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POPULATIONS AND HOME RANGE RELATIONSHIPS OF THE BOX TURTLE, TERRAPENE CAROLINA (LINNAEUS)

By

LUCILLE F. STICKEL

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COMMITTEE IN CHARGE:
PROFESSOR PETER OKKELBERG, CHAIRMAN
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PROFESSOR CARL D. LARUE
ASSOCIATE PROFESSOR WILLIAM H. BURT
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ASSISTANT PROFESSOR NORMAN E. HARTWEG

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INTRODUCTION

A quantitative field study of a local population of the box turtle, *Terrapene carolina* (Linnaeus) was made at the Patuxent Research Refuge, Maryland, during the years 1944-1947.

The main goals of the project were, first, an understanding of home range relationships, and second, a determination of the size of the population. The term, "home range relationships," is here used to include such topics as: (1) the presence or absence of defensive territorialism, (2) the ways the activities and home ranges of different individuals in the same area are related, (3) the size of the home range in the habitat studied, (4) the characteristic movement patterns of the animals in the home range, (5) the nature and extent of travels beyond the home range, and (6) the frequency of transients and the causes for them. The study has thrown some light on each of these topics.

The determination of the size of the population necessitated corrections for transients and for individuals resident on the margin of the study plot. Methods of making these corrections and calculations received special consideration.

The box turtle is especially well suited for study of the phases of population biology dealing with home range relationships. Details of travels can be followed for weeks or months by attaching thread-laying devices to their carapaces.

Their normal activities are not detectably altered by the attachment of these trailers, or by handling and marking. Box turtles can be collected readily without the disturbance of trapping or shooting that is often necessary in studies of birds and mammals. All the animals resident in an area can be collected several times in the course of a season. Under favorable conditions a large number can be collected in a few hours. The turtles are active only in the daytime, so they can be observed during their entire activity period. They are long-lived, so it is possible to study many of the same individuals year after year. It is therefore possible to make more detailed home range and population studies of the box turtle than of many other animals.

CHAPTER I

HISTORICAL BACKGROUND

Before proceeding to the details of the present study it is desirable to survey the historical and theoretical background that has grown from field studies of many kinds of vertebrates. An attempt will be made to trace the development of ideas important to this phase of population biology, and to discuss these ideas in relation to the different groups of terrestrial vertebrates.

Birds. - The idea of territorialism among birds was reintroduced to biologists in 1920 when Howard published his book, Territory in Bird Life. The important ideas expounded here were: (1) that pairs of birds inhabit a particular restricted area during the breeding season, (2) that this area is defended, and, (3) that it is defined to a certain extent by the locations of the singing stations of the male. These ideas provided not only the basic concepts but the fundamental methods for bird population studies. Both were immediately taken up by ornithologists for testing and elaboration. Many additions were made to the list of birds whose behavior fitted this pattern. Examples were found of variations and apparent exceptions. With these concepts established, other types of studies became possible: first, the size of a population could be found by counting singing males at the breeding season, and second, bird behavior could be studied not only as life history, but as individual behavior in relation to community organization. Actually, counts of birds did not take the form of a systematic census until much later, for Kendeigh (1944) credits Williams (1936) with the first field mapping of bird territories as a census method. Today, the breeding bird census, made by counts of singing males, is a standard method in field ornithology.

In the twenty years following Howard's publication, a number of highly specialized bird studies were made. It was shown that the germs of the territorial idea had been present in the literature before Howard, but the fact remained that he had independently conceived and presented the ideas, and his influence was much stronger than that of his predecessors.

It is not the province of the present paper to discuss the many findings of ornithological population research. The significance of these studies, their historical development, and their bearing on modern ornithological thought are ably covered in a paper by Nice (1941).

Critical workers were not long satisfied with the identification of individual birds by location alone. Many problems of social structure at the breeding season and in successive seasons required positive methods for identification of individuals. Bird banding made this possible. Bird banding in the United States was organized on a systematic basis about 1920, and was readily adapted to population study. The general use of colored bands, begun in the 1930's

(Hickey 1943), was of even greater importance for local population study. By this means individual birds could be recognized without repeated trapping.

The preceding discussion of the development of ornithological population research is oversimplified. For a more thorough discussion the reader is referred to Nice (op. cit.) for theoretical discussion and to Kendeigh (op.cit.) for a discussion of method and a critique of modern procedure. The point that is made here is that the principle of territorialism and the method of banding have been the basic tools in bird population research. Among mammals, reptiles, and amphibians the process has been similar, with advances in ideas paralleling those in method.

Mammals. - Some mammals have been shown to hold and defend territories, but for many species this behavior has not been demonstrated. Territorialism received particular notice among the mammals whose habits were largely diurnal, such as antlered game. A number of early observations are cited and discussed by Heape (1931). It was noted relatively early that even those animals that defended particular areas also spent some time on neutral ground. Seton (1909) used the term "home range" to describe the home area of an animal, whether this area was defended or not, and stated that, "No wild animal roams at random over the country; each has a home-region even if it has not an actual home." He gave estimates of the size of this range for several mammals.

This concept of home range as distinct from territory is very useful in understanding and describing the behavior of animals. In a discussion of home range and territory in mammals, Burt (1943) emphasized the distinction with the following definition, "Home range . . . is the area, usually around a home site, over which the animal normally travels in search of food. Territory is the protected part of the home range, be it the entire home range or only the nest."

The development of population studies of mammals was handicapped by the difficulty of observation, for many mammals are nocturnal and secretive and can seldom be studied by direct observation. Into this category fall most of the smaller mammals whose ranges are small enough to make their behavior susceptible to careful analysis. Development of methods of trapping and marking, as well as techniques of procedure were required. As late as 1924 one of the objectives of a small mammal study was to find if the animals could be trapped and re-trapped a number of times (Johnson, B. M.1927). In the same year, travels of small mammals were studied by live-trapping and releasing them at a distance from the point of capture (Johnson, M. S. 1926). Both workers marked the animals so that individuals could be recognized. Similar methods were used by Murie and Murie (1931, 1932) in their studies of the travels of small mammals.

Population research in a broader sense, involving study of individual behavior and the size and behavior of the population as a whole, began with Dice's suggestion (1938) of the live-trap quadrat method of studying small mammal populations. The method involved the use of numerous live traps at regularly spaced intervals, and systematic trapping. From recaptures of individuals and the total trapping results, many facts concerning the population and the individual animals were derived, including reliable data on movements and on the size of the population. Burt (1940) applied these methods successfully to a study of the small mammals of a Michigan hardwoods. Since that time the same methods have been used in population studies of many species of mammals. Good examples of the use of these methods in small mammal study are found in Blair (1940), and for larger mammals in Allen (1942), Haugen (1942), and Stuewer (1943).

From the preceding discussion of home range and territory it might be concluded that individual animals are neatly compartmentalized in habit, and diagrammatic in pattern of behavior. This is far from the truth, for an animal population is in a constantly moving state. There are travels and changes accompanying growth and development of new generations, as well as losses to the population through death and emigration. Even within a limited time in a normal, established population, there are travels and movements outside the home range, often of unexplained nature. These travels should be viewed as a phase of animal behavior in coordination with the home range concept. Burt (1940) believed these travels were normal for small mammals.

Storer, Evans, and Palmer (1944) also found that travels outside the home range were not rare among small mammals, and gave examples of this behavior in several species. The problem is taken up again in a later section of the present paper.

Amphibians. - Studies of populations of amphibians have been largely confined to observations of breeding aggregations. Only very limited observations have been made on the travels of salamanders outside the breeding season. Test and Bingham (1948), in connection with a study of a local population of red-backed salamanders, cite records that suggest that at least some salamanders maintain home ranges. The difficulty of marking salamanders is probably a principal reason for scarcity of this type of observation.

There have been a few studies of travels of frogs and toads. One of the earliest of these (Breder, Breder, and Redmond 1927) showed that individual frogs (Rana clamitans) maintain home ranges outside the breeding season. They had recapture records for 31 frogs, released at the site of collection. These were collected a total of 161 times, and individuals were collected 2 to 14 times. Thirty had traveled distances less than 150 feet; one had traveled farther. They also made homing studies of R. clamitans that tend to support their other data. They showed that male toads (Bufo fowleri) have a well-developed homing instinct at least when in voice. The frogs and toads were marked with small numbered paper tags tied around the middle of the body. The numbers could be read in the field without disturbing the animals, and remained legible for about three months. In some instances aluminum tags and colored beads were used.

Noble (1931: 403-407) summarizes other amphibian laboratory and field studies that show restriction to home area and homing behavior.

Travels of Rana clamitans, primarily during the breeding season, have been studied by Raney (1940) and Ingram and Raney (1943). The travel distances they recorded were highly variable. Some frogs were retaken near the place of release and others were retaken thousands of feet away. The results of recaptures after a lapse of a year or more are of particular interest. Twenty-one individuals were retaken after one or two years in the same ponds where they were first found. The distances from the original collection sites varied from zero to 650 feet. Other frogs were taken in succeeding years at considerably greater distances and in different ponds. They report three cases of "homing" over distances of 400, 570, and 675 feet. The frogs were marked by metal fish tags clipped around the lower jaw.

The first recorded attempt to estimate the size of a frog population by marking and recapturing was made by A. P. Blair (1947). He recorded forty different frogs (Rana moorei) during five nights' collecting along part of a creek. Each frog was marked by toe-clipping and the individual travel distances were recorded for recaptured animals.

Twenty-three frogs were recaptured one or more times, most of them near the place of first capture. However, the data did not prove suitable for estimates of population size, either because of habits of the frogs or methods of collecting.

Reptiles. - Few detailed population studies have been made of reptiles. Demonstrations of territorialism in this group have been confined to alligators, lizards, and *Sphenodon*. Snakes and turtles have been shown to have home ranges, but there are no available data pointing to territorial behavior.

Von Haast (1881) studied the habits and behavior of *Sphenodon* on the Chicken Islands, and his findings are described by Gadow (1910: 299),

> The Tuatara excavates its own hole, and this is shared sociably by various kinds of Petrels. . . . Whilst very tolerant of the bird with its egg and young, it does not allow another of its own kind to live in the same hole, which it is ready to defend by lying in such a manner that the head is placed where the passage widens out into the chamber. On putting one's hand or a stick into the burrow the Tuatara bites at them furiously.

Evidence of home areas and territorialism among alligators is given by McIlhenny (1935). He stated that alligators used the same wintering dens throughout life and that females often used the same nesting place year after year. Concerning defense of territory, he states,

> Large male alligators are very intolerant of the near approach to the place in which they live, of other large males, and I think most of the roaring they do is for the purpose of warning away any other who might

> invade their range. The males fight each other fiercely and it is not uncommon to find large males with a foot or leg missing, or a considerable section of its tail gone, or severe scars on its body, which could only be made by other alligators. I have often seen them fighting.

Some lizards are known to restrict their activities to relatively small areas, and to defend territories. Early papers dealing with this subject are listed by Evans (1938). More recently, additional population and ecological studies of lizards have appeared. Of particular excellence are studies of two different species of the genus Sceloporus. These are by Fitch (1940) on Sceloporus occidentalis and by Stebbins (1944, 1948) and Stebbins and Robinson (1946) on Sceloporus graciosus. In both studies the lizards were marked for permanent identification by toe-clipping. In the latter studies lizards were marked with colored indelible pencils for field identification. The studies of both species include observations on territorialism, home ranges, and population structure and change.

Miller (1944) found a population of at least sixty-two limbless lizards (Anniella pulchra) on a one-hundred foot square islet off Point Pinos, California. Repeat captures of ten marked individuals showed very short travel distances, 1.87 to 27.5 feet.

Evidence that snakes have home ranges is given by W. H. Stickel and J. B. Cope (1947). They offer explanations for opposite conclusions by previous authors.

A study of an unusually dense snake population was made by Seibert and Hagen (1947). In a single summer season they collected and marked the remarkably large number of 383 snakes on a 3.2 acre plot. These snakes were mainly Thamnophis and Opheodrys. Recaptured individuals had apparently traveled very short distances, an indication of home range behavior in these species.

Fitch (1947) found that in a population of rattlesnakes (Crotalus viridis oreganus) most recaptured individuals were taken at distances less than one-hundred yards from the sites of first capture.

There has been no satisfactory evidence of territorial behavior in any snake. Fighting between male snakes has been observed both in the field and in captivity. Male combat behavior in snakes is described by Shaw (1948). Lowe(1948) reviews the published records of combat between male snakes and discusses its implications. He considers the fighting to be territorial behavior. This fighting between males cannot by itself be considered evidence of territorialism as it is now generally defined (See page 6 above). The term "combat dance" used by Shaw (op. cit.) is a more satisfactory description of the phenomenon.

Home range behavior has been shown in both aquatic and terrestrial turtles, although detailed studies have been few. Studies of aquatic forms will be considered first.

A marine turtle of the West Indies, Chelonia mydas, was studied by J. Schmidt (1916). He found that individuals were often recaptured in the same locality where they were originally taken.

The *Chrysemys* population in part of Lake Mendota, Wisconsin, was estimated at five turtles per water acre (Pearse 1923). The estimate was based on the percentage of marked turtles recaptured in successive collections at fourteen stations along the shore. Records were kept of the travels of the marked turtles that were collected more than once. These showed that many *Chrysemys* were local in habit, and gave good evidence for the existence of home ranges in this species.

The most complete studies of travels and population behavior of aquatic turtles are those of Cagle (1944). He marked the turtles by filing notches in the marginal scutes, a method he devised and reported in an earlier paper (Cagle 1939). This method was used in conjunction with mass collecting and trapping. His findings concerning species composition and specialized behavior of aquatic turtles are excellent contributions to the population biology of these forms. Results relative to home ranges have particular bearing on the present study.

