no emigrating young were trapped. However, four which transformed in the marsh were later taken in the vicinity of the pond in the gravel pit, indicating that some emigration occurred.

Distance of Dispersal and Establishment of Home Range: Of the 472 young trapped while emigrating from Budzinski's

marsh in 1960, four (0.8%) were retaken in the study area in 1961 and four others in 1962, but none was recaptured more than once. Six (4%) of the 146 young captured by hand in 1960 and not known to have left the vicinity of the marsh were also retaken in the study area in 1961. Five of these were taken only one time each, but one individual was taken four times between July 26 and August 22 in an area about 20 x 5 m near the marsh, apparently having established its subadult home range there. It was not retaken in 1962.

Of 431 marked young which metamorphosed at Budzinski's in 1961, none of which was known to have left the study area, seven (1.6%) were recaptured in 1962. Four of these were retaken only once in the study area, but three had established home ranges in the vicinity of the marsh; one was taken four times between June 5 and August 10, a second four times between June 9 and July 27, and the third nine times from May 19 to August 19.

In the spring of 1962 more than 150 breeding adults were captured in five ponds outside the study area but in the vicinity of Budzinski's. Two of these, a male and female, which as young had emigrated from Budzinski's marsh in 1960, were found in breeding ponds 800 and 400 m from Budzinski's respectively. In addition, a male which had also emigrated in 1960 was found clasping a female in the gravel pit on May 5. This was his only recapture; he had not been taken in 1961 nor was he captured again in 1962.

In 1961 and 1962 a large influx of "foreign" young into the study area was shown by trap captures. That these were not local frogs returning after a dispersal was evident both by their size and the direction of the movement. In both years the frogs came from the west or northwest and averaged 6-8 mm longer than local young, indicating that they were from another pond where metamorphosis had occurred earlier. None was marked.

The origin of the 1961 influx is not known with certainty, but in 1962 the probable source was located, a large marsh 800 m northwest. A sample of young taken from this marsh immediately following the immigration showed no significant difference in mean size from those which moved into the study area, but both samples differed significantly from the young known to have transformed at Budzinski's. This agreement in size, the general direction of the movement and the fact that no other source of frogs could be found within a 1.5 km radius of Budzinski's toward the west or north indicates that this was the origin of the frogs. As the general direction in both years was the same, the 1961 immigration may have originated in the same source, or it may have come from another marsh approximately 0.8 km NNW which was discovered in 1962, but contained no young that year.

In 1961 the movement of young toward Budzinski's probably began in the night of July 20 when a 9 mm rain fell. On the morning of July 22, five "foreign" frogs were found to have been trapped entering Budzinski's pasture during the preceding

night; on July 23, six were trapped; on July 24, 30. On July 25, after a 1 mm rain during the night, two more were trapped entering the pasture, ahd six fell into traps as they moved eastward and southward from the study area, apparently continuing the journey in the same direction. One hundred ninety-seven other immigrants were captured by hand in the study area. Twenty trapped while entering the pasture were recaptured later by hand; the mean number of days between entering and their last capture in 1961 was 7.05 (range, 1-28). Four were recaptured again at Budzinski's in the spring of 1962, apparently having hibernated there, and one of these established its home range as a subadult near the marsh, for it was taken eight times between May 19 and August 5, 1962. Two others were taken in 1962 in another pond 0.8 km south of Budzinski's, a straight line dispersal distance from their pond of origin of over 1.2 km. Actually they must have moved well over 1.6 km, for the study area was not on a straight line between the two ponds.

In 1962 the pattern was similar. The movement towards Budzinski's probably began in the early morning of August 4 when a light rain (8 mm) fell, lasting until daybreak. On the morning of August 5, three young were found to have been trapped as they entered the study area during the previous night; on the morning of August 6, 26 had been trapped; on August 7, 32; on August 8, four; and on August 9, two. All came from the northwest. During this period these "foreign" young, readily identified by their larger size, were abundant

throughout Budzinski's pasture, especially around the ponds in the gravel pit; there was no water in the marsh at this time. In a 2.5 mm rain in the early morning of August 8, four were trapped leaving the gravel pit, moving eastward. Of the 67 trapped as they entered the area, 33 were subsequently recaptured by hand, all but eight near the pond in the gravel pit. The mean number of days between the time these first entered and their last capture was 6.5 (range 1-15) indicating that most did not stay long.

If, as seems reasonable in light of evidence presented later, the movement of all young toward Budzinski's in 1961 began in the rain in the night of July 20, the migratory frogs must have negotiated the 800 m in a period ranging from approximately 30 hours for the most rapid to more than four days for the slowest, the peak of the arrivals coming during the third night following the rain. Since dispersal occurs only at night (see later) the five animals in the traps on the morning of July 22 probably moved the distance in less than 12 hours of travel time, as the dark period in northern Michigan at this time of year is approximately seven hours long and the rain began about five hours before daybreak. In 1962 the first frogs also arrived during the night following the rain, having moved the distance in something less than 10 hours. The bulk of the frogs did not arrive until the third and fourth nights following the rain, however, and a few stragglers took as long as five days.

As an indication of the extreme dispersal distances sometimes involved, three captures made in 1962 by Peter Lee are of interest. In the course of his study Mr. Lee collected more than 100 adult Leopard Frogs at Nichol's Bog, 5.2 km SSW of Budzinski's. Among these he found three males which had been marked. As no other marking studies were being conducted in the area, they could only have come from Budzinski's. That these "numbers" were not the result of accidentally lost digits is evident by the patterns they showed, one animal having toes on two feet clipped, and two animals having clipped toes on three feet. On certain feet two non-adjacent toes were gone, exactly the toes which would be clipped in marking. In none did the toe combinations present an impossible "number" combination as would be expected had their loss been accidental. In addition, the sizes of these animals fit into the established growth pattern; all were in the lower size range of adults as would be expected of third season frogs, and their numbers were those of young of 1960 at Budzinski's. All were trapped while leaving the study area and none was seen again. There seems little doubt that they actually were frogs which metamorphosed at Budzinski's in 1960 and emigrated. Movement must have been overland for no bodies of water connect the two areas.

Dispersal in Relation to Density: In 1960, evidence was obtained which may indicate that dispersal of young Leopard Frogs is density related. Though the data are open to some question and to other interpretations, they are presented because

they may indicate that such a relationship exists in an animal which is neither antagonistic nor overtly aggressive to other individuals of its species.

From trap data it is possible to estimate the number of young in the marsh for each day in August, 1960. On August 20 and 22 the entire marsh area lying between the four traps was searched and all young captured were marked and released. From these data it is possible to estimate the number of young present on August 20 using the proportional method (Lincoln, 1930): $\frac{125}{x} = \frac{13}{122}$ $x = 1173$. This seems a reasonable estimate since movement into and out of the area (as determined by trap captures) was negligible between the two census periods and all tadpoles had metamorphosed.

Considering the traps to be four arcs of a circle with 50 m radius surrounding the marsh, and knowing the lengths of these arcs (7.32 m each), it is possible to estimate the number of young entering and leaving the area of the circle. Using the standard formula $C = 2\pi r$ to determine the circumference of the hypothetical circle, a factor of 10.79 is derived by which the trap samples can be multiplied to estimate the total number of young entering or leaving the area. All frogs trapped on the marsh side of a trap were considered to be leaving the region, while those trapped on the opposite side were considered to be entering it. The day-by-day population estimates based upon the estimated number entering and leaving (which were based on known number trapped), projected both backward and forward from August 20, are shown in Fig. 31.

Figure 31 Daily changes in number of young in Budzinski's marsh in August, 1960. Rainfall in millimeters is shown by arrows (T = trace).

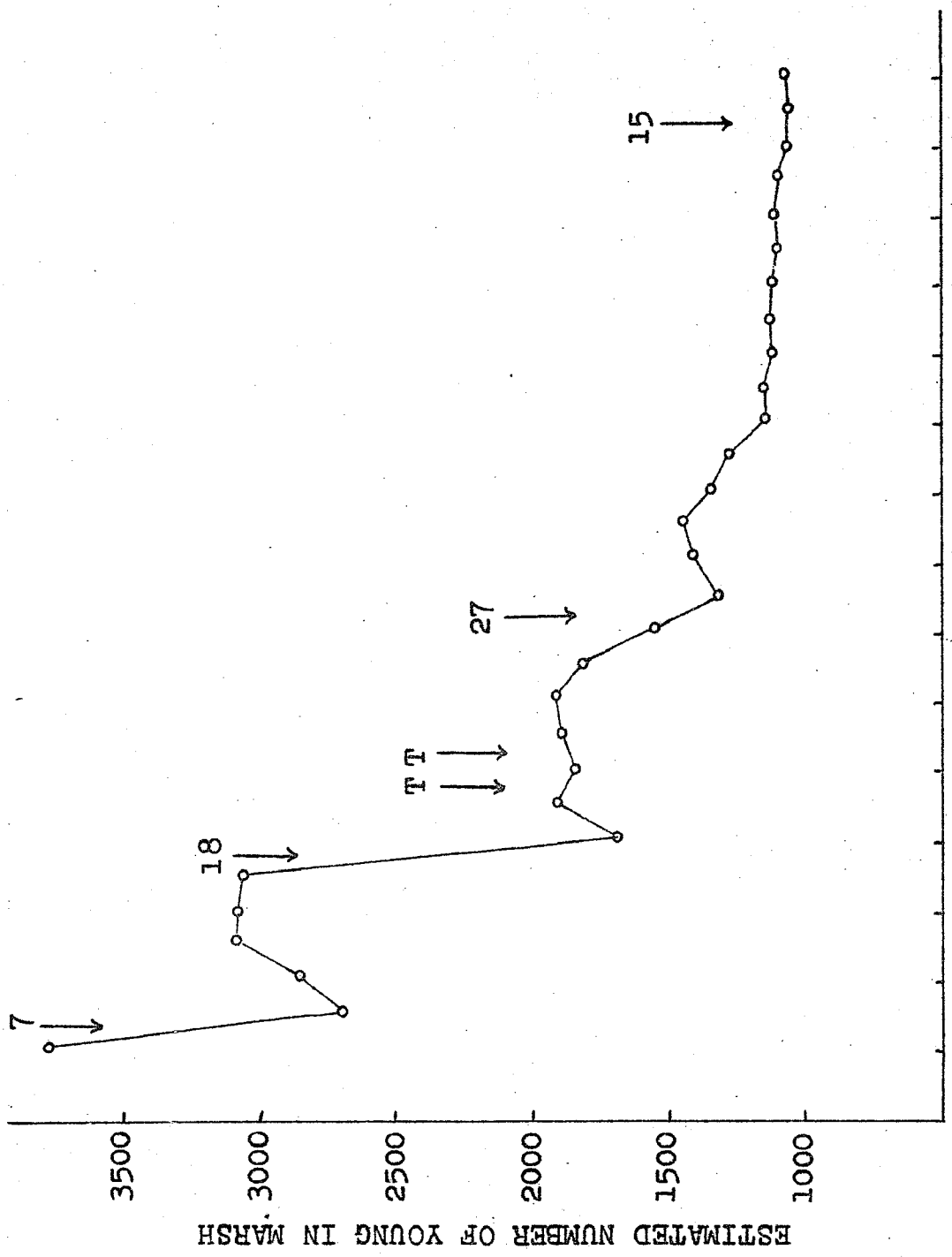

ESTIMATED NUMBER OF YOUNG IN MARSH
3500
3000
2500
2000
1500
1000
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
DAYS IN AUGUST 1960
7
18
T T
27
15

FIGURE 31

No great degree of accuracy is proposed for these figures, but they probably show the general trend in decline of the population with each emigration, and at least indicate the general magnitude of the population except during the first week of August. The projected estimates of young present before August 10 are probably too high due to the fact that an unknown proportion of these "frogs" were present at this time as tadpoles and cannot be considered as involved in the density of the young metamorphosed frogs. In making these population estimates it has been assumed that the only factors affecting the population size in the area are emigration and immigration. This is probably unrealistic since some undoubtedly were lost to predators, but there is no way to determine the magnitude of their effect. The estimates also do not take into account the addition of new frogs by metamorphosis, and since tadpoles were still present in the marsh in early August this cannot be disregarded. On August 10, however, a search of the marsh revealed only a few remaining tadpoles (7 were seen). Thus, the population estimates after this time are probably reasonably accurate, being affected only slightly by metamorphosis. Only the data from that point on will be considered here, for no reasonable way of correcting the earlier population estimates is available.