He found that *Amyda*, *Pseudemys*, *Chrysemys*, *Chelydra*, and *Sternotherus* had home ranges within which they normally remained. Some individuals of *Pseudemys* and *Chrysemys* were found to include parts of more than one body of water within the home range. These two species were also shown to have some homing ability when artificially transported to places outside their normal ranges. When the water level fell drastically in one of the lakes being studied, many turtles left the lake. These apparently traveled at random in different directions. Others may have stayed, buried in the mud. After the lake was drained and refilled, ten turtles were retaken in the same area of the lake where they had been collected and released one to three years previously.

Estimates of the size of normal populations were not made. In an earlier paper the number of turtles concentrated in a section of drainage ditch at low water level was calculated by the collecting ratio method of Pearse (Cagle 1942).

Woodbury and Hardy (1948) studied a semi-isolated population of the desert tortoise (Gopherus agassizii) in Utah. They estimated this local population to consist of approximately three-hundred tortoises, a density of about one tortoise for each four acres of land. They found that each tortoise had a small home range usually covering about ten to one-hundred acres. Ranges of different individuals overlapped and there was no evidence of territorialism. Evidence of home range behavior in Gopherus was also given by Grant (1936) and Bogert (1937).

Important data concerning the population biology of the box turtle are found in the study made by J. T. Nichols (1939). He collected and marked the turtles near his Long Island home and recaptured a number of them in the same vicinity after several years. Most of the turtles were taken some distance away from the collection point before they were released. There were eleven recoveries of turtles removed one-half to three-quarters of a mile from the collection point. Many others were not captured again. All of the recaptured turtles had returned home and the second collection was within a few hundred yards of the place of original capture. Other turtles were released where they were found, and twelve were recaptured. Recaptures for these turtles also were only a few hundred yards from the original site. These data show that at least some box turtles remain in a limited range for many years.

More casual observations had earlier indicated that box turtles remain in limited areas. Such records are those of Schneck (1886) and Medsger (1919).

A unique method of studying turtle behavior was used by Breder (1927). She attached a spool of thread to the posterior marginals so that the spool dragged along the ground behind the turtle and the thread unwound as the turtle moved. She had a limited time for the use of the technique and encountered mechanical difficulties with the device which caused threads to break, but nevertheless secured some interesting data. She tried the trailing device on four turtles, All were released some distance from the places they were collected. Most of them traveled in the direction of the place of collection, thus showing signs of homing behavior.

Two individuals were brought back to the starting point two or more times, but persisted in heading back in the same direction. One of the turtles was released only seventy-five feet from where it was collected and was apparently still within its home range. This turtle traveled in a more irregular manner than the ones released farther from the places of collection.

Taken as a whole, population studies of reptiles and amphibians are few, and of relatively recent date. It is probable that the population studies of reptiles and amphibians have been influenced rather strongly by those on other vertebrates.

CHAPTER II

METHODS

Two supplementary methods were used to secure population and travel data concerning the box turtle. The first was to census the animals by intensive collecting on a systematic basis. The second was to follow the detailed movements of selected individuals by means of a trailing device.

Census. - The collection data were used to estimate the size of the population, to find the size and locations of the home ranges of individual turtles, and to determine interrelationships of home range areas.

In order to use collection data in these ways it was necessary: (1) to mark individual turtles so that each could be positively identified on recapture, (2) to record locations quickly and accurately, and (3) to make numerous collections well distributed over the study area.

Marking. - Each turtle was marked by filing notches in its marginal scutes according to the code system used by Cagle (1939). A very large number of combinations of marks is possible, and a recaptured turtle can be identified with certainty. Marginals four through seven were not included in the marking plan as these form part of the bridge joining carapace and plastron. Marks were filed with a half-round bastard file. This file has some advantages and apparently no disadvantages over the square-edged metal file. The square-edged file is easily clogged with the bony material of the turtle's shell and rapidly loses its efficiency unless cleaned frequently. Patience and strength are needed to file a suitably deep notch even with a clean file, and there is danger of fracturing the horny covering of the bone. The half-round file is essentially self cleaning, and a notch of any desired depth is made quickly and easily, with little danger of fracturing the horn. The v-shaped notch seems equally as satisfactory as the square notch of the square-edged file. These marginal notches are visible in several of the photographs.

Locations. - Collecting locations were recorded with reference to markers placed at 82.5 foot intervals over the study plot. The U. S. Geological Survey has surveyed the entire refuge, placing bronze-cement numbered markers at 330 foot intervals, thus dividing the area into 2.5 acre plots. Placing tag markers at one-quarter plot intervals resulted in the 82.5 foot grid pattern. The terrain and natural landmarks of the study plot became very familiar, and this simplified spotting a marker after a turtle had been found. Except during the earliest part of the work, distances could be paced and locations recorded within one or two minutes.

Records. - Besides location and code number, various other data were recorded at the time a turtle was collected. Date, time of day, habitat, behavior, and sex were recorded for all turtles. New turtles were measured and marked. Sex of adults was determined primarily by the plastron depression, which is ordinarily deep and conspicuous in males and absent or slight in females. Other secondary sex characters such as height and shape of carapace, and eye color were used to verify the determinations.

Collections. - Much of the collecting on the study area took the form of systematic, standardized census trips. The object was to secure comparable data for use in estimating population size. A census trip consisted of an intensive two-and-one-half to three hour search of the study plot by two collectors, each responsible for half the area. Every effort was made to cover the plot thoroughly and uniformly, and to secure as many records as possible. Between thirty and fifty collections were made on most census trips. Uniformly distributed, intensive collecting is possible only when the participants are thoroughly acquainted with the area being searched, and familiar with turtle collecting.

Partial, or check censuses were made when there was not time for a complete census, or when the number of turtles available to collecting was small. In these check censuses a number of localities in different parts of the study area were searched. Many additional records were obtained incidental to other work in the area. All collecting was done in a way that left brush and other natural cover undisturbed.

The most intensive field work was in 1945. In this season collections were made on 77 different days from March to October. Thirty-two of these were systematic census trips and 19 were check censuses. In this year 283 turtles were collected a total of 991 times. Collections were made on 71 different days in 1944 and totaled 572 records. In 1946 there were 546 collections. The collections for the three seasons totaled 2109.

Trailing. - The second method used in the study of population behavior was detailed observation of the travels of individual turtles. This was accomplished by the use of a trailing device. The data obtained by this method were used to study the relationship of the individual to its home range and to the ranges of other turtles, and to determine extent and routes of travel. These observations of travel behavior were also useful in interpreting the data obtained by collecting.

Turtle travel routes were plotted on graph paper in the field. The location markers discussed above were used as reference points in the mapping. Detailed route maps were prepared for 456 turtle days. These provide a clear demonstration of actual turtle behavior. The longest record for a single turtle was 161 days, July 3 to October 24, 1946 and May 1 to June 18, 1947. Ten other turtles were followed for periods of one to forty-four days.

The trailing device is pictured in Figure 1. When the turtle moves, the spool unwinds and the turtle's route is marked by a trail of thread. The idea of using a thread trail to study turtle behavior was proposed by Breder (1927). The trailer she used was a device hooked into a hole bored through one of the posterior marginal scutes. The spool of thread dragged on the ground a number of inches behind the turtle. Under the field conditions encountered in the present study, this design was unsatisfactory, for turtles almost immediately caught the device on obstructions and were tethered. A workable trailer was developed in the summer of 1944.

The trailer is easily made from a six ounce (85 by 62 mm.) can. A metal housing is cut to fit smoothly on the carapace of the individual turtle. Two wire hooks to hold a spindle, and a guide loop for the thread, are soldered to the inside of the housing. A short metal rod cut from an iron bolt is used for the spindle. An ordinary thread spool is cut down at the core to hold about 550 yards of number eighty white thread, and this is placed on the spindle. The whole is fastened on the turtle's back with strips of waterproof adhesive. The trailer does not catch when the turtle walks under or between obstacles, for it forms a smooth extension of the carapace, neither higher nor broader than the shell itself. Turtles carrying trailers move and behave normally; recorded movements of turtles with and without trailers

Figure 1. Box turtle with trail-laying device. A metal housing is cut from an 85 by 62 mm. can to fit smoothly on the carapace of the individual turtle. Two wire hooks to hold a spindle, and a guide loop for the thread, are soldered to the inside of the housing. A short metal rod cut from an iron bolt is used for the spindle. An ordinary thread spool is cut down at the core to hold about 550 yards of number eighty white thread, and this is placed on the spindle. The whole is fastened to the turtle's back with strips of waterproof adhesive. The trailer does not catch when the turtle walks under or between obstacles, for it forms a smooth extension of the carapace, neither higher nor broader than the shell itself.

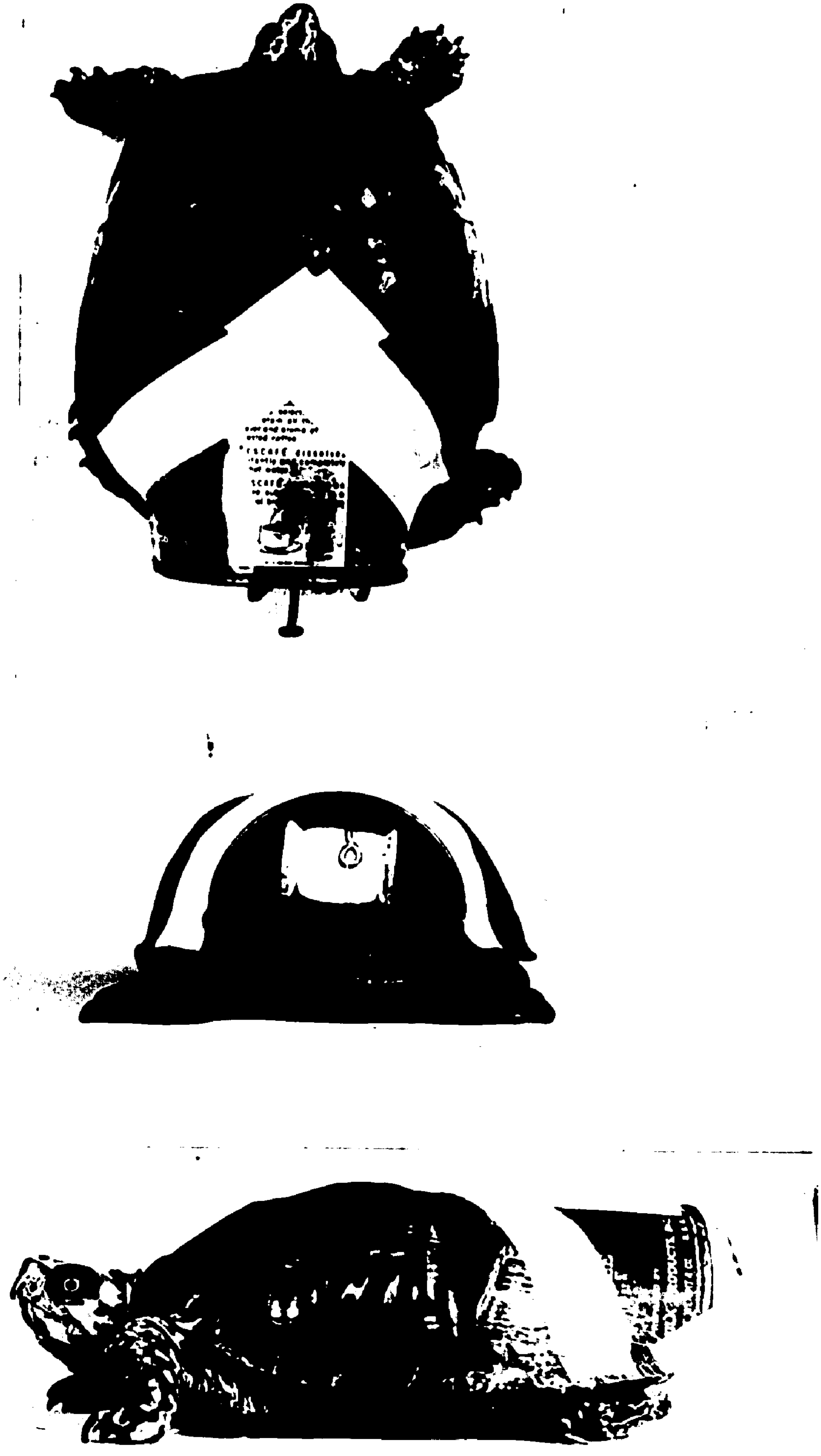

Figure 1

do not differ.

New spools of thread were easily supplied in the field. Adhesive was changed occasionally, usually after rainy weather. An old electric mixer was adapted to produce a mechanical winder for re-winding the spools. Trailers were applied in the field and the turtles were then visited about once daily, usually in the evening.

CHAPTER III

DESCRIPTION OF AREA

The Patuxent Research Refuge, near Laurel, Maryland comprises 2650 acres of land along the Patuxent River. Most of its area is wooded, although parts are agricultural land and residential area. On the north and northeast the refuge is bounded by the extensive wooded portion of Fort George Meade, and on the south and southwest by U. S. Forest Service land. In other directions are mixed woodland and small farms. The refuge represents a fairly natural situation for the region, and affords a good opportunity for the study of animals under undisturbed conditions.

Plant communities of the refuge have been described by Hotchkiss and Stewart (1947), who have also summarized the more important physical and physiographic features. Therefore, it will be necessary here to mention only the more important general features, before proceeding to a description of the particular area where the present studies were made.

Geologically, the refuge lies within the Fall-line Clay Hills District of the Atlantic Coastal Plain Province (Harper 1918, Fenneman 1938). Physiographically, the area comprises three principal types, flood plain, terrace, and uplands. The flood plain extends one-quarter to one-half mile back from the river, and in most places joins flat stretches of terrace, with bluffs of fifteen feet or less at the juncture. Some places the bluffs are higher and the flood plain adjoins the uplands. From the terrace level the land slopes to the broad hilltops of the uplands.

Box turtles have been found in all habitats, but are by far the most numerous on the flood plain. For this reason an area near the river was chosen for special study. The study plot was a 29.1 acre area (Figure 2) located in the portion of the flood plain classed as well-drained bottomland forest.[1]

The turtle study area is fairly typical of much of the refuge bottomlands. On a hot midsummer day, its temperatures are in striking contrast to those of other parts of

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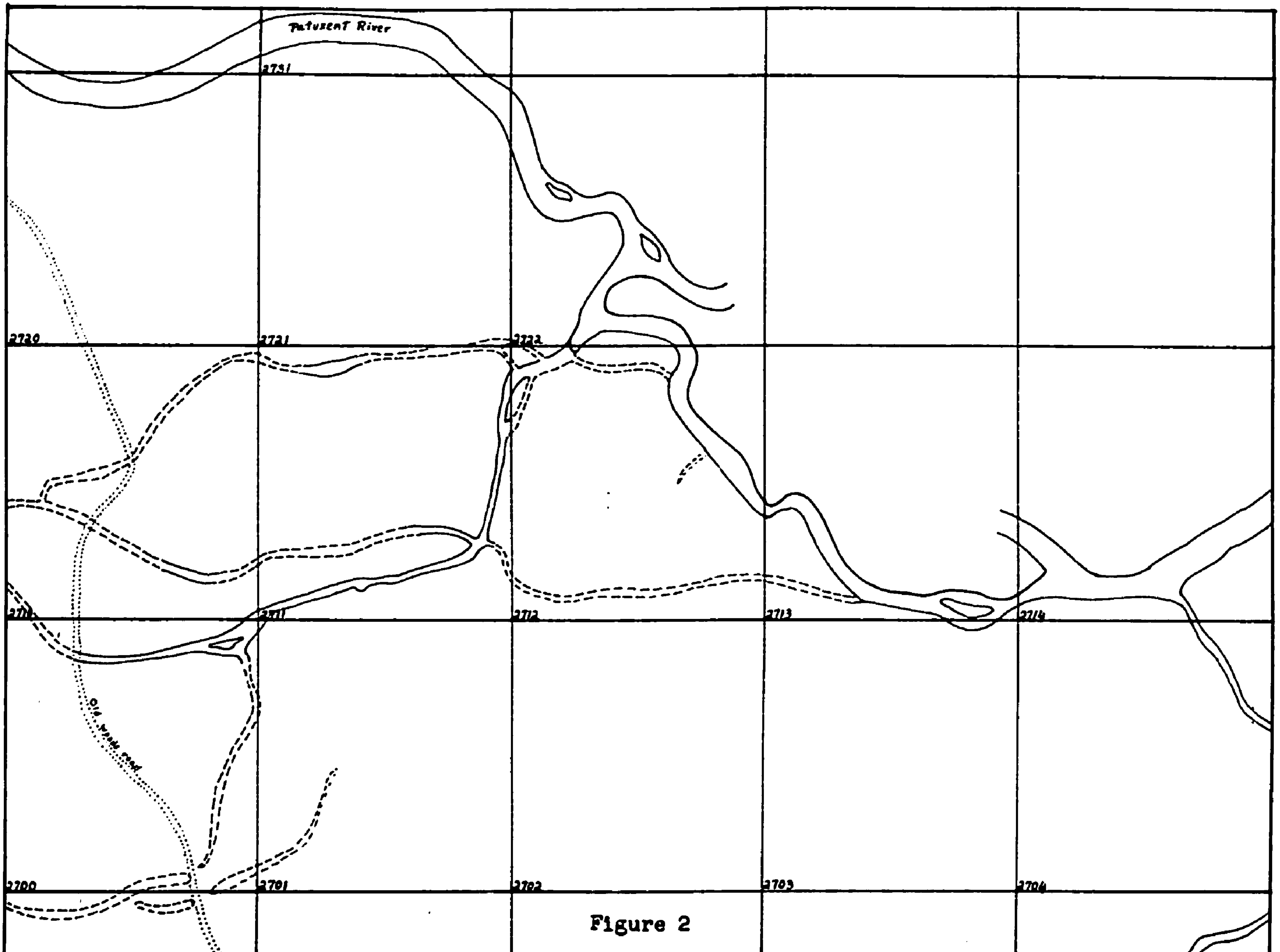
[1]Botanically these bottomlands are characterized by the large number of plant species that occur commonly. No single species dominates in numbers. The principal species of trees, shrubs, and herbs listed by Hotchkiss and Stewart (1947) for this plant community include:

Trees	Shrubs and Vines	Herbs
Carpinus caroliniana	Lindera benzoin	Arisaema triphyllum
Betula nigra	Toxicodendron radicans	Erythronium americanum
Fagus grandifolia	Viburnum prunifolium	Laportea canadensis
Quercus palustris		Claytonia virginica
Ulmus americana		Ranunculus abortivus
Liriodendron tulipifera		Podophyllum peltatum
Liquidambar styraciflua		Impatiens biflora
Acer rubrum		Viola affinis
Fraxinus americana		Circaea quadrisulcata
		Cryptotaenia canadensis
		Galium aparine

Figure 2. Map of box turtle study area. The study area comprises 29.1 acres of the wooded bottomlands of the Patuxent River. It appears on this map as all the land south of the river. The squares drawn on the map are 330 feet on each side and each marks off 2.5 acres. The major natural drainage channels are shown by broken lines. These, and many other minor channels are filled with water in the spring and at other times of high water. Most of them are dry the greater part of the year, although a few hold some water at all seasons. There is no flow in the channels except at high water, and during dry seasons water is present only as isolated pools along the course of the more permanent ones. The parts that tend to retain water most of the time are shown as solid lines.



Patuxent River
2731
2720
2721
2722
2711
2712
2713
2714
2700
2701
2702
2703
2704
Old woods road

Figure 2

the refuge. Temperature rarely exceeds 85° Fahrenheit and daily midsummer maxima are ten to fifteen degrees below those of the open hilltop. Humidity is prevailingly high.

A dense tree canopy diffuses the light so that in most places sunlight appears only as small flecks or patches. Lianas of grape festoon the trees and shaggy, wrist-thick stems of poison ivy vine ascend the tree trunks. The ground underfoot is soft with moisture under its cover of leafy material. The same leafy layer also fills numerous pits and ground depressions to the surrounding level. These pits vary in depth and size, but are usually eight to twelve inches deep and one to three feet across. They appear to have their origin in the burrowing activities of small mammals. In many places, especially about old rotted-out stumps, these burrows honeycomb the ground. In time the earth is so weakened that the surface collapses and pits or holes appear. Other pits are formed when a woodchuck burrow is abandoned, or a yellow-jacket nest is dug out by a raccoon.

Heaps of woody debris, fallen tree branches, logs and stumps are everywhere (Figure 3). Trees and tree branches are brought down in storms. A falling tree often carries along a great tangled mass of grape and poison ivy vine that forms a large dense viny tangle, like the one pictured in Figure 4. A single falling branch resulted in the tangle shown in Figure 5. Heaps of wood and debris are piled around bush clumps and tree bases at times of high water (Figure 6).

Figure 3. Wooded bottomlands near the center of the study area. Fallen trees, like the one shown in the background, are fairly common in the study area. Their fallen branches provide shelter and the break they cause in the leaf canopy admits sun to the forest floor and promotes shrubby growth. *Lonicera japonica* and some shrubby *Viburnum prunifolium* around the fallen crown of the tree shown here have formed a loose tangle that is a frequently used shelter and sunning area. The trees in the foreground are *Liriodendron tulipifera*, one of the important constituents of the overstory. Botanical features of the bottomlands are discussed on page 26.

Figure 3

Figure 4. Viny tangle made by a fallen tree with its burden of grape vine. These tangled areas are common in the bottomlands and are used extensively by turtles for shelter and sunning.

Figure 4

Figure 5. Viny tangle at the base of a small tree. This particular tangle was formed by a single falling branch carrying down a mass of vines. Turtles were frequently found beneath its shelter.

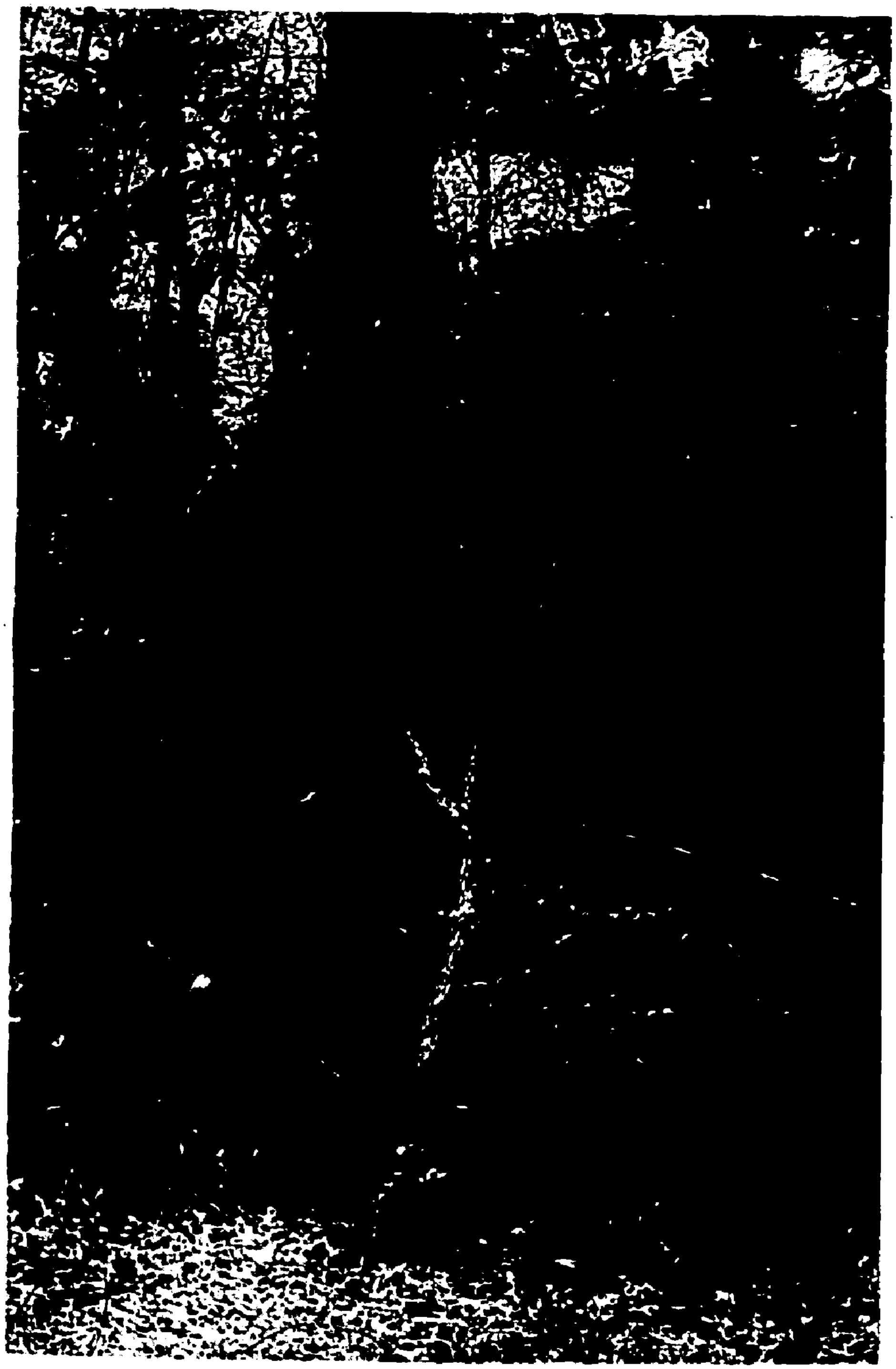


Figure 5

Figure 6. Leaf-filled dry channels. The heaps of debris piled at the tree bases were deposited by water flowing in these channels at flood time. The channels are filled with swiftly flowing water at several different times in a season. The debris piles provide good turtle cover, but are not used as extensively as are more permanent brush piles. This picture also shows the festooning grape vines that are typical of many parts of the bottomlands.

Figure 6

In these respects the appearance of the land changes, for each windstorm or flood brings down new branches, moves debris heaps about, and otherwise changes the distribution of this natural cover.

Another type of cover is found in certain woods openings. In these, _Rubus_ and _Smilax_ combine with a brushy growth of _Viburnum prunifolium_ to form dense spiny thickets. Some of them are so nearly impenetrable that they can be entered only with the aid of machete or clippers.

The turtle study area, like the flood plain generally, is laced with a network of natural drainage channels. In 1945 the majority of these held water through the summer. In some other years the majority have been dry in midsummer. Even in the driest years water remains in some of the deeper channels (Figures 7 and 8). Normally there is little flow, but after heavy rains there is a strong current. It is usual for the bottomlands to be partially flooded several times a year. At these times the portion of the flood plain nearest the bluff is submerged, and the gullies and channels of the better drained portions are full. Some of the lower parts of the well drained bottomlands are also inundated, but much land is emergent. Rarely, perhaps once in many years, the river overflows its banks and covers the entire flood plain. Even these floods are of short duration. Conditions become essentially normal within a few days.

Figure 7. Semi-permanent channel at low water. After a hard rain this becomes a flowing stream for a day or two. Usually it contains more water than shown here. Water is always present in the bottomlands in the numerous pools like this one. The water table is high and the ground itself is always moist.