It is evident from Fig. 30 that the magnitude of the emigrations gradually decreased, until only three young were caught as they left the marsh on August 29 even though conditions were such at that time that a mass emigration could

have been expected to occur (see next section). Considering the two known emigration periods after August 10 and the probable one for August 29, a gradual decrease in the proportion of the population emigrating is evident as the population size decreased. (Table 5). No more mass emigrations occurred after the estimated density of population dropped to approximately 2.6/sq m though weather was suitable at least on August 29.

The possibility of dispersal being related to density is further supported by data gathered in 1961. In that year the estimated number of young metamorphosing in the marsh was 751 (calculated by proportional method), roughly three-quarters the number present on August 29, 1960. This estimate was not affected by the addition of metamorphosing frogs for it was made at the time the marsh dried up; movement in and out of the area was also negligible. Despite the fact that weather conditions were apparently suitable on at least six nights in July and August no mass emigrations such as those in 1960 occurred. The 39 frogs trapped at various times as they left the area all moved eastward, apparently the result of a need for water.

One further observation concerning the possible affects of density is of interest. On several nights in August of 1961, after the marsh had lost all of its standing water, young were found as far as 10-12 m from it in the grass. After about 9-10 a.m. most had returned to the marsh where the soil remained very wet. It seems likely that this "spreading" was a prelude to dispersal. Possibly the animals tend to avoid

Table 5

Dispersal of young Rana pipiens from Budzinski's marsh in 1960. Population estimates on August 2 and 6 are probably too high due to unknown proportion of population present as tadpoles (see text).

	No. of emigrating young trapped	Estimated number emigrating	Estimated no. of young in marsh at beginning of emigration period	Estimated density in marsh	Percent of population emigrating
August 1	103	1111	(3753)	(9.4/sq m)	(29.6)
August 6	133	1435	(3020)	(7.6/sq m)	(47.5)
August 11-13	93	1003	1898	4.7/sq m	52.8
August 16-19	45	484	1445	3.6/sq m	33.5
August 29	2	22	1046	2.6/sq m	2.1

crowding, even though they show no apparent antagonism. Consequently, when conditions are suitable they tend to move away from the mass. In a small population they would not have to move far before the crowding was alleviated, the density being decreased because of the larger area occupied; as a result they may have no further inclination to disperse. In a very large population, on the other hand, they would have to move much farther before the population became diluted to the same extent.

Sedge Point

In 1960 a large number of young metamorphosed in the Sedge Point Pools, and again in 1962 a fair number transformed there. None was produced in 1961, probably due to heavy predation, and no data were collected. Most information on dispersal was obtained by repeatedly searching the vicinity of the ponds, the lake shore, and to a lesser extent, the swamp north of the area. In 1960 three traps in the woods between the pools and the swamp, and in 1962 four traps in the woods and two on the beach (Fig. 8), provided additional information. The beach traps, one 40 m west of the west pool and the other 40 m east of the east pool, were placed so that they extended approximately 2 m into the lake and 5 m onto the shore to trap frogs moving parallel to the lake's edge.

Occurrence and Pattern of Dispersal: When Sedge Point was first visited on July 11, 1960, newly transformed and transforming young were seen to be emerging in large numbers

from the east pool and a slough which earlier had been cut off from the lake as the water receded. Both still contained large numbers of tadpoles, all in late stages of development. On July 13 and 18 the entire study area and the lake shore from 200 m west to 200 m east of the point were searched; young were concentrated largely in the east pool and in and around the slough (Fig. 32). Those on the lake shore probably had emerged from the slough, or from the lake if the tadpoles had wandered out before it was cut off. Though tadpoles were numerous in the west pool only four young were found there.

In contrast, when the study area and lake shore were searched again on July 22, following a heavy rain, only two young were found in the east pool, none in the slough. Twenty-seven were taken along the lake shore among dense sedges where young frogs had not been found previously. In further searches on July 25 and 29, the latter made with the aid of nine persons associated with the Vertebrate Natural History class at the University of Michigan Biological Station, young were found concentrated largely along the lake shore south and east of the point, and, to a lesser extent, in the swamp. Due to the large area of the swamp and the difficulty of locating frogs in the water, many were undoubtedly missed, but the 13 captured there, and 16 trapped during the rain on the night of July 21 while moving northward toward the swamp, indicate a sizeable emigration in that direction.

The 13 frogs captured in the swamp were not scattered at random over its entire area. Ten were found in two regions,

Figure 32 Capture sites of all young captured at Sedge Point on July 13 and 18 (above) and on July 22, 27 and 29, 1960 (below). Broken lines indicate edge of woods.

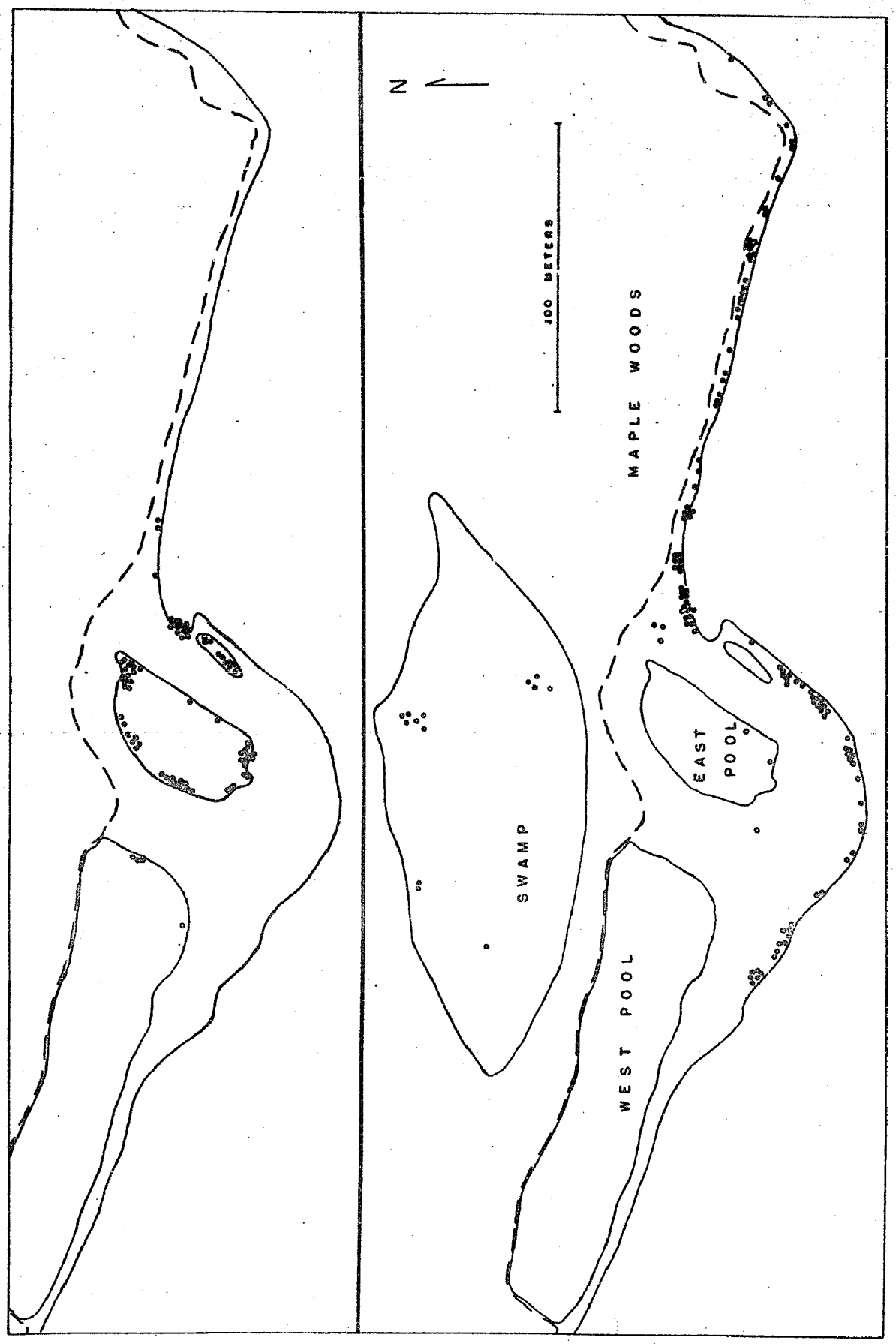


FIGURE 32

each about 10 x 10 m, where the canopy was open, small islets of moss emerged from the water, and several dense clumps of grass grew. The remainder of the swamp, where only three frogs were found, was bare of ground vegetation. Two of the 10 captured in the part of the swamp where grass grew were recaptured in the same region less than 5 m from their first capture site 26 days later, on August 24. One of the three found in late July in the portion of the swamp in which no grass grew was also recaptured on August 24 in the swamp, but it had moved approximately 40 m back toward the beach pools. It thus appears that the two young in the grassy region of the swamp, after dispersing from their place of metamorphosis, stopped moving and established themselves, at least temporarily. It is probably significant that they stopped in a region which supported vegetation similar to that in the habitats where Leopard Frogs are usually found. By contrast, the frog taken twice in the bare part of the swamp did not remain stationary.

In 1960 no young were captured more than once in the pond where they metamorphosed, and, in fact, only 12 were taken in the east pool after the July 21 emigration, though it was repeatedly searched. Emigration must have been nearly complete. In 1962, however, several young did not leave their pond of origin, at least not during the period of the study. Of 69 captured at least twice in 1962, six (9%), which had been captured in late July, were still in the pond where they transformed on the last census on August 26.

Movement along Lake Shore: After the initial dispersal from the pools there was a definite trend of movement along the lake shore, mostly eastward. This is shown in Fig. 33 in which the capture sites of all marked young of 1960 that moved more than 20 m (roughly the mean diameter of adult home ranges at Sedge Point) between their first and last capture are plotted. Eleven of the 15 captured more than once at the lake shore shifted positions 30 to 240 m from their previous locations. That there was some movement from the shore-line inland is evident from the captures of four which moved into the swamp. In 1962 a similar tendency of young to disperse along the lake shore was noted (Fig. 33). None was found in the swamp, probably because it was completely dry when the young emerged. Three, however, were trapped moving northward into the woods (not shown on map) indicating some dispersal in that direction.

Evidence gathered in 1962 indicates that the dispersing frogs did not necessarily move parallel to the lake shore as was suspected from their repeated capture at various points along it. Rather, they apparently left the shore, presumably moving into the woods, and only later returned to the lake. That movement along the beach did not occur to any great extent was clear from captures in the two beach traps. Though they captured more than 100 young Rana clamitans, these traps caught no Rana pipiens, yet three marked young are known to have by-passed the traps in moving to new locations along the shore. In addition, when the shore line was thoroughly

Figure 33 Movements of all newly metamorphosed Leopard Frogs at Sedge Point in 1960 (above) and 1962 (below) which were known to have moved more than 20 m. Circles indicate first capture; dots and arrowheads show subsequent locations. Broken lines in lower figure indicate approximate water levels in August, 1962.

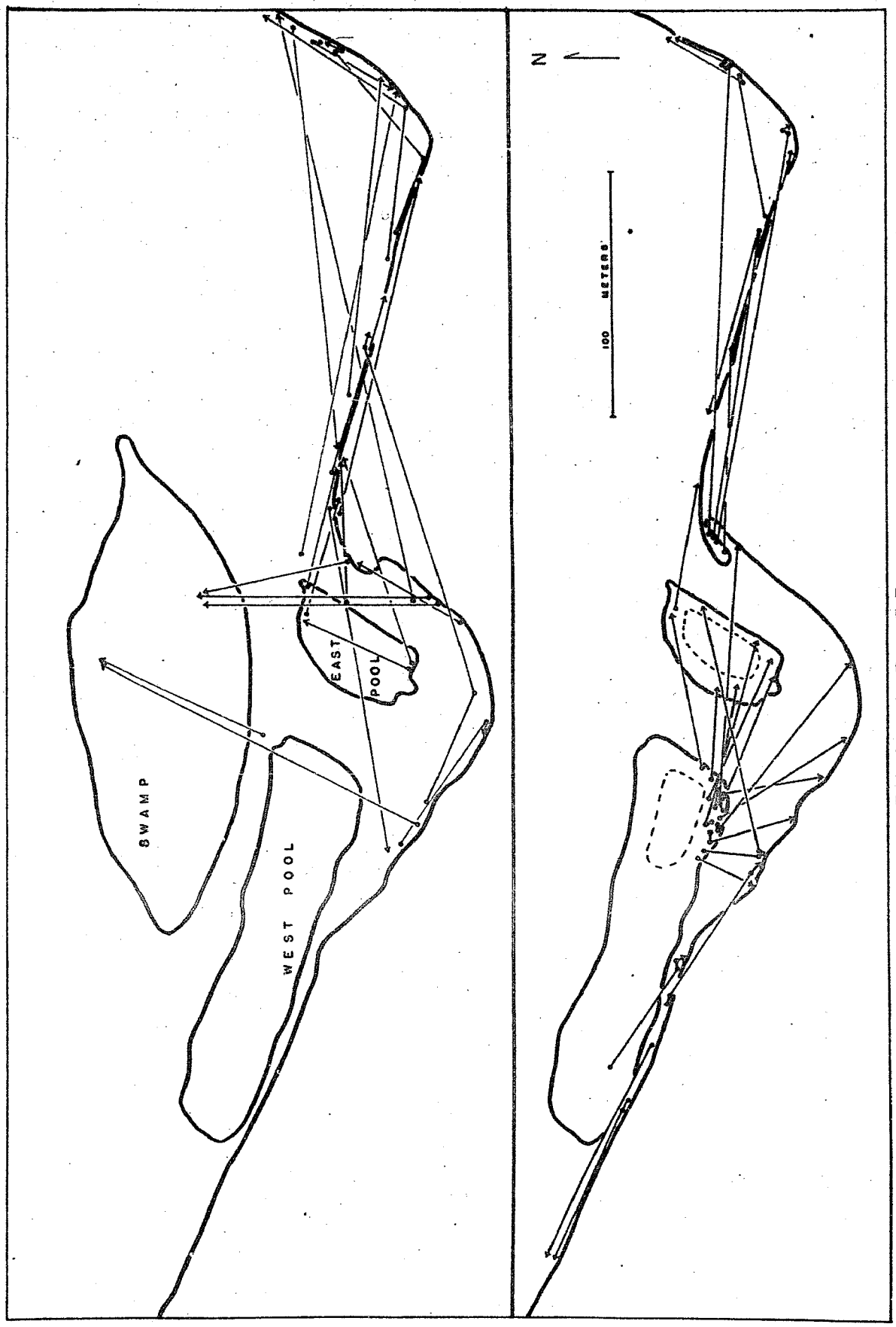


FIGURE 33

searched on August 4 following a heavy rain during the previous night, not a single frog was found. When re-searched on August 7, young were again taken at the shore indicating that they had left the lake and moved into the woods in the rain.

Ten young captured at the shore prior to the August 4 search, were retaken at the lake's edge again later in August. Five had moved to new locations 20-85 m from their previous sites. Five others, however, were recaptured less than 10 m from their sites of capture on the shore previous to August 4. These may have been missed in the search or they may have left the region and returned. It is very likely that they moved a short distance into the woods during the rain, preventing capture on August 4, and returned at some later time to the beach. In any case, it appears that these few may have developed an affinity for particular regions, similar to that shown by older frogs to their home ranges. The attachment was probably temporary, however, for two of the five moved in later rains to other places.

Most young tended to remain in small regions of the shore during fair weather. All movement between locations greater than 7 m apart occurred in periods when rain fell; presumably the movement was coincident with rainfall.

In both 1960 and 1962 young were captured much more commonly along the lake shore south and east of the point than to the west, and, in general, movement of frogs dispersing along the shore was eastward. Only five of the 20 frogs which moved to new locations on the lake shore (Fig. 33) were

captured farther westward on their last capture than on their first. In 1960, none was taken on the lake shore west of the point, but in 1962 two moved in that direction.

Movement eastward may have been passive in part, for the prevailing wind and wave action along the beach was from the west. Small frogs entering the lake when strong waves were beating the beach always came to shore again downwind from their original site, though seldom more than 1-2 m. The cumulative effect of being moved a few meters each time it entered the water could, however, result in movement of a frog over a fairly long distance.

Pronounced vegetation and substrate differences probably were largely responsible for the young frogs seldom being found along the lake shore west of the point. Whereas the shore east of the point supported dense growths of Spartina sp. and Carex americanus providing ample cover and, in fact, making capture of the young quite difficult, the west shore was almost bare of vegetation along the water's edge. Only occasional sparse sedge clumps, nowhere approaching the dense growth of the east shore, provided cover for the frogs. The substrate of the two regions also contrasted markedly. To the east the beach was sandy, generally moist as much as 1 m from the shore on calm days, and often with scattered mats of decaying aquatic vegetation washed ashore by the waves, but to the west the shore was composed of bare rocks and sand, seldom moist on calm days more than 10-20 cm from the water's edge. Frogs which dispersed along the west shore probably did

not find conditions suitable for their continued survival because of a lack of cover, and did not remain long.

Distance of Dispersal and Establishment of Home Range: Seven of the 325 young marked in 1960 were recaptured in 1961. Two, captured but once in 1960 along the east lake shore, were taken only one time in 1961. The other five, however, established their home ranges on the east side of the east pool in 1961 (Fig. 34). Why all five should have settled on the east side is not clear. It may have been related to the fact that the majority had dispersed to the east, and in returning this was the closest suitable site. It might also have been due to the general scarcity of resident adults along the east edge of the pool, for most adults had their home ranges between the two pools where the soil was always moist and a very dense cover of grass grew. The east edge of the pool had much less cover, supporting only a few willows (Salix sp.), milkweed (Asclepias scariaca) and scattered poison ivy (Rhus radicans). Perhaps, the newcomers were "forced" to take the less desirable habitats because the more habitable ones were already occupied. If this was so it implies that there may be some sort of aggressive action among adults to keep subadults out of their area, or that subadults tended to avoid older frogs.

The small number of 1960 young recaptured in later years indicates that most either did not survive to their second season or moved completely away from the study area. Though nos. 270, 456 and 457 (Fig. 34) almost certainly metamorphosed at Sedge Point there is no way to be certain that nos. 176 and

Figure 34

Capture sites of the five Sedge Point young of 1960 which were recaptured more than once in 1961. Dots indicate locations of captures in 1960; circles indicate captures in 1961; lines connect consecutive capture sites. Numbers designate frogs. Dates of capture in consecutive order:

176: Aug. 10 (1960) - July 30-Aug. 5-24 (1961)
192: Aug. 10-25 (1960) - June 30-July 9-17-Aug. 1 (1961)
270: Aug. 21-24 (1960) - June 30-July 5-9-Aug. 1-7 (1961)
456: Aug. 25 (1960) - July 11-Aug. 3-7-15 (1961)
457: Aug. 25 (1960) - July 9-15-Aug. 1-5 (1961)

Approximate edge of maple woods is shown by broken line.

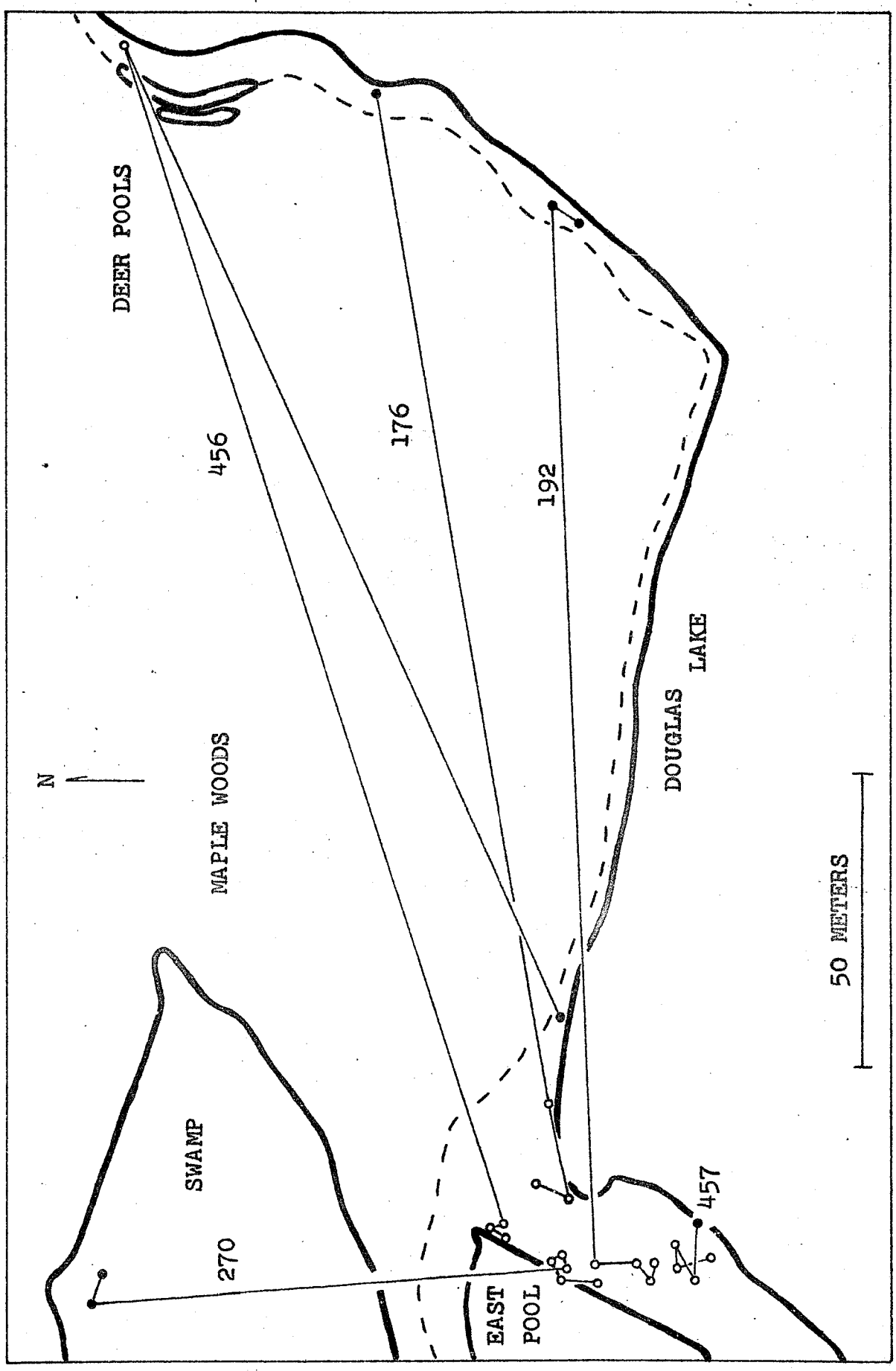

DEER POOLS
456
176
192
N
MAPLE WOODS
DOUGLAS LAKE
50 METERS
SWAMP
270
EAST POOL
457

FIGURE 34

192 were not "foreign" frogs, from Deer Point pools, 400 m northeast along the shore. It is likely that nos. 192 and 270 came (returned?) to Sedge Pools in the fall of 1960, hibernated there, and established themselves at the edge of the pool in the summer of 1961. No. 456 probably spent the winter in the Deer Point pools, for he was captured there early in the summer of 1961. As Deer Point supports a population of Rana pipiens and the area surrounding it seems to be equally suitable to Sedge Point for the establishment of a home range, it is not clear why he returned to Sedge Pools.

No. 457, in contrast to those just discussed, was captured no farther than 30 m from the east pool. In 1960 it was captured only once, along the shore, and in 1961 had a home range near the place it had been captured the previous year. If it, too, left the area for a period in late summer or fall of 1960, there is no evidence to indicate it.

None of the 1960 young which had occupied home ranges at Sedge Point in 1961 were recaptured in 1962. However, three additional 1960 young were taken in the study area two years later, each only one time. One other was found in May, 1962, in Deer Point pools, about 400 m northeast of Sedge Point; she had probably spawned there.