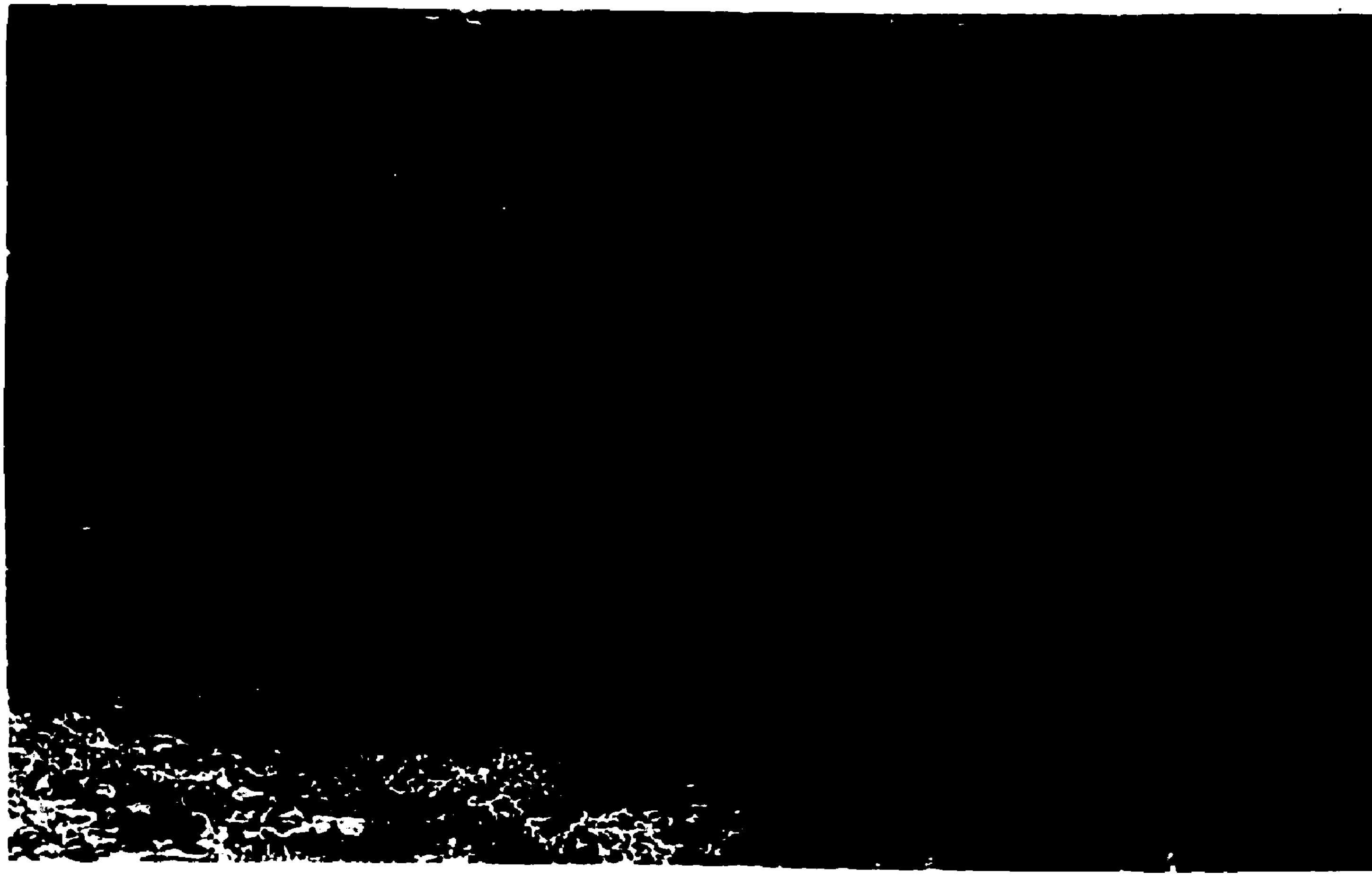


Figure 7

Figure 8. A large semi-permanent channel, well filled but not flowing. Turtles enter the shallow water of the channels readily and are occasionally found in the water or in the mud and water at the channel's edge.

Figure 8

CHAPTER IV

BEHAVIOR IN RELATION TO ENVIRONMENT

The abundance of box turtles in the bottomlands probably depends on a favorable combination of environmental features. The behavior of the turtles in relation to shelter, food, and weather will be reviewed in this section as a background for the discussions that follow.

One of the most conspicuous features of box turtle behavior in the bottomlands is the extensive utilization of cover. This is not confined to taking shelter at night. During the day, turtles that are not actively moving are almost always found in and around the brush piles, heaps of debris, and tangles of vines and briars that are characteristic of the bottomlands. Grape vine tangles make a dense cover that is frequently used. One particularly dense tangle of this sort, formed about a tree base when one of its branches fell and dragged down a mass of vines is shown in Figure 9. Not all trees are encumbered with vines, and when these or their crowns or branches fall, a thinner type of cover results. Turtles are frequently found in these places. Figure 10 shows a portion of a fallen tree with a turtle resting beneath its branches.

The thicket partly shown in Figure 11 is one of the most used areas of the study plot. At some times of the year

Figure 9. Box turtle coming out of a dense viny tangle where it had spent the night. This tangle was formed by a single branch with its vines. It is in a sunny place near the river, and is a favorable turtle locality.

Figure 9

Figure 10. Adult male box turtle under the partial shelter of a fallen tree crown. Even when brush or branches are few and seem to provide little shelter, these sites are preferred to strictly open areas. The particular turtle shown in this picture has the horny carapace worn away to the bone toward the rear, and this shows as a lighter area. One of its code marks is visible anteriorly.

Figure 10

Figure 11. Small portion of a Rubus-Smilax thicket on a gully bank near the middle of the study area. This thicket covers a ground area about twenty-five by fifteen feet and reaches five feet in height. Six to ten turtles have often been found here within a few feet of each other.

Figure 11

it is common to find six to ten turtles there. The thicket covers an area of about twenty-five by fifteen feet, and is on the edge of a shallow gully. At the highest point the mass is more than five feet tall. It is formed by a complex of *Rubus*, *Smilax*, and *Viburnum prunifolium*. The vines of *Rubus* and *Smilax* interlace in a continuous tangle. At the ground level the old *Rubus* canes form a loosely packed layer. This layer contains a network of passages and trails made by the turtles. Several well marked turtle paths lead from the thicket to the gully.

The gully bank for about twenty-five feet adjacent to the tangle is open, and is a favorable sunning area. The combination of the dense thicket and the sunny bank is apparently a good one, for this region is one of the best collecting spots in the study area.

Turtles are active only during the day. As evening approaches they seek places to spend the night. A particular type of construction for this purpose I have termed a "form." It is a well shaped cavity in leaves, debris, other ground cover, or even soil. The turtle makes the cavity by digging with the front feet and pushing and moving about from side to side. A form may be used only once or it may be used repeatedly at intervals of several days or longer. Different turtles are sometimes found in the same form on succeeding days. A turtle in a form is often completely concealed; at other times the rear of the carapace projects. Within, the head and front legs of the turtle are sprawled out in sleep. Forms are easily recognized after a few samples have been seen. Figure 12 shows a turtle leaving a form in leaves and sticks. Forms are most often constructed in the midst of brush or viny debris, or in heaps of leafy material piled against logs or stumps. Less frequently they are made in the leafy or grassy ground cover away from other shelter.

Use of a form is not invariable, although it is by far the commonest type of nightly retreat. Turtles often push up against a log or tree base, wedge themselves under branches, or crawl into a heap of leaves or debris, without leaving any evidence of their presence when they depart. Some turtle resting sites are shown in Figures 13 through 17.

Weather conditions influence turtle activity, although they do not govern it completely. The most favorable conditions are high humidity, warm sunny days, and frequent rains. The most unfavorable influences appear to be low temperatures and drought. The favorable conditions prevail in the bottomlands for extended periods during the summer. Turtles can be found moving about at almost any hour of a long summer day. In the cooler weather of spring and fall, movements are more closely restricted to the midday period.

Although some turtles are active on most summer days in the bottomlands, not all turtles are active every day. Periods of activity are alternated with periods of

Figure 12. Juvenile turtle leaving a "form" in leaves, sticks, and earth. Turtles frequently spend the night in such cavities, which they construct by digging with the front feet and pushing and moving about from side to side. Some forms are used only once. Others are used several different times by the same turtle at separated time intervals. The same form may be occupied by different turtles on succeeding nights.

Figure 12

Figure 13. Turtle resting site. Turtle pushed against and partly under an old river birch log. A turtle will often spend the night in a location such as this one. The code marks of this turtle show plainly on right marginals eight and nine.

Figure 13

Figure 14. Turtle resting site. Turtle pushed against a log under a network of vines and a thin covering of leaves, some of which were removed to make the photograph. A turtle may spend a single night in such a location, or if conditions are not favorable to travel, it may remain for days. This same viny tangle is shown more fully in Figure 4.

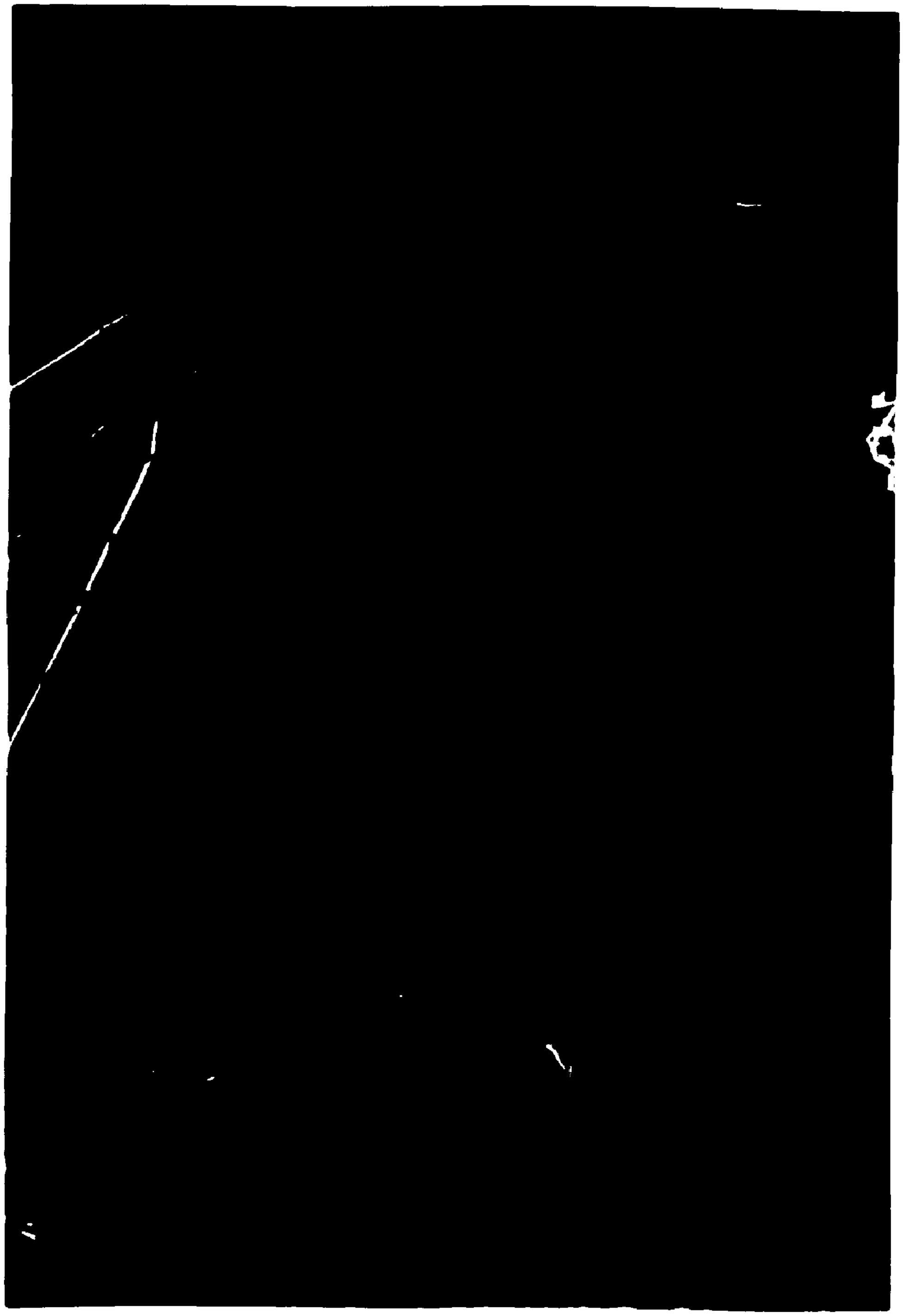


Figure 14

Figure 15. Turtle resting site. Turtle amidst brush and sticks and crowded under a slender branch, but otherwise unconcealed. Such an exposed position is not commonly used.

Figure 15

Figure 16. Turtle resting site. Turtle on the elevated ground at a tree base, and pushed against the tree. Elevated tree bases are favored localities, particularly during the day.

Figure 16

Figure 17. Turtle resting site. An unusual refuge site in the hollow base of an old rotting stump.

Figure 17

quiet. In dry weather or unusually hot or cold weather a turtle may stay in its form for days or weeks. This behavior is especially conspicuous in the fall when the active days are often fewer than the inactive. Under the very favorable conditions of parts of midsummer there may be some activity each day for many days before a day or two of rest. Even under the most favorable conditions not all the turtles are active. On the best collecting days some turtles are invariably found in forms or partly concealed in debris.

These varied activity habits were first noticed in connection with the results of collecting trips. They were later shown in the records of trailer turtles. Some of the activity records for different months are shown in Table 1. These contrast the days when there was some activity with the days when the turtles remained in their forms.

Water and sun may be important for other reasons than their stimulus to activity. Places where openings in the canopy have allowed sun to reach the ground are frequently utilized as sunning areas. The sunny areas that also have protective cover in the form of brush, vines, or tall weeds seem to be favored over completely open areas. The best sunning areas in the study plot are gully banks, margins of the old woods road, and

TABLE 1

TURTLE ACTIVITY

Fall 1944

Turtle Code Number	Sex	September 28	29	30	October 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
424	♂					–	–	–	–	–	+	–	+	+	+	+	+	+	+	–	+	+	–	–	–	+	–	–	+	hibernation	
629	♂					–	–	–	–	–	–	–	–	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–	+	–	+ hibernation
593	♂	+	+	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	+	–	–	–	–	–	–	+	–	–	–		
627 (subadult)	?♂		+	+	+	+	–	–	+	+	+	+	–	+	–	–	+	+													
634	♀																					+	–	–	–	+	–	–	+	+	hibernation
635 (subadult)	?♀					+	–	–	–	hibernation																					

Summer 1945

Turtle Code Number	Sex	May 21	22	23	24	25	26	27	28	29	30	31	June 1	2	3	4	5	6	7	8	9	10	July 6	7	8	9	10	11	12	13	14	15	16
515	♂	–	–	+	–	–	–	+	+	–	+	–	–	–	+	+	–	–	–	–	+	+											
424	♂																						+	+	+	+	+	+	?	+	+	+	
629	♂																						+	+	+	+	+	–	+	+	+		
192	♂																						+	+	+	+	+	+	+	+	+	+	+
476	♀																						+	+	?	+	+	+	–	+	+	+	+
492	♀																						+	+	+	+	+						

woods openings formed by falling trees.

Warm shallow water is present in many of the natural drainage channels through the summer. Turtles enter these readily, sometimes apparently to bathe or soak. They are occasionally found sitting quietly in the middle of the stream, head and top of carapace above the water. One turtle carrying a trailer made several short excursions into shallow water. Several times I have found a turtle near the bank of a gully, partly covered by mud and water. I have never found large numbers of them in mud or pools. These groupings have been reported to occur in some places where summer weather is warm and dry (Overton 1916, Engelhardt 1916, Hurter 1911).

The box turtle is an omnivorous feeder (Surface 1908, Allard 1935). It would seem that the bottomlands forest should provide abundant food. Beetles and other insects are common, as are spiders, millipedes, harvestmen, and snails. Mushrooms and may apples are available in season.

The foods that are most important to the box turtle probably vary with the season and the habitat. Notes were made of all feeding observations in the bottomlands as a possible clue to important foods there. Altogether I have records of sixty observations. Forty-three of these refer to turtles feeding on mushrooms. More than half of these records are for the first two weeks of July, when mushrooms are plentiful. This is an indication that mushrooms are one of the staple foods, but should not be interpreted to mean that they represent as high a proportion of the food as would appear from the field notes. Feeding on insects and other small prey would be difficult to observe, and probably was overlooked frequently. The seventeen records of other foods were for may apples, millipedes, snails, caterpillars, earthworms, and beetles.

CHAPTER V

TERRITORY AND HOME RANGE

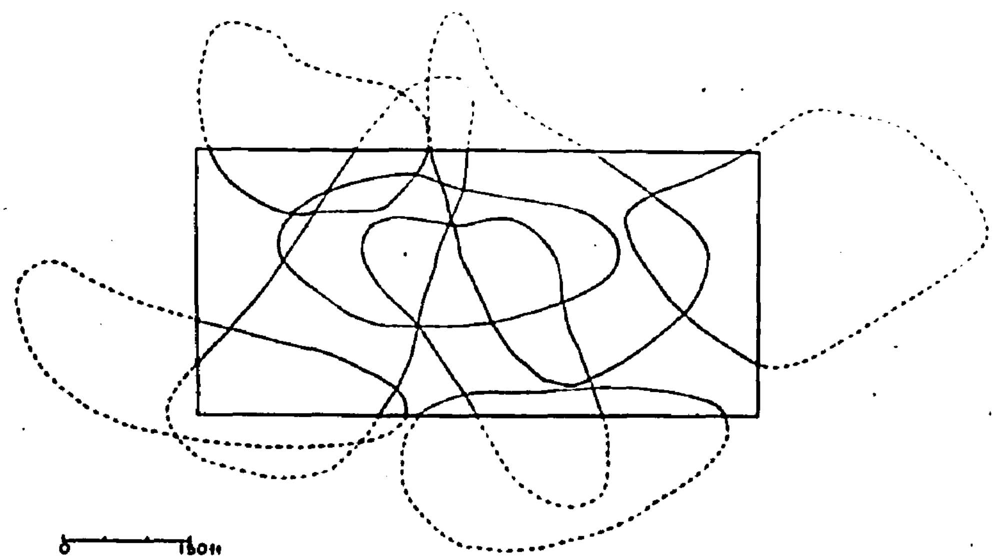
Most species of animals whose field behavior has been studied carefully have been found to have home ranges; their day to day activities are largely restricted to a limited area. Some have been shown to hold territories; they defend a part or all of the home range.

Home ranges and territories of various vertebrate animals are discussed in a previous section. The findings of the present study concerning home range and territory in box turtles are described below.

Territory. - Box turtles apparently do not hold territories, and in fact show social tolerance. No turtle seems to occupy any piece of ground to the exclusion of other turtles. Ranges overlap grossly, and are sometimes completely superimposed. All sexes and ages appear to be equally tolerant of the others' presence. Adults and juveniles of one or both sexes often occupy the same area. The ranges of fifteen of the turtles occupying parts of a five acre plot in the study area are shown in Figure 18. Ranges overlap to an even greater degree in most other parts of the study plot.

Turtles are frequently found near each other, not

Figure 18. Ranges of fifteen turtles occupying part of a five acre plot in the study area. Ranges overl grossly. Those in the upper figure represent males and in the lower figure represent females. Both fig ures show the same area. These were not the only turtles that used this area, but only those that wer collected as many as five times in the 1945 season alone. Broadly overlapping ranges and the very tol- erant behavior of turtles toward each other give no evidence for territorialism.



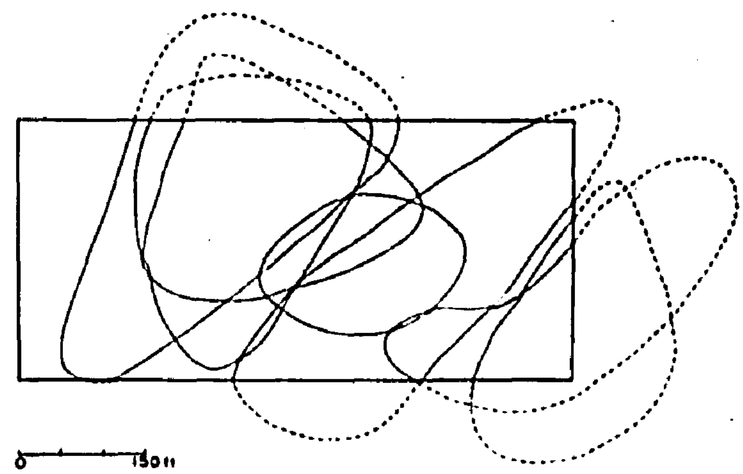


Figure 18

uncommonly in groups of three or four. These are not breeding groups, for they may contain members of only one sex, and sometimes include juveniles. Sometimes the turtles are so close together their shells nearly touch, but at other times they are spaced more widely. The turtles may be together because the location is particularly desirable, but they must be tolerant of each other, or the groups would not occur. The amount of grouping is somewhat variable. For example, on the collecting trip of August 29, 1945, thirty-five per cent of the forty-eight turtles collected were in the vicinity (within twenty feet) of one or more others. On October 17, 1945, sixty-three per cent of the thirty-eight turtles collected were near one or more others.

No turtles were seen fighting although more than two thousand collections were made. There were four 1945 records of males on top of other males or following them. Two of the aggressor males were later found in courtship behavior with females, so the behavior was most probably attempted mating activity, and irrelevant to the problem of territoriality.

Allard (1935) described a fight that took place between two captive male box turtles and Latham (1917) described a fight that took place between two wild individuals. However, from the records of the present study it appears that fights rarely occur in nature. They certainly do not occur often enough to demonstrate territorial defense or aggression.

Females usually lay their eggs some distance from their normal ranges and, after laying, display no further interest in the eggs or site. Whether a female would defend the site where it was actually preparing a nest or depositing eggs is not known.

Home range. - Box turtles living in the study plot showed definite home range behavior. Most, if not all, of the adult animals occupied specific home areas. There was a strong tendency for the turtles to retain the same home ranges from year to year. Even numerous collecting records cannot be expected to show the exact limits of range in every direction. For this reason slight shifts in position of range or small extensions or decrease of range will not be accurately shown by collections alone. Beyond these possible slight shifts there appeared to be no change in range among 106 turtles collected three or more times in each of two successive years. Most recorded ranges in succeeding years overlapped broadly or were nearly identical. There may have been weekly or monthly changes in the exact amount of land traversed, and in the shape of the home range area, but such changes were not detected. There were no records of turtles changing their ranges completely, and no evidence that residents of the study plot moved away. All turtles that could be definitely rated as residents of the plot in 1944, on the basis of four or more collections in the area in that year, were retaken there in 1945. Examples of record maps made from collecting data are shown in Figures 19 through 23.

Box turtles tend to remain in their home ranges, even under adverse conditions. This was demonstrated when flood waters covered the bottomlands in July 1945. Rains began July 14 and continued more or less steadily through July 19. The Patuxent River overflowed its banks, and the bottomlands became a swirling mass of water for one-quarter to one-half mile back from the river. The study plot was completely submerged to a depth of two to three feet. The flood peak came July 18. On July 19 and 20 most of the land was still under water, but the water level was lower, and there were elevated portions not submerged. On these two days, 25 turtles were collected in the study area. Most of the turtles proved to be within their normal ranges, despite the severity of the flood. Eighteen of the 25 turtles collected July 19 and 20 were collected between 5 and 14 times each in the 1945 season, so their ranges were fairly well understood. Of these 18, one turtle apparently had been carried by the flood waters, for she was found 670 feet from the nearest portion of her normal range. She was found in her usual home range 11 days later, and was collected there 8 more times that season (Figure 24).

Figures 19 through 22. Sample maps of home ranges based on collection records of adult box turtles. Maps of these four individuals are typical of records obtained for most of the resident study area turtles. Solid lines connect consecutive collection points in a single season. Broken lines connect the records of different years.
1944 records: ◐ 1945 records: ● 1946 records: ○

Figure 19. ♀ 393:
1944 - June 21 to October 19; 12 collections
1945 - April 3 to October 17; 6 collections
1946 - September 10; 1 collection

Figure 20. ♂ 546:
1944 - September 5 to September 22; 4 collections
1945 - July 12 to October 18; 7 collections
1946 - August 29 to September 12; 6 collections

Figure 21. ♂ 478:
1944 - July 27; 1 collection
1945 - April 3 to October 29; 11 collections
1946 - September 10; 1 collection

Figure 22. ♂ 505:
1944 - August 3 to October 7; 3 collections
1945 - April 3 to October 19; 12 collections
1946 - July 8 to October 7; 4 collections