Discussion

As with most species of vertebrates, dispersal in Leopard Frogs is largely a function of the young, for older frogs showed strong tendencies to remain in relatively small regions. Thus most of the exchanges of individuals between populations,

hence gene flow, appears to be brought about by movements of the young very soon after metamorphosis.

Evidence indicates that young Leopard Frogs may disperse over greater distances than have been previously reported for most species of anurans. Hundreds of young entered and passed through Budzinski's in 1961 and 1962 after moving more than 800 m from the place where they metamorphosed, and two of these were known to have moved at least 1.6 km. The three marked frogs found at Nichol's Bog must have moved over 5 km. Maximum dispersal distances of young reported for other species based on recapture data have generally been much less than a kilometer. Jameson (1955) reported the dispersal of young Syrrhophus marnocki up to 328 yds before establishing residence. The same author (1956) found one juvenile Hyla regilla which dispersed 260 yards; most dispersed less than 200 yards. One Bufo valliceps was found in its second year about one-half mile from its place of metamorphosis (W. F. Blair, 1953). Although young of Rana pipiens may, in fact, be exceptionally vagile, the relatively short dispersal distances reported for other species of anurans do not necessarily indicate that the animals do not move greater distances; these data probably reflect, at least in part, the meager chances of recapturing an individual which has moved more than a few hundred meters, since, in general, the area of search is limited because of practical considerations.

The rate at which dispersing Leopard Frogs moved was found to be quite rapid. A few of the fastest "foreign" young

which were trapped entering Budzinski's in 1962 apparently moved 800 m in little more than 24 hours, but the bulk in both 1961 and 1962 moved the distance in from 48 to 72 hours. Such relatively rapid movement would enable the young frogs to cover considerable ground in only a brief time during and after rains. Those which dispersed again in later rains could conceivably cover several kilometers before hibernating in the fall.

As they dispersed, young Leopard Frogs apparently moved quite as readily through wooded areas, not the usual habitat of Rana pipiens, as through grasslands. (Though some adults did have home ranges in very wet wooded swamps, none were known to occupy the drier forest). That woods did not act as barriers to dispersal is evident from the number of young captured while moving into the maple woods north of Sedge Point. Similarly the "foreign" young which moved into the Budzinski study area probably passed through about 400 m of beech-maple forest, though some may have moved down a gravel road. Dispersal through unfavorable habitats is also characteristic of some other animals. Howard (1949) found that young Prairie Deer Mice (Peromyscus maniculatus bairdii) dispersed through woods. Anthony (1923) observed picas (Ochotona) on several occasions "miles from anything that could be regarded as their natural habitat." Although Martof (1953b) found in his study that young of the highly aquatic Rana clamitans tended to disperse along a stream, in the present study young Rana clamitans were commonly captured in the traps along with

Rana pipiens indicating that they too dispersed overland, away from their usual aquatic habitat. Jameson (1955), however, found that in the Cliff Frog (Syrrhophus marnocki) most juvenile dispersal occurred along rock exposures, the normal habitat of the species.

In spite of their willingness to disperse through more or less unfavorable regions, young appeared to show a preference for grassy vegetation types, consistent with the habitat in which Leopard Frogs are most commonly found. This was shown by the fact that ten of the 13 captured in the swamp at Sedge Point in 1960 were in regions where dense clumps of Spartina sp. and islets of moss emerged from the water, two remaining for at least 26 days. The tendency to aggregate among the grass may have been the result of the presence of cover, largely lacking elsewhere in the swamps, or possibly the islets, on which the animals could rest. Whatever the attraction, the tendency to colonize regions similar to the usual habitat of the species would be advantageous, for such regions would be most likely to provide conditions necessary for continued survival.

Dispersing frogs did not always settle down in the first suitable site which they encountered. This was clear from the fact that many which moved to Budzinski's in 1961 and 1962 dispersed again in the next rain. It is not unlikely that some continued to do so for several weeks; such repeated dispersal could conceivably carry these animals over several kilometers before hibernating in the fall. Also the repeated

shifting of young along the lake shore at Sedge Point indicates that dispersal does not always stop at the first suitable site reached.

Evidence from Budzinski's in 1960 was presented which may indicate that crowding has an effect upon the percentage of young in a population which disperse. Bovbjerg (1959) after studying dispersal in crayfish proposed the hypothesis that "animals demonstrating intraspecific aggressive behavior, territoriality, or spacing will disperse in ... a density related fashion. Conversely, those species without these behavioral attributes will disperse in a manner not related to density or fail to disperse ...". Leopard frogs would be expected to fall into the second category, for no overt aggressiveness or antagonism has been clearly demonstrated. Observations of movements of young (described in detail later), however, suggest that crowding does affect movement, for when large numbers of young were together the movement of one often disturbed others, causing them to turn and jump. Whether the disturbance of one frog by another would ultimately result in dispersal from the region or only short movements in the local area is not known.

Though environmental factors such as crowding and aggression have often been considered to have an affect upon dispersal of animals, less attention has been paid to the possibility that individual animals of the same species vary in their inherited inclination toward dispersal. Certainly there was a wide range of behavior among the young frogs, for some dispersed

long distances, often moving again and again; others dispersed only once and then settled down; still others did not disperse at all. It is entirely possible that in certain individuals there is an innate restlessness which is lacking in others. Howard (1960) has suggested this hypothesis to explain the non-random dispersal distances which Dice and Howard (1951) reported for Prairie Deer Mice (Peromyscus maniculatus bairdii), most of which dispersed long distances or not at all, while only a few moved intermediate distances. Burt (1949) states in regard to mammals "if ... there is an inherent desire to wander, it most certainly is not developed to the same degree in all individuals of a species." Though an inborn predisposition to wander has not been clearly demonstrated for any animal it is probable that variations within species in this respect do exist. In fact, it is possible that the lack of mass emigrations from Budzinski's in late August, 1960, was not due to decreased density at all, but was the result of the earlier departure of all frogs with a tendency to disperse, leaving behind only those frogs lacking such a predilection. With the data obtained it is not possible to be certain which explanation is the correct one.

Recency of metamorphosis did not appear to be a crucial factor in determining the predilection of young to disperse. Incompletely metamorphosed young, many still with tails (up to 15 mm long), were commonly trapped as they dispersed, as were numerous young which had obviously metamorphosed several weeks prior to dispersal. Thus, it is unlikely that young

lose the urge to disperse (assuming they have it) as they grow older, at least during their first season.

Some idea of the relative importance of the dispersing and non-dispersing frogs as replacements in local populations can be deduced from the young which later established home ranges as subadults in the study areas. At Budzinski's only one (0.4%) of the 140 known to have entered the study area from another pond in 1961 established a home range there. Four (0.9%) of the 431 local frogs of 1961, for which there was no evidence of emigration, did so. These facts suggest that dispersing frogs may account for a smaller proportion of the replacements in local populations than do those which fail to leave their place of metamorphosis. Probably a larger percentage of dispersing frogs is lost through predation, dehydration, and other causes than of those which remain where they metamorphosed, so that survival among the dispersing frogs is much lower.

Even among those which emigrated, dispersal distance was not always extreme. This is indicated by the recapture in Budzinski's study area in 1961 and 1962 of eight frogs trapped leaving Budzinski's in 1960. Though all were recaptured only once, the fact that they were taken at all suggests that they had settled in the vicinity, probably not more than a few hundred meters from the pasture. Likewise at Sedge Point some frogs which dispersed did not move far and at least two (possibly four) returned to Sedge Point after emigrating. Such return to the place of origin had no parallel at Budzinski's,

for none which were known to have left the study area established a home range there in subsequent years. Probably the greater tendency to return to Sedge Point was the result of few habitats in the vicinity favorable for continued occupation. The point was entirely surrounded by the lake to the south and forest extending more than a kilometer north. Aside from Deer Point pools, 400 m northeast, and Hook Point pool, 550 m northeast, both on the lake shore, no other breeding populations of Rana pipiens were known within a radius of a kilometer.

Climatic Factors Affecting Dispersal of Young

Dispersal of young Leopard Frogs was shown in the previous section to be unevenly distributed in time. On particular nights large numbers of animals dispersed together, these periods of mass movement separated by nights when few or no frogs left the area (Fig. 30). The more or less synchronous emigration of large numbers of frogs suggests that climatic conditions were important in regulating the time of occurrence of dispersal. Because of the complex nature of environment, and individual differences among frogs, an analysis of the roles of the various climatic factors in regulating emigration of young is difficult. No single weather condition was invariably associated with dispersal, implying that emigration is not entirely dependent upon one particular environmental factor but may occur under more than one set of conditions. Despite the difficulties involved, it seemed worthwhile to attempt to determine the influence of some of the major environmental factors on the activities of young. Information about environmental effects on dispersal was collected both in the field and from laboratory experiments; evidence from the two sources will be presented separately.

Field data

Most of the field data on influence of weather upon dispersal were obtained in 1960 when large numbers of young

emigrated from Budzinski's marsh and Sedge Point pools. Records of rainfall, temperature and relative humidity in the study areas were kept, and a record of barometric pressure was obtained from the United States Weather Bureau, Pellston, Michigan, 16 km WNW of Budzinski's and 5 km WSW of Sedge Point. The correlation of the time of occurrence and magnitude of dispersal, as determined by trap captures, with climatic records, permitted a partial analysis of the factors influencing emigration. No mass emigrations comparable to those in 1960 occurred in 1961 and 1962 due to the small numbers which metamorphosed.

Rainfall:-- Of all the meteorological factors considered, precipitation seemed at the outset the most likely to influence activity in animals so dependent upon moisture as are frogs. Several occurrences in the field indicated that rain did indeed play an important role in initiating dispersal. Not only did the two largest mass emigrations, (August 1, 6) and a third, smaller one (August 13), from Budzinski's in 1960 occur on rainy nights, but dispersal from the east beach pool at Sedge Point in the same year also apparently took place in a rain. In addition, immediately after a rain in 1962 when the lake shore at Sedge Point was searched no young could be found, although several had been taken there only a few days previously and many were again back at the shore four days following the rain, suggesting that they left the area temporarily during it. Most of the shifting along the shore occurred in periods of rainfall.

In addition, direct observations of young showed clearly that their activity was influenced markedly by precipitation. In more than 30 hours, approximately nine in rains, I spent observing young from a blind in Budzinski's gravel pit, a good indication of the nature of their activity was obtained. A summary of their behavior is presented below.

In fair weather small Leopard Frogs typically were more or less sedentary, not unlike adults (described earlier), often sitting for several hours in the same spot, changing locations only to feed or when disturbed by predators. During rains, however, they became much more active; three more or less distinct reactions were observed. The most obvious, and the one manifest by almost all frogs at the onset of rain, was a general, apparently non-directional, increase in activity. As rain began, the small frogs made short leaps in a more or less random manner but did not leave the general area. Those moving often stimulated others to become active by hopping close and apparently disturbing them. They in turn jumped, and in a dense population a chain-reaction usually developed, each frog jumping when disturbed and in turn disturbing others. The total result gave an appearance best described as a general milling of the animals. It was impossible to follow individuals for very long so it is not known if all frogs were involved or if some simply sat while the others moved about. I suspect all did some moving, though movement may not have been continuous for any individual.

Some of the frogs, however, crawled under objects or into dense clumps of vegetation as though seeking shelter from the rain. This shelter-seeking reaction was most pronounced in light drizzles, during which many frogs were successful in getting out of the rain. Those which succeeded generally remained under shelter and did not move about further. In intense precipitation some frogs still attempted to escape the rain, but there was less success, and activity remained at a high level.

Occasionally from among the actively moving frogs one could be seen to execute a rapid series of leaps in a straight line away from the rest and disappear into the surrounding vegetation. This is interpreted to be true dispersal movement, for of the three reactions mentioned only this one would be likely to result in emigration from the pond. In the single diurnal rain in which behavior was watched (1.25 hrs in and after a very light sprinkle which lasted only 15 min) none of the frogs was seen to leave the group of approximately 20 young being watched. In crepuscular or nocturnal rains, however, such behavior was more common, possibly as many as 5-10% of the population leaving the mass in a two hour observation period in an intense rain. Even for as long as an hour after a rain had stopped (observations were not continued longer) an occasional frog could be seen to disperse from the pond, although the active milling usually stopped with the rain.