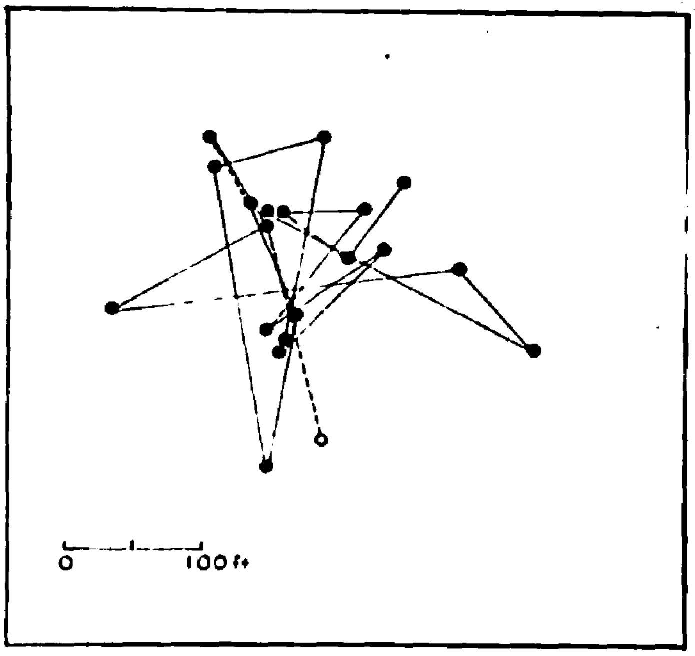


Figure 19

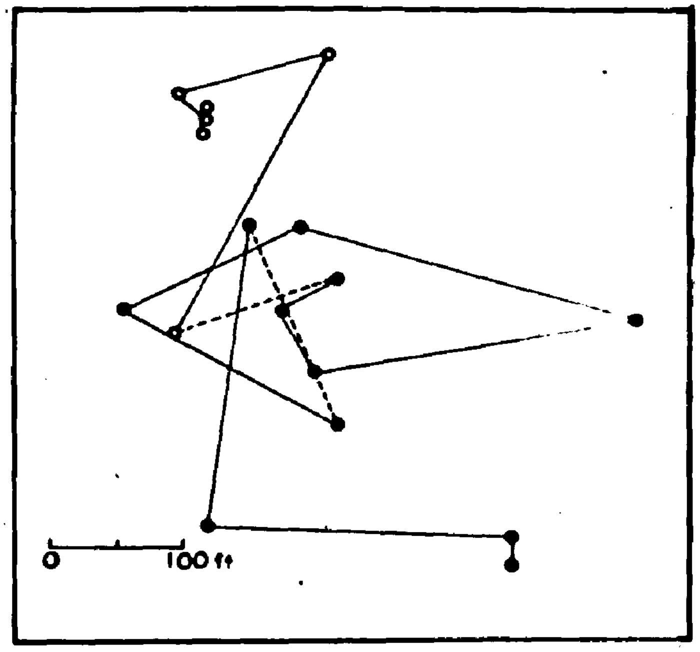


Figure 20

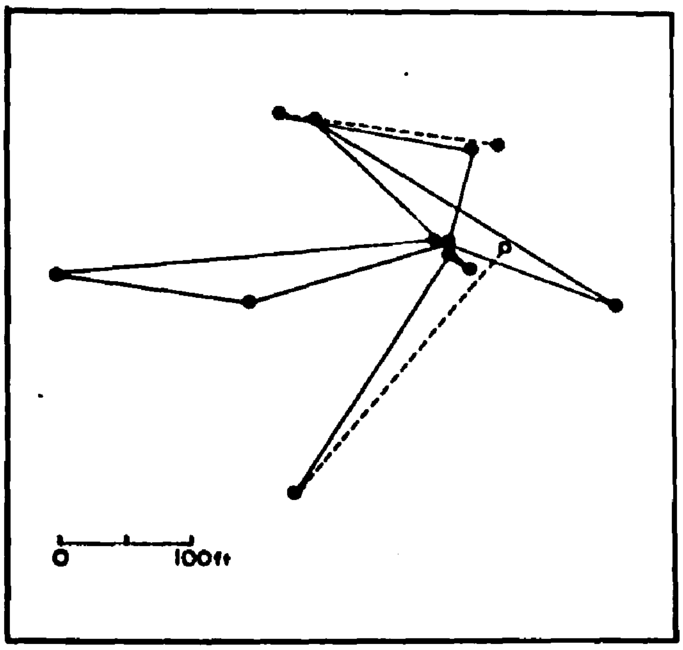


Figure 21

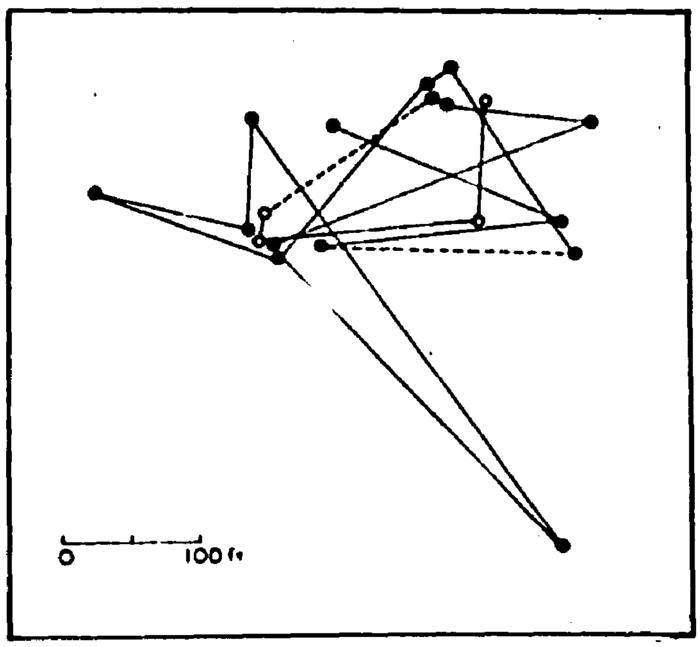


Figure 22

Figure 23. Sample map of home range based on collection records. The range of this turtle is larger than the average, but is otherwise typical. 1944 records: ⊕ 1945 records: ● 1946 records: ○

♀ 426:
1944 - July 3 to October 7; 7 collections
1945 - April 3 to September 26; 8 collections
1946 - July 8 to September 13; 4 collections

Figure 24. Map of collection records of a turtle displaced from her normal range by a flood. Records in the home range both preceded and followed the flood record, which was 670 feet from the nearest recorded part of the normal range. 1944 records: ⊕ 1945 records: ● 1946 records: ○

♀ 597:
1944 - September 15 to October 7; 3 collections
1945 - May 13 to October 19; 10 collections (flood collection on July 20).
1946 - September 3 to September 13; 3 collections.

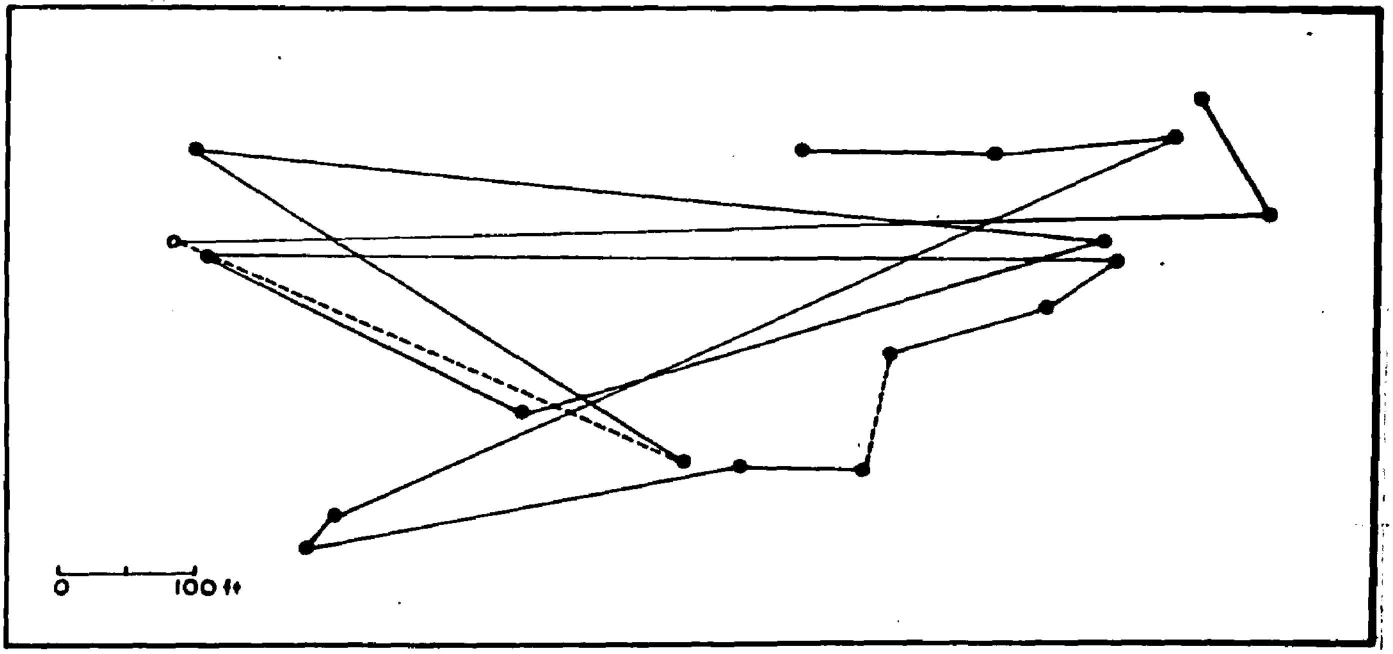


Figure 23

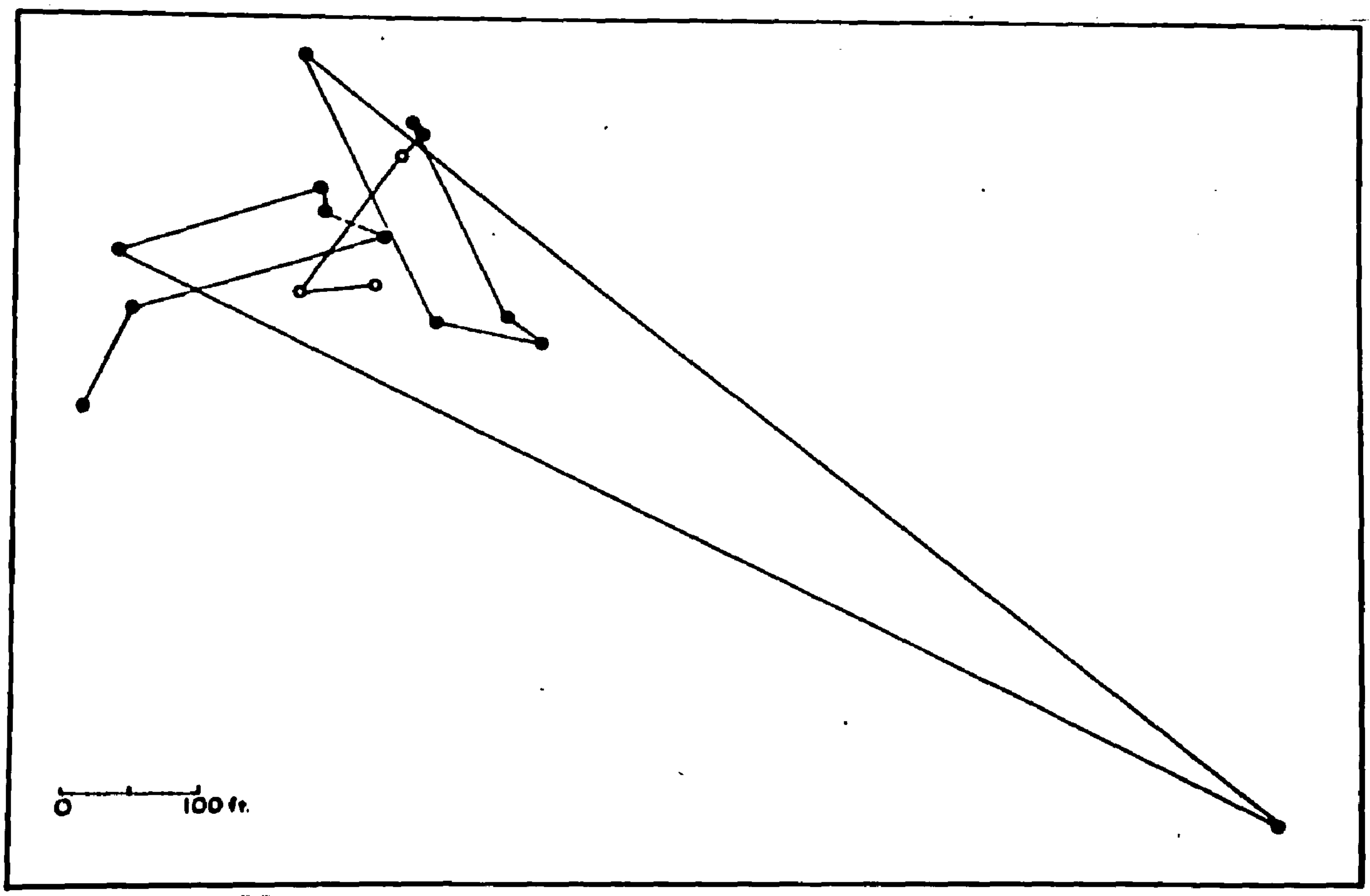


Figure 24

Two others may or may not have been moved by the flood for they were found 170 feet from the nearest known parts of their home ranges. The remaining 15 evidently were not displaced, for their flood records were within their normal ranges.

Seven of the 25 turtles found during the flood were collected fewer times in the 1945 season, so their status in the population was less clear, and their flood records less subject to interpretation. Nevertheless, with two exceptions, collecting localities at flood time were less than 150 feet from their other collection points.

These findings concerning home ranges are in accord with those of Nichols (1939). He found box turtles in the same general localities after many years. He records one instance of fifteen years, one of ten years, and a greater number for shorter periods.

Turtles with established ranges in the study area occasionally left their ranges for short periods, and turtles from other places occasionally passed through the study area as transients. These travels present a separate problem, and are discussed below. They are mentioned here to show that constancy to the home range is not invariable.

The above discussion refers primarily to adult turtles. The age when the home range is established is not known. In the present study, juveniles were collected infrequently, and there were too few repeat captures to answer the question with certainty. However, a few juveniles seemed to have established ranges. A turtle 88 mm. long in 1944 was collected within the same 100 foot area a total of 7 times. It was taken 3 times in 1944, once in 1945, and 3 times in 1946. Another, 97 mm. long was collected once each in 1944 and 1945 and 3 times in 1946; all records were within 325 feet. Some other juvenile records are shown in Table 2. The paucity of data concerning juveniles may be an indication that some turtles of this age behaved differently from those described above.

CHAPTER VI

SIZE OF HOME RANGE

Discussion. - Size of home range is a significant variable in an animal population for it expresses the effect of a complex of environmental features. The size of the home range with the size of the population constitutes an expression of the status of the population and an index to the suitability of the environment.

The factors that govern the size of the home range are largely unknown. There have been few detailed comparative studies of home range variation in any species. Nevertheless, it may be worth while to consider some of the factors that may influence range size.

(1) Environment. Food, shelter, and other physical features of the environment influence range size. There is evidence that range sizes are larger in unfavorable habitats than they are in favorable ones (Stickel, L. F. 1948). It is logical to expect variations in the suitability of environment from place to place. Seasonal or annual changes might also produce variations in a single locality.

(2) Physiology. The individual's needs will determine the distances of travel under a given set of environmental conditions. At one extreme, in very poor habitat, the energy expenditure required to secure food might exceed the energy

value of the food (Leopold 1933). Food and shelter might not be available within a reasonable distance of each other. At the other extreme, when there is an abundance of food and shelter, other physiological needs (perhaps, for example, exercise requirements) might cause an animal to travel over a larger range than would be necessary to secure food or shelter.

(3) Population size. Range sizes might tend to be smaller in densely populated areas than in sparsely populated ones, because of the pressure of crowding.

(4) Territoriality. The desire of individuals for exclusive use of property of a certain minimum extent may under some conditions limit the minimum size of range (Burt 1940).

Turtle ranges. - The average size of the home range was calculated from the 1945 records. A single season's records were used so that range shifts or population changes would not influence the results. Collections in 1945 were more numerous and better distributed over the study plot than the collections of other years, and gave the most nearly complete data. Quantitatively similar calculations could not be made for 1944 and 1946 because of the differences in collecting pressure. However, the mapped travels of turtles in these two years showed a very close similarity to the 1945 records. There seemed to be no difference in range size in the three separate years.

Most of the collecting in 1945 was done on systematic census trips, when the entire study plot was carefully searched. When collecting is done in this way, turtles are likely to be found in many different parts of their ranges, and the range size will be estimated more reliably than it would be if collecting were casual. Collections were made on seventy-seven days from March to October. Nine-hundred and ninety-one records were secured, a greater number than in any other season.