Since the young frogs always became active almost simultaneously with the start of precipitation, there seems no doubt that the activity was a direct response to the rain; apparently rainfall is a causative factor in initiating movement rather than one which simply allows it to take place.

Barometric pressure:-- Although the largest emigrations from Budzinski's marsh in 1960 occurred in conjunction with rains, some young frogs were trapped while leaving the area on almost every night in August. Since the periods in which dispersal was greatest (Aug. 1, 6, 11-13, and 16-19) showed a close correlation with rapid drops in barometric pressure (Fig. 30), it seemed possible that pressure changes might also be an important factor in initiating activity. The lack of mass emigrations when the pressure fell after August 19 may have been due to the lowered density of frogs (see previous chapter). In an attempt to determine if changes in barometric pressure could stimulate young frogs to become active a series of laboratory experiments was conducted; these are described later.

Light:-- Dispersal of young was almost totally confined to the dark part of the diel period, as determined by the scarcity of trap captures during daylight. Of 472 frogs trapped while leaving the marsh at Budzinski's in 1960, only three fell in the traps between 8 a.m. and 8 p.m. Thus, it appears that a very low light intensity is necessary for dispersal activity. The fact that no dispersal movements were

observed in the single diurnal observation in a rain is probably significant, but the lack of such movements might also have been because the rain was of short duration and low intensity rather than because of the higher light intensity.

Since light intensity measurements were not taken, the photic level above which emigrations do not occur is not known. Neither was it determined if bright moonlight or starlight inhibited activity, as no records of cloud cover were kept. It was found, however, that migratory movements of adults, once initiated by a rain, usually continued until daybreak even though the sky cleared and the moon shone brightly. It is likely that young responded similarly.

Since the "foreign" frogs which entered Budzinski's in 1961 and 1962 were trapped on several consecutive nights, but none was taken during the daylight, it is probable that dispersing frogs stopped during the day in wet places and did not resume moving until the following night, in a manner similar to that of the migrating adults. No evidence was obtained that they migrated during daylight, even when overcast or rainy, though Martof (1953b) found that Rana clamitans became hyperactive before a rain and concluded that "the activity demonstrated before a rain was no doubt greatly stimulated by the decrease in light that generally accompanied precipitation."

Though the amount of light undoubtedly affected the time of occurrence of emigrations, low light intensity by itself was not sufficient to initiate such activity, for mass dispersal did not occur on every night.

Temperature: That temperature affects the activities of a poikilothermic animal scarcely needs confirmation; it is not surprising to find a significant correlation between the number of frogs trapped while leaving Budzinski's marsh in 1960 and the minimum temperature during the night ($P < .02$). There is no doubt that temperature plays an important role in regulating dispersal, for emigration would not be expected to occur unless the weather was suitably warm, even if other conditions favored such activity.

Although in general the largest emigrations occurred on nights when the temperature remained fairly high, dispersal was not confined to these nights. Even when the temperature fell quite low during a night a few frogs were trapped as they emigrated. On the nights of August 15 and 24, when the minimum temperature was 10 C, the lowest temperature recorded in August, 1960, one and two young respectively were trapped; on the night of August 8, when the temperature fell to 11°C, eleven were trapped while leaving the marsh. It is very likely that on such cold nights most dispersal movement which occurred took place in the few hours following sunset while the weather was still relatively warm.

In general the temperatures on rainy nights in summer remained high, and did not show the sharp decline through the night which generally occurred on clear nights. It is very probable that the greater number of frogs trapped on nights with precipitation was, at least in part, due to the higher temperatures, allowing the frogs to be more active

as a result of their higher metabolism. Also, the longer time over which activity could continue, the result of the temperature remaining at a high level all night, allowed more movement to occur.

It is unlikely, however, that warm weather alone initiates mass dispersal, even though it is a necessary condition if emigration is to occur. The lowest minimum temperature on any of the nine nights, August 1, 6, 11-13, and 16-19, which together accounted for 80% of all the young frogs trapped while leaving the marsh in August, 1960 was 15 C; 29 were trapped while they emigrated on the rainy night of August 13 when the minimum temperature was 15 C. The minimum temperature was above this level on seven other nights when fewer than ten animals per night were trapped.

Atmospheric Moisture: There is no doubt that atmospheric moisture affects the behavior of Leopard Frogs, the higher humidities allowing the animals to be active away from water without risking rapid water loss. However, high humidity alone did not initiate dispersal movements, for there was not a single night during the three summers of the study when the relative humidity in the grass failed to reach 100%.

Dew: Though Leopard Frogs utilized dew as a water source, its presence appeared to play no part in initiating dispersal. Dew formed only on clear nights, while emigrations usually occurred on overcast and rainy nights.

Evaporation: The effects of relative humidity, temperature and wind can be combined into a single function, evaporation. In 1962 two Piche evaporimeters were used at Budzinski's, one placed in the grass near the marsh, the other south of the field among the sumacs, each with its evaporating disc 5 cm from the soil surface, where conditions closely approximated those encountered by the frogs.

Due to the high relative humidity it was not unexpected to find no evaporation occurring during most nights; in fact on nights with heavy dew the evaporimeters took on water. Only a single night, one with considerable wind, showed a measurable amount of evaporation. There is no evidence that low evaporation alone stimulated dispersal, for most nights fell in this category. It is likely, however, that a night during which water loss to air was high would be unfavorable for emigration and retard its occurrence.

Laboratory Experiments

The evidence that both rain and barometric pressure changes might be important in stimulating movements of young prompted a series of laboratory experiments. These were conducted in the winter of 1961-62 in Ann Arbor using recently transformed young, raised in the laboratory from eggs artifically stripped from Leopard Frogs obtained from a Wisconsin supply house.

Experiment I: A chamber 3.05 x 0.61 x 0.61 m with the upper side open was constructed of plywood. A 45 x 25 x 5 cm

enamel pan, its bottom covered with sand, was placed at one end to form a "pond." The remainder of the chamber was sodded with sedges and grass, ranging in height from 10 to 30 cm, to simulate natural conditions; the sedges were placed in the third of the chamber nearest the "pond" while grass provided cover elsewhere. The soil was kept continually wet by frequent watering. To the end of the chamber opposite the "pond" was attached a 15 cm wide runway which opened through a 15 x 25 cm opening cut in the center of the end of the chamber, the bottom of the runway flush with the surface of the sod in the chamber. The surface of the runway was covered with dry sand and gravel to approximate conditions on a gravel road. At the end of this 1.8 m long runway another, smaller chamber (0.61 x 0.61 x 0.61 m), sodded with grass but containing no water, was attached. Two treadles, one at each end of the runway, recorded the passage of frogs on a 24-hour kymograph, from which the time of crossing could be determined. The main chamber was constructed so that simulated rainfall, produced by nozzles attached by means of flexible garden hose to a mixing faucet, could be controlled by adjustments of the faucets and nozzles. The nozzles allowed the water to be dispersed as individual droplets falling randomly throughout the main chamber, but neither the runway nor the small chamber received "rain." A recording hygrothermograph kept a constant record of temperature and humidity in the large chamber while a microbarograph recorded pressure changes. Fluorescent lights, controlled by an automatic time switch

set for seven hours dark, 17 hours light (approximate summer conditions in northern Michigan), provided illumination. Thermostatically controlled heating in the room kept the temperature nearly constant, never varying beyond 20-24 C. A thin sheet of polyethylene over the chamber kept the humidity between 70 and 80% except during and immediately after "rains," when it reached saturation. For observing activity after dark a set of low intensity red lights, providing sufficient illumination for observation, but apparently not affecting the behavior of the animals, was utilized.

Small Leopard Frogs, within seven days after metamorphosis was completed, were placed in the "pond" in the main chamber and their behavior observed. Confinement did not seem to alter the usual daily activities of these frogs for they seldom move about in nature. Typical behavior in periods of no rain, both day and night, was to remain sitting in the same location for the entire duration of an observation (usually two hours).

During "rains," however, most frogs moved about the chamber in a more or less random manner similar to that observed in the field. What appeared to be dispersal movements of the same type as those seen in the field also occurred, for occasionally a frog which had been moving randomly would suddenly execute a rapid series of hops in a straight line from one end of the chamber to the other. Upon reaching the wall it usually leaped at it several times as if trying to get out, but finally moved off in another direction to

resume the random movements. Shelter-seeking behavior such as was seen in the field was also observed in the chamber during "rains." On one occasion when "rain" (a light drizzle) was allowed to fall in only one-half of the chamber for 15 minutes before it was begun in the other half, the three frogs receiving the water directly became active immediately, but two at the opposite end of the chamber did not leave their usual spots. Only when they, too, received the rain did they become active. In addition, one of the three which began moving in the "rain" stopped upon reaching the end of the chamber where no "rain" was falling; the other two continued to move actively in the "rain" until each eventually found refuge under clumps of sedges where they, too, stopped.

In Tables 6 and 7 are given the conditions for each occasion when a frog left the main chamber and entered the runway. Although the runway was open and available to the frogs throughout the 104 days of the experiment, frogs were recorded entering it on only 24. Those emigrations which occurred on nights when "rain" fell are listed separately from those which took place at other times. All "rains" began within 30 min. after the lights went off and lasted for 15-30 minutes. Although "rainfall" was not measured at each observation, in general, the intensity of drizzles was approximately 0.3 mm "rain" per minute while in hard "rains" approximately 1.5 mm fell per minute.

Of the 114 passages through the runway, 80 (70%) occurred on nights when "rains" fell. This does not differ

Table 6

Environmental conditions in experimental chamber and emigrations of young frogs on the 14 nights when "rain" fell. Relative humidity on all nights was 100%.

Date	No. of frogs in chamber	Precipitation Duration Min.	Precipitation Intensity	Pressure changes*	No. of crossings recorded	Comments
Feb. 19	3	15	Drizzle	741-746-749	2	
Mar. 1	4	20	Hard	760-764-764	4	
11	4	20	Hard	747-737-730	6	
20	4	20	Hard	743-743-738	4	
26	4	20	Hard	749-749-749	4	
29	5	20	Drizzle	743-742-744	2	
Apr. 2	8	20	Drizzle	747-754-757	3	(1 in small chamber following morning; returned next night)
6	12	30	Hard	748-747-743	5	(1 in small chamber following morning; returned in daylight)
15	10	30	Hard	744-750-752	2	
17	10	30	Hard	753-749-746	3	
22	10	30	Hard	745-742-745	7	(1 in small chamber following morning; returned in daylight)
25	9	30	Hard	745-745-745	5	
May 7	8	30	Hard	750-749-747	19	(4 in small chamber; returned in daylight)
17	19	30	Drizzle	754-753-753	14	

* Center figure indicates pressure (mm Hg) at time of rain; outside figures indicate pressure at time the lights went on on mornings preceding and following the rain. In all cases where two or more consecutive figures are identical the pressure showed no fluctuations of greater than 1 mm in magnitude in the interval.

Table 7

Environmental conditions in experimental chamber each time a frog entered the runway in absence of "rain."

Date	No. of frogs in chamber	Precipitation	Pressure changes*	Rel. Hum. (in %)	No. of crossings recorded	Comments
Feb. 27	4	none	749-748-745	80	1	(crossed in day; returned following night)
Apr. 28	9	none	741-741-742	80	#	
29	8	none	742-744-745	75	1	(in small chamber following morning; returned in daylight)
30	8	none	Variable (see Fig. 35)	80	6	(concurrent with pressure change; tornado)
May 4	8	none	747-749-749	80	1	(in small chamber following morning; returned next night)
13	8	none	748-746-746	70	#	
16	19	none	753-754-754	75	#	
19	19	none	Variable (see Fig. 35)	100	23	(heavy thundershowers outside)
21	19	none	745-744-745	80	1	(in small chamber following morning; returned in day)
23	18	none	744-738-738	75	1	

Frog entered near end of runway but did not traverse it.