Box turtles normally traverse their ranges within a period of a few days. It is theoretically possible to find the size of the range, or at least its maximum diameter, by a relatively small number of collections. In practice this is not strictly true. When only a few collections are available, it is impossible to determine which turtles have their home ranges completely within the study plot, and which ones have their ranges partly inside and partly outside the area. Further, there is no way to distinguish between these resident turtles and the transients that are traveling through the area. Records of transients would be especially difficult to interpret, although the records of the marginal residents might have more influence on calculations. In a season's collecting, the permanent residents of the area will be collected more times than the transients or border residents. The number of collections per individual can therefore be used as an aid in selecting the turtles whose records are used to calculate the average range size. For the present calculations the travel records were grouped according to number of collections, and the groups were studied to find the ones most suitable.

Among males, there was no significant difference in the ranges of turtles taken three times and those taken any greater number of times. Trips outside the home range for egg laying or other purposes complicated the records of female turtles. Non-resident turtles traveling through the study area were sometimes collected at two or more points in their travels. As a result, the average travel range of female turtles collected twice exceeded the travel range of those taken three or four times. Also, the average range of those taken three times exceeded the range of those taken four times. Averages for female turtles taken four, five, or six times were not significantly different from each other. Individuals collected more than six times were too few for reliable comparison. In this group there were some turtles with well defined ranges who made travels outside the home range so their maximum travel distances were unduly great.

A conservative procedure was decided upon; calculations of range size were based on the records of turtles collected at least six times. On this basis there were 440 records for fifty-five turtles, an average of eight collections per turtle. Four examples of travels outside the home range made by female turtles were excluded from the data before calculation. Travel distances are shown in Table 2.

The mean range (average maximum diameter of home range) of adult males in the study area in 1945 was 330 feet, with a standard error of the mean of 26 feet. Standard deviation was 137 feet. One standard deviation on each side of the mean includes home range sizes between 193 and 477 feet. The ranges of two-thirds of the population can be expected to lie between these limits. The coefficient of variation is 41.5.

The mean range of adult females is 370 feet, with a standard error of the mean of 29 feet. The standard deviation is 149 feet, so two-thirds of the population should have ranges between 221 and 519 feet. The coefficient is 40.3.

There is no significant difference between the size of male and female ranges: the difference between the means contains its standard error 1.04 times. Therefore, the records of the two sexes can be grouped and studied together in problems related to range size.

The range sizes found in the present study are of the same magnitude as those found by Nichols (1936) on Long Island. Twelve of the box turtles that he released at the site of capture were recaptured six months to six years later. They were retaken from less than 150 feet to as much as 750 feet from the places of original capture. The average distance for the twelve was 390 feet.

TABLE 2

BOX TURTLE RANGES AND COLLECTIONS

IN 1945

Maximum diameter of known range (feet)	Number of Collections in 1945: 2		3		4		5		6		7		8		9		10		11		12		13		14		15	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
0-50	2	4		2																								
51-100	2	4	3	2	1		1	1																				
101-150	4	1	1	3	2	4	2		1	1			1															
151-200	5		4	1	5	2	1			1	3			1														
201-250	2	3	1	3	2	1	2	5	1	2	2			1[B]	1				1									
251-300	1	1	1	2						1	1				1	1[E]	1			1								
301-350	1		2			3	2	2[A]		2	1		1					1		1						1		
351-400		1		2	2	1		1	1	3	2	1			1		1											
401-450		1		3			1	1		1									1		1							
451-500	1	1	1	2	2				1			1	2	2[C]														1
501-550				1			2				1	1													1			
551-600					1		1	1	1							1												
601-650																												
651-700				1										1[D]														
701-750				1								1																
751-800	1																											
1000		1																										
1060			1																									
1470					1																							
1540			1																									
2310		1																										
2400		1																										

[A]Increased to 765 ft. on trip away from home range
[B]Increased to 770 ft. on trip away from home range
[C]Increased to 855 ft. when carried by flood
[D]Increased to 1380 ft. on egg laying trip
[E]Increased to 985 ft. at peak of flood

Range size among juveniles has not been established, nor has it been found whether all juveniles have home ranges. The 1945 travel records for juveniles 107 mm. and smaller are shown in Table 3. The shortest and longest travel records for juveniles do not differ appreciably from those of adults collected an equal number of times. Juvenile travel records for other years were similar to these.

The long travels are proportionally more numerous among these juveniles than among adults. Perhaps this is the result of sampling error owing to the smallness of the series, but it is also possible that it is an indication that more juveniles than adults are prone to extensive wanderings. The small number of collections per juvenile may indicate that young turtles travel extensively, or it may simply reflect the fact that they are difficult to find.

TABLE 3

TRAVELS OF JUVENILE TURTLES

Code number	Length mm.*	Times coll. 1945	1945 distances feet	Collections other years
522	88	2	520	none
594	97	2	1360	Once in 1944, 125 ft. from the nearest 1945 record.
825	103	2	280	Three times in 1946, overlapping the 1945 records.
830	104	2	455	none
653	106	6	170	Once in 1944, 5 times in 1946, overlapping the 1945 records.
410	107	3	1230	Once in 1944, 290 feet from the nearest 1946 record. Three times in 1946, within 245 feet. Two of the 1945 records overlapped the 1946 records.

*Measurements are made in a straight line from anterior to posterior margins of carapace. Measurements in this table are for the year the turtle was first collected. Therefore several of the turtles were larger than this in 1945.

CHAPTER VII

MOVEMENT PATTERNS IN THE HOME RANGE

Very little is known about the daily travels of any animal, except that they are usually limited to a definite home range. It is not surprising that this subject has been studied so little, for most animals are difficult to observe. Many are nocturnal, and almost all are wary. In contrast to other animals, the box turtle is almost ideally suited for studies of travel and range relationships, for it can be made to map its own travel routes.

In the present study the use of a trailing device has been the principal technique in determining movement patterns of the box turtles. The trailer, a small light structure that is attached to the turtle's carapace, is described in detail and illustrated in the section on methods. As the turtle moves, a spool of thread unwinds, and makes an exact and detailed record of the turtle's travels. Routes can be followed for days or weeks. The behavior of a turtle carrying a trailer appears absolutely normal. Its method of walking, speed, and other actions are the same as for turtles without trailers. The distances traveled are entirely comparable.

The principal difficulty of the method is that only a few turtles can be studied this way at any one time. Locating the turtles each day and supplying new thread occupies about two hours per day for five turtles if they all live in the same vicinity. When their paths are divergent, or they live at distances from each other, the time required is greatly increased. More prohibitive is the problem of mapping the travel routes. In the study area markers at regular intervals simplified the mapping but it was nevertheless very time consuming.

Detailed travels of eleven turtles were followed and mapped for 456 turtle days. The longest record for one turtle was 161 days. The ten others were followed for periods of one to forty-four days.

Systematic collecting in the study area provided more indirect data concerning turtle movements. All collection sites were mapped and the maps were used in making interpretations of some of the trailer data. Generalizations concerning travel behavior are based on evidence gathered by the combination of methods.

The normal movements of a turtle in its home range form a complicated pattern:

(1) There are numerous turns, doublings, detours, and criss-crossing paths. These appear in the routes of every turtle followed with a trailer in its home range for as much as one day of activity (Figures 25 and 26).

Figure 25. Travels of an adult male turtle during eight days of midsummer, July 7 through July 14, 1945. The devious path, with its turns, doublings, and detours is characteristic of the travels of turtles in their home ranges. The maze of paths at the middle left of the map was made by the turtle returning to this same place at different times, while traveling in various directions in between times. The same stretch of path was thus traveled seven different times in the eight days. The tendency to retrace the same particular route at different times is typical of behavior of turtles in their home ranges.

♂ 424:
(1) Place collected July 5 and released July 6 at 7:00 p.m.
(2)(3)(4) July 7
(5) July 8
(6)(7)(8) July 9
(9)(10)(11) July 10
(12)(13) July 11
(14)(15) July 13
(16) July 14, 3:45 p.m.

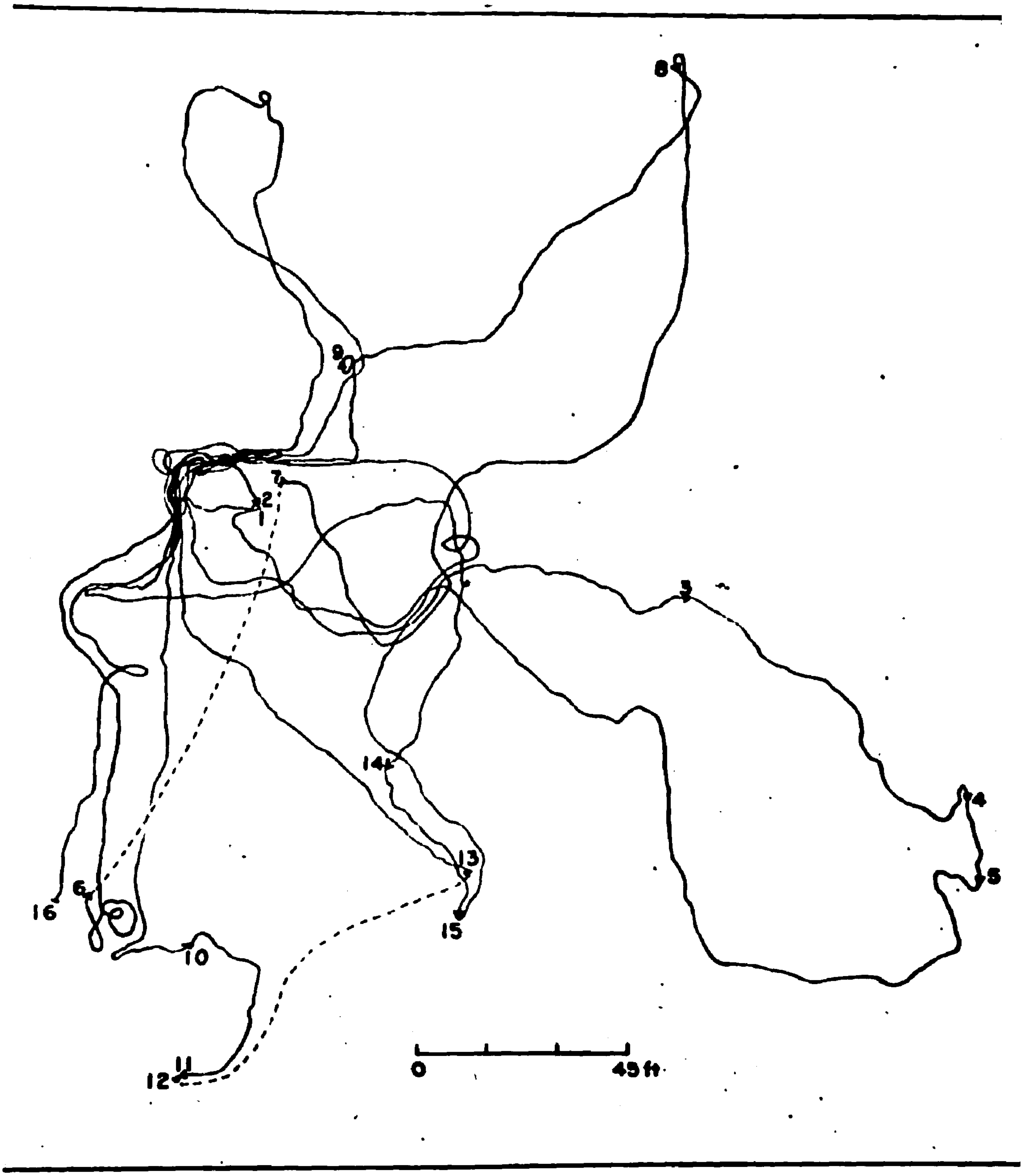


Figure 25

Figure 26. Collections and trailer records in the home range. This map shows the collecting localities from 1944 to 1946 as well as the detailed travel route during eleven days of midsummer 1945.