* Center figure indicates pressure (mm Hg) at time lights went out on date given; outside figures indicate pressure at time lights turned on on the mornings preceding and following. In all cases where two consecutive figures are identical the pressure showed no fluctuations greater than 1 mm in magnitude in the interval.

greatly from the data obtained at Budzinski's in 1960 when 62% of the frogs trapped as they left the marsh did so on rainy nights. On every one of the 14 nights when "rain" fell in the chamber, at least one frog (i.e. 2 crossings) left the main chamber irrespective of whether barometric pressure was rising, falling, or steady. The relatively few emigrations early in the experiment were probably due to the small number of frogs in the chamber at that time. As more frogs metamorphosed and were added to the population, the number crossing during rains increased.

Occasionally frogs traversed the runway, or entered one end in the absence of rain, accounting for 30% of the crossings. These individuals may have been "exploring," as suggested by three which entered only the near end of the runway, then retreated again to the large chamber. Perhaps some, more restless than others, were attempting to disperse.

On two occasions, when there was no "rain" in the chamber, activity increased considerably over its usual level. On April 30, six, and on May 19, 23 crossings were recorded. The movement on April 30 occurred at the time of passage nearby of a tornado which was accompanied by a drop of 4 mm of mercury in a six-hour period, followed by a very rapid rise of 2.5 mm in about 10 min. (Fig. 35). The first emigration was recorded shortly after the rapid rise in pressure, at about the time the lights went off. The movement on May 19 began as the pressure began to fall rapidly, following the passage of several thunderstorms which were accompanied by

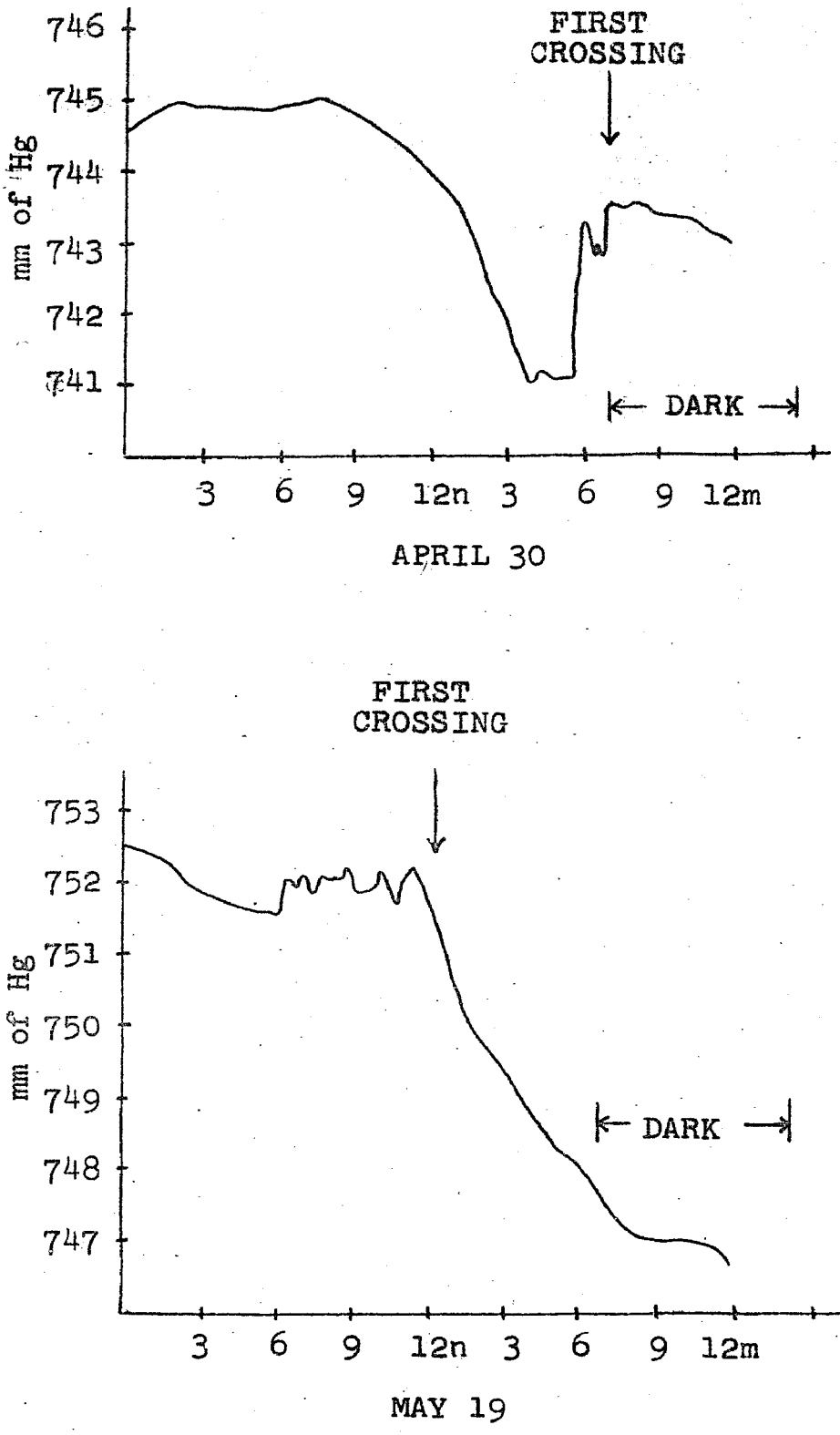


Figure 35 Changes in barometric pressure in experimental chamber, April 30 and May 19, in relation to dispersal.

rapid fluctuations in pressure of the magnitude of about 0.5 mm of mercury (Fig. 35). Six of the 23 crossings occurred before the lights were scheduled to go off. Although no records are available and I was not present to see, it is possible that during or following the thunderstorms a general power failure caused the lights to go out temporarily, perhaps accounting for the emigrations before the lights were supposed to have gone off. In view of the rapid changes in pressure on these two occasions whereas other conditions remained constant (except relative humidity, which on May 19 rose to 100%, the result of a general increase in atmospheric moisture accompanying thundershowers outside) it is probable that the animals detected and reacted to the pressure changes. It is doubtful that the increase in humidity on May 19 initiated the movement, since on three other nights in May the humidity rose to saturation but no movement was recorded.

Experiment II: To test further the hypothesis that a change in barometric pressure can stimulate activity, a second experiment was designed. For this an aktograph consisting of a circular surface 20 cm in diameter with contacts dipping into vials of mercury and recording on a kymograph was constructed. The apparatus was placed under a bell jar, into which the frogs to be tested were introduced, and the bell jar sealed. The pressure within the bell jar was regulated by withdrawing air through a hypodermic syringe. Wet paper toweling kept the humidity in the chamber at saturation. All tests were run in temperatures between 20 and 23 C, the

greatest temperature fluctuation recorded during a single test being slightly more than 1 C. A cardboard box over the entire apparatus excluded most of the light, simulating conditions at night.

Because of the design of the aktograph, only changes in position of 6-7 cm or more, or leaps in which the animal temporarily left the platform, recorded as movements. Shifts of position involving no change in location, or a change of less than 6-7 cm, did not record.

Frogs within seven days after metamorphosis were tested one at a time on the aktograph for four-hour periods. Each was tested twice, once with the pressure falling at the rate of 4 mm Hg per hour and again while the pressure remained stationary. The two tests for each frog were run at the same time of day on two consecutive days. Eleven of the animals were subjected to the falling pressure first and 12 to the constant pressure. In all, 23 frogs were tested.

In Table 8 are presented the data derived from these 23 frogs. There was a marked degree of variation in activity among individuals, for while three did not move at all during a four hour test period, two moved more than 300 times under the same conditions. While, in general, those frogs which were extremely active under one set of conditions were also the most active under the other, the correlation between the amount of activity under the two sets of conditions was not statistically significant ($P > .10$).

Table 8

Number of recorded moves made by 23 recently metamorphosed Rana pipiens under experimental conditions with atmospheric pressure constant and again while dropping at the rate of 4 mm Hg per hour. Asterisk indicates animals subjected to falling pressure first.

Frog	Pres. Constant	Pres. Dropping	Order of Tests
1	2	51	
2	0	67	*
3	83	153	
4	340	106	
5	6	44	
6	4	26	*
7	365	138	
8	120	125	*
9	49	101	
10	0	23	*
11	6	15	
12	0	38	*
13	5	4	
14	21	6	
15	8	25	*
16	12	8	*
17	53	6	
18	29	4	*
19	74	36	*
20	88	2	
21	184	53	
22	7	7	*
23	75	2	*

Eleven of the frogs tested showed the most activity in decreasing pressure but an equal number was most active when the pressure remained constant. One moved the same number of times in each test. No statistically significant relationship between the amount of activity (as measured by the number of moves recorded) and the conditions of pressure was found ($P > .05$). Neither could any significant association between activity and the natural pressure changes to which the animals were subjected prior to each test be discovered. Previous experience with the testing apparatus appeared to be unimportant in determining the amount of activity manifest by the frogs, for no statistically significant tendency among the group of 23 frogs to increase or decrease their activity on their second tests (irrespective of pressure conditions) could be found ($P > .05$).

Thus, these data fail to support the previous hypothesis that pressure changes stimulate activity. These results may be misleading, however, for it is likely that the failure to obtain a correlation may have been due to several factors: (1) The confined nature of the chamber, allowing a frog to make at most two or three hops in any one direction was not conducive to dispersal movements which take the form of a rapid series of hops in one direction; (2) the lack of other individuals may have retarded movement, for observations indicated that the presence of other frogs often increased activity; or (3) the handling of the animals in placing them in the bell jar, as well as the completely unnatural environment, may have influenced their behavior.

Discussion

Noble (1931) and others have suggested that migration may take place without external stimulation in some species of amphibians. Noble pointed out that some salamanders, for instance, retain their normal periodicity of egg laying in the laboratory and "probably, therefore, in their desire to migrate." Though he was concerned with breeding migrations, the same might apply in dispersal, for it has been suggested by Howard (1960) that young animals possess an innate desire to wander. If this is true, then it is possible to assume that the "stimulus" to disperse is internal (perhaps hormonal) and always present, but the response (emigration) is only manifest when favorable conditions permit the animals to leave the ponds. Such an internal restlessness can neither be proved nor disproved from data gathered in this study.

Evidence was obtained, however, which shows that at least one environmental factor, rain, actually stimulates activity and does not simply permit it to occur. This was evident from the observations, both in the field and in the laboratory, that almost immediately at the onset of rain, frogs, which had previously been quiescent, began moving very actively. Such behavior was not observed at any other time, though the passage of several frogs across the runway in the experimental chamber on two nights with rapid pressure fluctuations, suggests that activity must have been at a high level on these occasions as well. Apparently rainfall is an important causative factor in initiating movement, thus

explaining in part the tendency for large numbers of frogs to disperse on rainy nights.

What it is about rain which acts as a stimulus is less clear, however. The increase in activity was not the result of increased humidity alone, for atmospheric moisture in the field reached saturation every night, yet mass movements did not always occur even when temperatures were sufficiently high. In addition, frogs in the chamber which did not receive rain directly did not become active even though the humidity increased to 100%. The shelter-seeking behavior of many young indicates that the drops striking their bodies may act as irritants, thereby stimulating activity. The suggestion of Martof (1953b) that they respond to the falling drops as though they were elusive prey seems unlikely to apply here, for no indication of attempts to feed on falling drops was noted. Although two instances of frogs striking at water droplets rolling slowly down a grass blade were seen, this behavior was so rare as to be of no effect in migrations.

Observations of other investigators also implicate rainfall as being an important factor in the dispersal of young Rana pipiens. Fitch (1958) has reported that "... during and just after heavy rains there is a mass dispersal [of newly metamorphosed Rana pipiens], with relatively few remaining behind ... successive waves of migrants emanate from the breeding ponds throughout the summer ..... Within a few hours after heavy rains, frogs have been caught in funnel traps on slopes and hilltops hundreds of yards from the ponds, where probably the trip was begun." Scott (1938) found dead

Rana pipiens and Acris crepitans on an Iowa road adjacent to a marsh after a storm. He estimated the density to be 10 per sq yd. Although he failed to indicate the size of the frogs, judging from the number of animals and time of year, the Rana pipiens were probably young dispersing from the marsh in the rain. Whitaker (1961) while studying Zapus hudsonicus, trapped numerous small Rana pipiens in mouse traps and found that they were more commonly taken following rains.

An association between rain and emigrations of young of some other species of amphibians has also been demonstrated. Blair (1953) found that juvenile Bufo valliceps were stimulated to disperse by a heavy summer rain and Martof (1953b) concluded that most dispersal of newly transformed Rana clamitans was accomplished during rains. Jameson (1955) found very small individuals of Syrrhophus marnocki only on nights following summer showers, suggesting that rain is an important factor in dispersal of that species. The influence of rain on movements, particularly breeding migrations, has also been reported for many species of amphibians (Blanchard, 1930; Packer, 1960; Fitch, 1956; Pearson, 1955; Pyburn, 1958; Martof, 1953b; and others) suggested that the influence of rain on the activities of amphibians is a rather general one.

Inconclusive evidence was also obtained which suggests that young Leopard Frogs might also be able to detect pressure changes and respond to them in the same manner as to rain, i.e. by becoming more active. Since rainfall is often accompanied by a fall of the barometer it is not unlikely that

the animals respond to both, perhaps either alone acting as a stimulus to some frogs, but the occurrence of both together initiating the most pronounced activity. The possibility that pressure changes might affect behavior of amphibians has been seriously considered by only a few investigators. Bogert (1960), however, recognized its possible importance for he states that "changes in ... atmospheric pressure may be effective in arousing migration behavior in some species, or they may be necessary supplements to rainfall as the primary stimulus to others."

Certainly many organisms, probably including frogs, are sensitive to pressure changes. Oliver (1955) mentions that Beck was able to induce mating behavior in Scaphiopus h. holbrooki by lowering the pressure in a vacuum jar. Bogert (1960), referring to the same animal, states that "little attention has been paid to the possibility that the sudden lowering of atmospheric pressures stimulates breeding activity in the species. The drop in pressure commonly accompanying periods of abnormally heavy rainfall would, however, offer a more plausible explanation than the absorption of water" for the initiation of breeding activities. Hicks (1949) states that in the Western Fox Squirrel (Sciurus niger rufiventer) the "degree of activity is, in general, related proportionally to magnitude of pressure," but "the specific effects of pressure isolated from the interactions of any other environmental factor are unknown."

Wellington (1946) after an extensive review of 78 articles concerning the effects of pressure changes on insects

concluded that "lowered pressure acts to increase the rates of various activities of insects, including undirected locomotor activity." Since his paper was published Stephen and Bird (1949) have indicated that periods of high pressure promote long distance flights in the cabbage worm butterfly (Pieris rapae), while it is stimulated to egg laying by low pressure, laboratory experiments demonstrating a definite increase in oviposition. Broadbent (1949) found that aphids flew more readily when barometric pressure was fluctuating than when it was steady.

Only in Packer's paper (1960) on Taricha rivularis did I find any previous attempt to correlate pressure changes with dispersal activity of amphibians. His is a negative conclusion for he found "no correlation ... between either changes in or the absolute level of barometric pressure and the magnitude or direction of movement other than those which can more easily and more precisely be defined on the basis of rainfall alone." This is not surprising since a fall in pressure is often accompanied by rain. As he does not present his data the possibility that pressure does affect these animals cannot be ruled out.

Although temperature is an important factor affecting activity there is no evidence that it initiates dispersal movement. The fact that mass dispersal only occurred when the weather was sufficiently warm is undoubtedly the result of the general effect of temperature changes on all bodily functions in a poikilothermic animal. Other investigators,

too, discount temperature changes as being the initiating cause of movement. Blanchard (1930) found rain to be more important than high temperatures as the migratory stimulus in Ambystoma maculatum even though such movements only occurred when the weather was warm. Packer (1960) found a correlation between temperature and the number of Taricha rivularis migrating but concluded that a "high relative humidity can overcome the inhibitory effect of a drop in temperature." Savage (1961) discarded temperature as a stimulus to migration in Rana temporaria with the following statement: "I doubt very much if the temperature effect is anything more than the result of the general 'poikilothermous effect,' and is no more a 'stimulus' to migration than raised temperature is a stimulus to digestion."

It is clear that at least three factors, rain, temperature, and illumination, and possibly a fourth, pressure, are important in regulating dispersal in young of Rana pipiens. In general, the greatest amount of dispersal takes place on warm rainy nights, but considerable numbers of young may also leave the ponds on warm nights without precipitation, perhaps stimulated by a drop in pressure. Emigrations on cool, clear nights when barometric pressure is high tend to be much smaller.

Discussion

Dependent upon age, season, and particular environmental conditions, Leopard Frogs in this study exhibited several different types of activity. In general, their movements can be separated into the following more or less distinct categories:

1. Travel to the breeding ponds from the hibernacula in the spring.
2. Movement within the breeding ponds, which may or may not be associated with mating behavior.
3. Post-breeding migrations to other ponds during the spring, probably occurring in conjunction with rains and involving only spent animals.
4. Shift from the spring habitat of the ponds to the home range in outlying areas.
5. Routine day to day movements in summer from one resting spot (form) to another within the home range.
6. Migrations from the home range in conjunction with nocturnal rains, followed by return to the range, usually within a few weeks.
7. Temporary return to ponds from the home range in summer, brought about by unfavorable moisture conditions.

8. Shifts to new home ranges late in second or early in third season, rarely involving adults.
9. Dispersal of young from the ponds.
10. Movement to the hibernating sites in late fall.

A few comments on several of these types of movements are in order here.

Although breeding migrations were not specifically studied in the present investigation, Cummins (1920) has reported information concerning this phase of the yearly cycle of Rana pipiens activity. His data indicated that migration to the breeding ponds took place both in the light and dark, for he trapped 22 frogs moving to the water in daylight and 17 at night. He concluded that the stimulus inciting migration and the factors controlling migratory behavior operate independent of light and darkness. This is in contrast to the behavior of Leopard Frogs in the summer, as determined in the present study, for they did not usually make long excursions overland during daylight, confining such activity to the dark part of the diel period. It is very likely that the tendency for the frogs to move more actively in daylight in early spring is a result of the lower nighttime temperatures at that time of year, which probably often inhibit nocturnal activity.

Among the frogs trailed in the present study only five showed substantial movement off their home ranges in daylight, two of them forced to return to the ponds for water,

two moving to their home ranges from the ponds in mid-June, and one returning to her home range after an excursion from it (Fig. 16, 3523). Certainly the two frogs which left their ranges to return to ponds did so out of necessity for water, the need for moisture overcoming their reluctance to move in daylight. The occasional daytime movements of the two frogs moving to their home ranges from the breeding ponds might have been partially the result of lower temperatures at night, but it is also possible that frogs off their home ranges are more restless so that the attraction for the home range overcomes the tendency to refrain from excursions in the daytime. A strong attraction to the home range, may also explain the continued movement after daylight of no. 3523, following a long nocturnal journey. There is little doubt that she could have reached the swamp before daybreak had she not been delayed twice by running out of thread, but this does not invalidate the possibility that her diurnal movement was prompted by an attraction to the familiar area of her home range.

Although much attention has been put on the fact that an animal's home range is the area over which it habitually travels in search of food or homesites, and with which it is familiar and thus better able to escape enemies, in addition the attachment to familiar areas is probably a psychological phenomenon. Not only does a home range satisfy the physical needs of an animal, which might be served equally well elsewhere, but because of a psychological association

with the particular area, an animal probably moves with assurance and has a sense of well-being, which is lacking in unfamiliar surroundings. Discordant feelings may be aroused when off its home range, so that an animal attempts to return home. Thus the tendency of the frogs returning toward their home range to be more active in daylight, and indeed the homing tendency itself, may be in large part the result of psychological unrest and a motivation to locate the familiar surroundings which to the particular animal represent "home."

Since all displacement from the home range in this study was accomplished by the animals themselves, there is no doubt that the frogs had opportunity to become familiar with the region over which they passed, enabling more or less direct return to the home range. It is very probable, in fact, that all Leopard Frogs are sufficiently familiar with a large region around their home ranges, the result of previous migrations, movement to and from the hibernating and breeding sites, and dispersal as young, to return home by fairly direct routes. The return of many animals year after year to the same area, after an absence of several months during winter and spring, suggests that the memory of the home range and motivation to return persist for long periods. The ability of Leopard Frogs to find their way home from totally unfamiliar areas was not investigated; presumably, return to the home area under such conditions, if it occurred at all, would involve random search until a familiar region was encountered.

The results reported in this paper, though clearly indicating a homing ability among Rana pipiens, did not identify the particular sensory mechanisms utilized in homing and in recognizing the home area when it is encountered. Both visual and olfactory cues may be important and, in fact, it is very likely that both play a role, the animal using either or both as the situation demands.

Sight is without doubt a vital sense in frogs, used in detecting both prey and predators. Laboratory experiments have demonstrated that visual cues play at least some part in orientation, for Yerkes (1903) found that Green Frogs (Rana clamitans) became confused when the colors of two alleys of a maze which they had previously learned were interchanged. Pache (1932) showed that Hyla arborea can distinguish form, a triangle from a circle, even without movement of the object; it is very probable that all frogs can and do distinguish differences in forms and outlines. Thus Leopard Frogs probably learn to recognize individual visual landmarks (isolated trees, telephone poles, etc.), as well as the more general outline of the horizon made by woods and topography, and use these cues to guide their homeward movements.

Though it is possible that Leopard Frogs may be sufficiently acquainted with the microhabitat (individual herbaceous plants, microrelief, etc.) on their home range that they can move more or less directly from place to place within this familiar region, it is improbable that such cues are used in orientation as the animals move across the less

familiar areas outside the home range. The fact that the three trailed frogs which returned to their home ranges after leaving them in a rain (e.g. 2761) did not return by the same route taken in leaving the area indicates that such details are not important; had they been, return would have followed nearly the same path. Certainly such details would be of no importance to frogs returning to their home ranges after hibernation and breeding, for the herbaceous plants and probably much of the microrelief would not be identical to those of the previous year. It is likely that any visual cues used in homing must be more permanent, and large enough to be seen from the dense grass. Trees, telephone poles, fence posts, houses, the outline of woods and topography were all likely landmarks in the area where this study was conducted. Celestial cues, including star patterns, moon, sun, all of which have been implicated in the orientation of other animals (Carthy, 1956; Sauer, 1958; Gould, 1957, Hasler, et al, 1958) probably played no part in guiding frogs, for long distance moves generally took place on overcast nights.

The ability of amphibians to detect and utilize odors as cues in orientation has only recently begun to be investigated. No work has been done with Rana pipiens, but Martof (1962) has demonstrated that Pseudacris triseriata tends to move toward the source of odors associated with its breeding habitat, and has also shown that Bufo fowleri can be conditioned to respond when an odorant is released. Twitty (1959) has demonstrated that California Newts (Taricha

rivularis) can successfully return to their home areas when blinded, but lose their ability to orient properly when deprived of the sense of smell. Savage (1961) has amassed substantial evidence over 30 years of study with Rana temporaria that the frogs migrating to the breeding sites are directed to a large extent by odor emanating from the ponds.

If frogs do orient by means of their olfactory sense, what is the source of the odor? It is possible that the animals themselves provide distinctive smells to their home ranges, through urination or body secretions. Such odors would probably, however, not be sufficiently permanent to permit recognition of a home range after a winter's absence, for the smells would dissipate rapidly. It is conceivable that the peculiar combinations of plants and micro-organisms provide distinctive odors to the various parts of the countryside, and would be sufficiently reliable, the same plants growing year after year for the lifetime of a frog, to permit recognition of the area. Savage (1961) has suggested that particular combinations of algae provide ponds with distinctive odors, detectable by frogs.

Dispersal in Rana pipiens appears to be largely a function of the recently metamorphosed young. Older frogs show strong tendencies to remain in the same region year after year and probably never go more than a few hundred meters to hibernate and breed; though they may not breed in the same pond each year, they probably do not move far. Young on the other hand may move as much as several miles before settling

down. Undoubtedly these first-season frogs are responsible for most of the exchange of genetic material between populations, the relatively great distances sometimes involved indicating that gene exchange is rather rapid in areas where water is abundant and no major barriers to movement exist. Thus, the gene pool of the species is probably fairly homogeneous over a wide area, accounting for the close similarities between individuals in populations over large sections of the continent and the small number of recognized subspecies although the species has the largest range of any North American anuran. It probably also falls largely to the young frogs, rather than adults, to invade and occupy new areas as they become suitable for habitation, thus extending the range of the species.

Thorson (1955) demonstrated that in Rana pipiens the largest individuals lose water much more slowly than the smaller ones. Evidence from the present study indicates that, in general, the larger frogs live at greater distances from ponds in less moist habitats than do the smaller ones, probably the direct result of the slower rate of water loss in the bigger animals, coupled with the ability to utilize moisture from soil and dew. The ability of the larger animals to tolerate drier conditions undoubtedly allows the species as a whole to range over a wider area than would be possible if all were so dependent upon ponds as sources of water as are the smaller frogs, thus permitting more frogs to exist in populations without increasing intraspecific

competition. Also, the occupation of different habitats by the recently metamorphosed young and the older frogs reduces competition between them, probably permitting a greater number of young to survive than might otherwise. In addition, the presence of sexual dimorphism in size allows the mature males and females to occupy somewhat different regions, thus reducing competition among them; this would seem to have a distinct selective advantage and may be the basis for the evolution of the different sizes of the sexes in this species.

Although the return of the frogs to the hibernating sites in fall was not observed in this study, such movements have been reported by Wright and Wright (1949, p. 490) of Rana pipiens in Minnesota. They record spectacular mass movements reportedly seen by local residents: "When the first frosts come, the frogs begin to leave the lowland meadows for the lake, the young ones first, the adults later.... [Mr. Carl Holm] has seen them moving in such numbers at this season as to form a band two rods wide and one-half mile long where no one could step without crushing frogs." These large concentrations of frogs resulted because "The land lies in such a way ... that there is a lane leading to the lake ..." apparently serving to funnel the migrating frogs from a large area into a narrow strip. It is not clear, however, if the spectacular masses described consist wholely of adult, of young, or of both. If adults occur in such droves, it is doubtful that these movements could be matched in Michigan, for adult Leopard Frogs seldom are present

here in such enormous numbers. Young, on the other hand, may be very numerous in late summer and early fall if survival to metamorphosis is high.

Rana pipiens, though commonly called the grass or meadow frog, appears to have a wider habitat preference than these names imply. Numerous captures of these animals were made in woods, especially in wet, swampy places, and on several occasions individuals were trailed into and through forests; at least five had home ranges in wet woods. The behavior, however, of the animals in woods differed from those in grassy fields, for wood-inhabiting frogs commonly crawled into crevices and cavities and beneath leaf litter so that they were hidden from view. It is likely that Leopard Frogs are more common in wet woods and swamps than is generally appreciated, but due to their secretive habits in such places are seldom seen. Heatwole and Getz (1960) reported finding this species in a hardwood (Ulnus, Betula, Acer) swamp, in a spruce (Picea) swamp, and at ponds in an oak-hickory forest. Wright and Wright (1949) indicated that they occupy grassy woodlands.

Summary and Conclusions

The purpose of this study was to determine the nature of the movements and spatial relations of Rana pipiens and the factors controlling them. Movements in two populations in Cheboygan County, Michigan, were studied by means of a trailing device for following individual frogs, by trapping, by weekly censuses of the study areas and by direct observation. In the summers of 1960 and 1961, and the spring and summer of 1962, more than 6000 frogs were marked for individual recognition by toe clipping.

Trailing was accomplished by means of a spool of thread, mounted in a holding device on the backs of adult frogs, which unwound as the animals moved, marking their routes. One hundred thirty-six frogs were trailed for a total of 681 frog-days (one frog/one day); individuals were trailed continuously for periods up to 35 days.

Budzinski's study area was within a 4.25 hectare pasture containing an abandoned gravel pit and small marsh, both having water much of the summer. The Sedge Point study plot was a 1.2 hectare region surrounding two beach pools on a point of land extending into a lake and bounded on its inland side by a red maple woods.

In spring, adult frogs preceded the young out of hibernation. During, and for three to four weeks after breeding, all sizes of Rana pipiens were confined to bodies of water

and did not occupy the fields as they did during summer. This seasonal difference in habitat may be the result of seasonal physiological changes, differences in availability of cover or food, or environmental temperature differences.

Despite the restriction of frogs to bodies of water in spring, considerable movement between ponds occurred, probably during nocturnal rains, and apparently involving only spent frogs. An almost complete exodus of frogs from one study area (Sedge Point) immediately after breeding was followed three to four weeks later by a gradual return to the area.

Sometime between May 21 and June 4 in 1962, Leopard Frogs at Budzinski's abandoned the ponds and began moving to their home ranges in outlying regions; a few did not reach their ranges until early July, possibly because a lack of rain in June prevented earlier movement. At Sedge Point 39% were on their home ranges within a week after emergence from hibernation in late April; this was possible because of extensive spring flooding of the area and the fact that over 90% of the resident frogs had ranges adjoining ponds, enabling them to remain in water while on their ranges.

Two adult females were trailed as they moved from the spring habitat of the ponds to their home ranges in a field and woods 150 and 400 m away. One moved in a nearly direct line to her range while the other followed a zig-zag route; both may have been following previously learned pathways. Much of the movements of both occurred in daylight and in fair weather.

In summer, frogs in their second season, or older, limited most of their activities to a home range. At Budzinski's, ranges of second-season frogs were less permanent than those of adults, for most females and many males moved to areas more remote from water upon reaching adulthood; the shift probably occurred early in their third season. At Sedge Point, where the region inhabited by Leopard Frogs was smaller and more confined by unsuitable habitats, second-season ranges were commonly reoccupied. Adults in both study plots tended to reoccupy the same home range year after year; only one adult, a female, was known to have shifted her range within a study area. One male, absent from his range in the second summer of the study, returned to it in the third year; presumably he occupied another range elsewhere in the year he was absent.

Within each study area the differences in range size between the adult males and females and subadults lacked statistical significance. The mean area of home ranges at Budzinski's were: subadults, 283 $\pm$ 146 sq m; adult males, 361 $\pm$ 277 sq m; adult females, 503 $\pm$ 159 sq m. At Sedge Point mean range areas were: subadults, 67.5 $\pm$ 76.7; adult males 78 $\pm$ 45 sq m; adult females, 112 $\pm$ 97 sq m.

The differences in size of home range between the two study areas were statistically significant. Evidence is presented that this may have been the result of different degrees of crowding, or in the availability of water. The possibility of territorial behavior among adult Rana pipiens

is considered, but the evidence is inconclusive; though home ranges overlapped, the defense of particular parts of their ranges cannot be ruled out.

In fair weather in summer, Leopard Frogs on their ranges in the fields typically spent more than 95% of a day's time sitting quietly in "forms," made by clearing the wet soil of dead vegetation. Several remained in the same form for more than 24 hours, two for more than five days.

Travel on the home range occurred only infrequently during each day, and usually consisted of a shift from one resting spot (form) to another, seldom more than 5-10 m apart and usually much less. Such movement took place at all times of the diel period, but almost two-thirds of the total distance moved by frogs on their home range was covered between 8 p.m. and 8 a.m., presumably during the night.

Movement within the home range formed complicated patterns of turns, doublings and criss-crossed paths. Many frogs returned repeatedly to particular parts of their range, often to certain forms which seemed to have some significance as homes. Occasional brief trips into adjoining regions uninhabitable by frogs may have been exploratory, or attempts to reoccupy former parts of the home range which were no longer suitable for occupancy.

Leopard Frogs which had home ranges in wet woods, seldom constructed forms, but instead frequently used crevices and cavities as retreats. It is suggested that Rana pipiens may be a more common resident in wet forests than is generally

realized, but is seldom seen in such places due to its secretive habits.

In nocturnal rains Leopard Frogs occasionally made extended excursions off their ranges. Such movement differed from home range movement in being direct, more or less continuous through the night, and often covering distances of 100 m or more; one trailed frog moved 159 m in a single night. These migratory movements stopped at daybreak, the frogs commonly remaining in the region they had reached for several days unless forced by unfavorable moisture conditions to move to more moist regions. Occasionally the migration was continued on the night following the initial movement; one trailed frog traveled 240 m in two consecutive nights.

Heavy rains of long duration in which almost the total population emigrated produced a marked, though temporary, effect on dispersion. Although Leopard Frogs were almost entirely confined to regions of moist soil in fair weather, during and immediately after heavy rains they scattered widely.

Migratory frogs, even those which reached areas suitable for permanent occupancy, showed a strong tendency to return to their ranges following nocturnal excursions. Of 30 subadult and adult frogs captured off their range during or after rains, 25 were later taken on their home range or had moved towards it.

The function of the nocturnal migratory excursions is not known; they probably enable the animals to become acquainted with a large area around their home ranges.

The most rapid rate of movement determined for a trailed frog during a migration was 46.6 m/hr. The distance traveled, hence rate of movement, showed a significant positive correlation with temperature. Rain appeared to be the environmental factor initiating migratory movement.

Adult Rana pipiens rarely frequented ponds during summer. Soil water, absorbed through the groin from the moist soil of their forms, was their primary source of moisture. Dew, obtained by sitting on wet vegetation, was also used.

Ten adults confined to each of two enclosures in a field away from ponds, one in which both moist soil and dew were available, and a second in which dew was prevented from forming, all were in good health after 33 days. They showed regular daily fluctuations in weight due to the net loss of body water during the day, and net gain at night.

Three adult Rana pipiens in a terrarium without access to free water, partially buried themselves when the soil moisture content reached 20-25% of dry weight. Such behavior probably served to retard further water loss. Similar behavior was observed once in the field.

Only 12 of the 136 frogs trailed left their ranges to move to ponds for water. Six of these moved on a windy night, the only night when a measurable amount of evaporation was recorded. Movement of all 12 was directly to ponds, indicating

that the animals either knew the location of water from previous experience, or that they were able to detect it from a distance without seeing it. Evidence was also obtained that newly metamorphosed frogs sometimes moved directly to other bodies of water when their place of metamorphosis dried, supporting the latter hypothesis.

In general the larger frogs occupied home ranges in less wet regions and at greater distances from ponds than did the smaller frogs. These data fit well with the laboratory findings of Thorson (1955) that small Leopard Frogs reached a critical level of body water more rapidly than did larger ones. Because of the difference in size of the animals, hence different degrees of dependence upon moisture, the regions occupied by subadults and adult females were almost mutually exclusive. The region occupied by the intermediate-sized adult males overlapped that of both subadults and mature females. Young-of-the-year were confined almost entirely to the vicinity of standing water in fair weather.

Although the sex ratio of newly metamorphosed young was 1:1, males were more abundant in adult populations (approximately 1.40:1), probably indicating a slightly greater mortality among females. In the vicinity of ponds in summer the proportion of males to females was even higher (from 2.50:1 to 4.33:1), since the larger females tended to reside at greater distances from standing water. Immediately after nocturnal rains in summer, the proportion of the sexes in the area of ponds was usually more nearly equal, the result of males migrating out and females moving in temporarily.

Several mass dispersals of recently metamorphosed Leopard Frogs took place in 1960, always on nights when the minimum temperature was above 15 C, sometimes, but not always coincident with rain. Evidence is presented, both from field data and experiments, that rainfall is an important environmental factor initiating dispersal; the effects of rain upon behavior of young is described. Evidence that changes in barometric pressure also may serve to initiate dispersal is presented.

Large numbers of dispersing young moved more than 1 km from their place of metamorphosis; three moved more than 5 km before settling down. Evidence was obtained, however, that young frogs which failed to disperse or which dispersed only short distances were numerically more important as replacements in populations than widely dispersing frogs.

Evidence that emigration of young Rana pipiens which were not known to be aggressive, was density related is presented and discussed.

Dispersing young at Sedge Point showed a strong tendency to congregate along the lake shore east of the point and to shift positions eastward along the shore. The tendency to aggregate in this area was the result of more vegetation and less rocky substrate than along the west shore. Movement eastward was probably passive in part, the animals being carried by vigorous wave action along the shore.

Dispersal movements were not confined to grasslands; young were found to move through forests as well. More settled down in regions where the vegetation was grass-like, however.

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