1944 records: ◉ 1945 records: ● 1946 records ○

♂ 192:
Collection data:
1944 - July 25 to September 28; 8 collections
1945 - April 17 to September 28; 10 collections
1946 - June 15 to October 7; 14 collections

Trailer records:
(1)(2) July 6
(3)(4)(5) July 7
(6)(7) July 9
(8) July 10
(9)(10) July 11
(11)(12) July 12
(13) July 13
(14) July 14
(15) July 15
(16)(17) July 16
(18) July 17

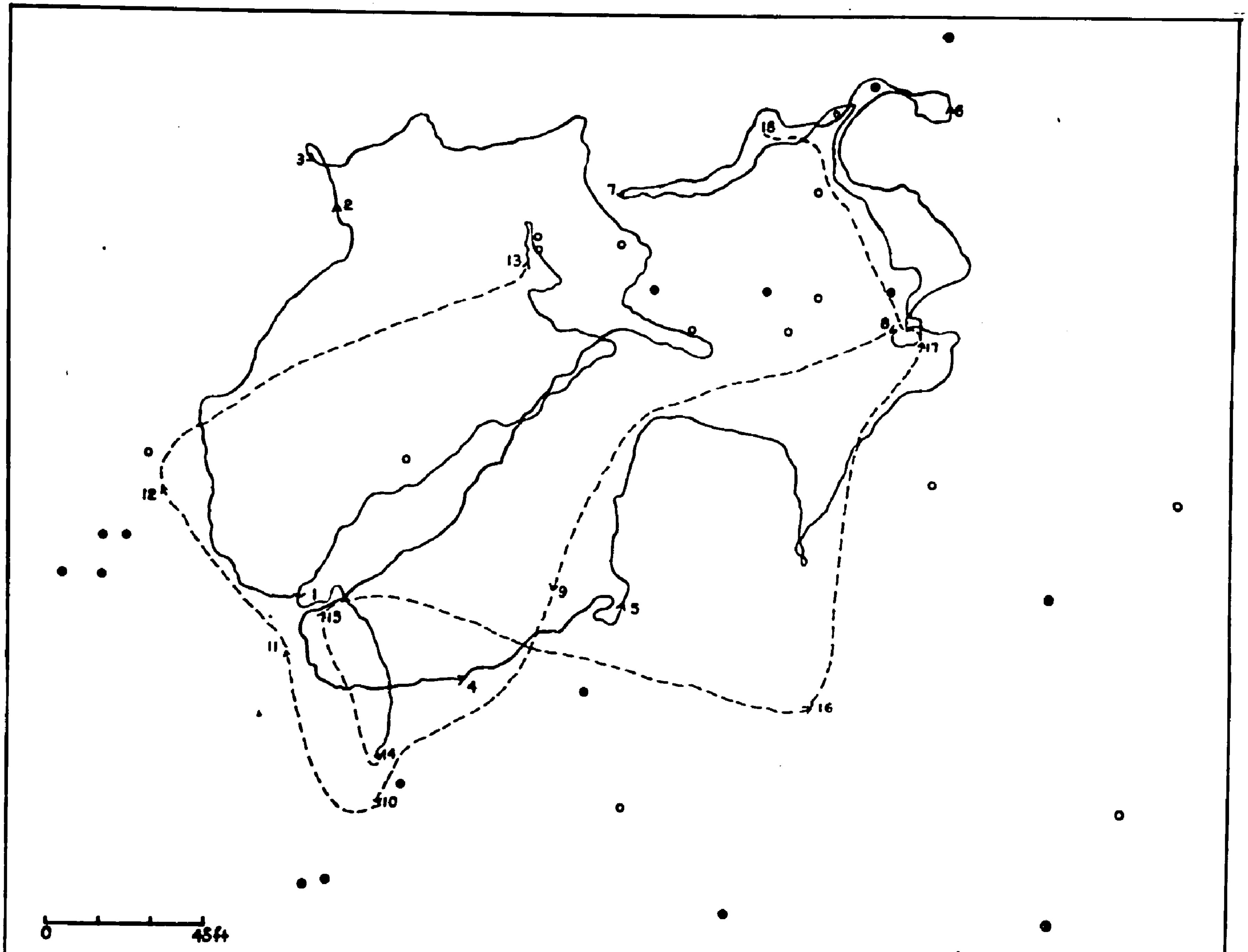


Figure 26

(2) There is an interspersion of fairly direct routes or traverses of the home range so that the principal parts of the range are visited in a relatively short time (Figure 26).

(3) There is a tendency for some routes to be traveled more frequently than others. At intervals of a day or more a turtle may return to a particular tree or bush. Each time it will make a turn or two around it, until finally an irregular web-like pattern results. The route may loop around the end of a particular log many times in different trips across the range. One turtle walked along a single short stretch of path seven different times in eight days, traveling over diverse areas between times. These travels are shown in Figure 25.

The distance a turtle travels in a day usually has very little relationship to the distance measured in a straight line. People occasionally report finding the same turtle in nearly the same spot at several different times, and conclude that the turtle is extremely sedentary. There are times when turtles travel very short distances, or none at all for some days, but if a day is favorably warm and moist the actual distance may be great in relation to the straight-line distance, or even to the total diameter of the home range. One of the trailer turtles covered 456 feet in a day without leaving its home range, which was less than 300 feet in diameter. The straight-line distance between the form the turtle left in the morning and the form where he spent the night was only 170 feet. This much travel on a favorable day is not exceptional.

There is some variation in the amount of its home range a turtle covers in a single day, but most turtles seem to reach or approach the extreme limits within a relatively short period.

Collection records show no correlation between the distance that is traveled and the time that has elapsed between collections. Maximum distances may be recorded within a few days or weeks, and minimum distances may be recorded after time lapses of months or years. The tendency to reach the limits of the home range in short periods was also shown by the trailer turtles. Three examples are given below.

Example 1. - The home range of ♂ 192 was determined by collecting records to be about 285 feet in greatest diameter in 1945. The records for two other years gave similar results: 265 feet in 1944 and 290 feet in 1946. During four days in July, 1945, while carrying a trailer, this turtle covered an area having a maximum diameter of 245 feet. This was only forty feet less than the distance recorded in collections from April to September of that year. The detailed route of travel for these four days and an additional seven days is shown in Figure 26.

Example 2. - Trailer records for ♀ 476 covered an area 390 feet in greatest diameter during a nine day period in July. Seven collections during the year showed a maximum range of 355 feet. The small difference is within the sampling error.

Example 3. - The home range of ♂ 629 was determined by collecting records to be about 235 feet in diameter. During five days in July, while carrying a trailer, it covered an area 185 feet in diameter. Trailer records for four additional days did not increase the distance.

The general tendency to cross and re-cross the entire home range at frequent intervals is not followed by all turtles. Other types of travel are best illustrated by trailer records, but are also suggested by the collecting records.

A simple variation is to cover only a part of the range at a time. Movements within this area follow the patterns described above. There was one striking example of this among the trailer turtles. A male turtle, number 424, had a total seasonal range of about 510 feet in greatest diameter. For twenty-nine days, May 21 to June 18, he remained in and near a single brushy entanglement at the extreme northern portion of his range. During this time all his travels were within an area ninety-five feet in diameter. A few weeks later this turtle was in the most southern part of his range. A trailer was again attached and his route was followed for eleven days, July 5 to 15. During this time his activities were limited to an area 260 feet in diameter, which was very intensively covered. This eleven day route is shown in Figure 25.

Some turtles may have two home ranges, and travel between them at infrequent intervals. The single example of this behavior was provided by an adult female turtle. In the summer of 1946 she was collected far distant from her normal range, and a trailer was attached in hopes of finding an explanation of her travels. This turtle had been studied by collections in 1945, and one of these 1945 records had also been well removed from the others. The travels of this turtle were recorded from July 3, 1946, until hibernation on October 24, and from the time of leaving hibernation May 1, 1947 until June 18, 1947, a total of 161 days.

She was collected July 3, 1946, on a hilltop roadside. A trailer was attached and she was released within an hour at the same place. The first part of her route (Figure 27) was related to egg laying. At 6:45 p.m. on July 6 she was found digging an egg hole in a gravelly clay spot on the shoulder of a little used road, 1045 feet from where she had been released. By 7:45 p.m. the egg hole had been filled with earth and the turtle was in a form a short distance away. In the days following she traveled an irregular route, mainly through an old pine field, and on July 13 reached the edge of the bottomlands bluff.

The trip through the bottomlands to her previously known range was completed by July 22. There she remained for nearly a month, criss-crossing her range and following a twisted zig-zag route, all typical home range behavior (Figures 28 and 29).

On August 17, following a rain, she started southward and in three days traveled in a fairly direct route to a place 480 feet distant where her movements again took on the typical home range pattern. She stayed here for one month before starting north again (Figures 29 and 30).

The northern trip occupied four days. Again in her northern range she exhibited typical home range behavior. By this time the weather was less favorable for turtle travels than it had been in midsummer and the daily movements were shorter. The night of October 23, she covered herself with earth and began hibernation in her northern range. The place of hibernation was only thirty feet from the spot where she had hibernated in the winter of 1944-45 (Figure 30).

She left the place of hibernation on May 1, 1947 and traveled about ten feet that day. She remained in the northern part of her range until May 27, traveling intermittently. Between May 27 and 29 she traveled south over the same general path used previously in north-south trips, but instead of stopping in her usual summer range she continued into an old pine and sweet gum field. Her route in this field was similar to the route she followed in 1946 when she was returning to the bottomlands after laying eggs. On June 18 she was at the edge of the field, not more than fifty feet from the egg laying site of 1946. The trailer was removed on this date, and no further trailer records were made. No turtle collection trips were made during the remainder of the summer. However, this turtle was collected again October 10, 1947 in the northern part of her range in the bottomlands.

To summarize: In the time this turtle was under observation in 1946 a northern range of four-hundred feet diameter was occupied for a total of fifty-nine days, in two separated intervals, while a southern range of the same size was occupied for twenty-eight days. The two ranges were more than four-hundred feet apart at the point where they approached each other most closely. Travels in the early part of 1947 followed a similar pattern.

It is not likely that many turtles divide their time between separated areas, but the behavior is probably not unique. Collecting records for most turtles are well distributed through the season, and have, except in a few cases, given no indication that the turtles left their ranges for appreciable periods. One collection record for this particular turtle had been far from the others, but until the travels were followed with a trailer interpretation was impossible, for turtles as well as other animals occasionally make brief trips away from their home ranges.

Other records of turtles collected far from the places that were known to be their normal ranges are discussed and described in the following section.

Figures 27-30. Maps of the travels of adult female box turtle, number 539, for 113 days, from July 3, 1946 until hibernation October 23. She divided her time between two separated ranges: a northern range of four hundred feet diameter was occupied for a total of fifty-nine days in two separated intervals and a southern range of approximately the same size was occupied for 28 days. Two trips between the ranges occupied three and four days each.

Figure 27. The turtle was collected June 3 on a hilltop roadside (1) and from there traveled through brush, woods, and an old pine field to a little used road. She traveled along this road (1-3) with occasional deviations into the adjoining pine field, and on July 6 at 6:45 p.m. was digging an egg hole on the gravelly clay road shoulder (3). By 7:45 p.m. the hole had been filled and the turtle was in a leaf form in the woods a short distance away (4), where she stayed all the next day. On the day following she traveled a short distance, where she was found in a leaf form at 3:00 p.m. (5).

On the next day, July 9, she crossed the old road into the pine field again and in succeeding days followed an irregular route through the field to the edge of the bluff separating uplands and bottomlands (1

The part of the route shown in this figure lies so of the area shown in Figures 28 to 30. Its position can be seen from the guide numbers at the side of the map and from the code numbers marking the turtle's route.

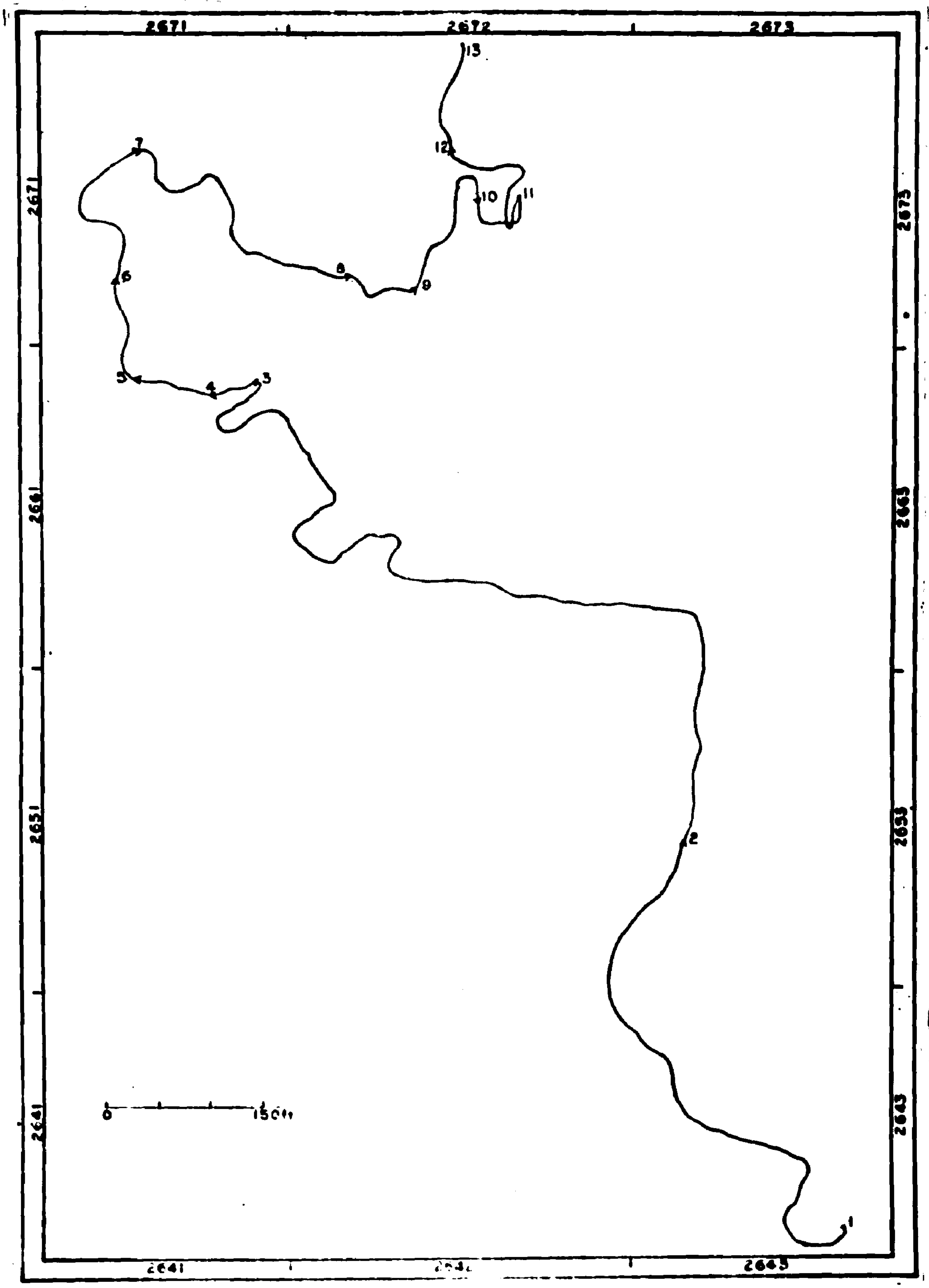


Figure 27

Figure 28. - She entered the bottomlands July 13 (13-14) and traveled some each day until on July 22 she reached the home range where she had been col-cected several times in the previous year (14-23). Here her travels took on a pattern typical of home range behavior. She remained in this area for nearly a month, July 22 through August 16(points 23-32 on this map and 32-40 on the map in Figure 29, which is a continuation of the same route and shows the same area).

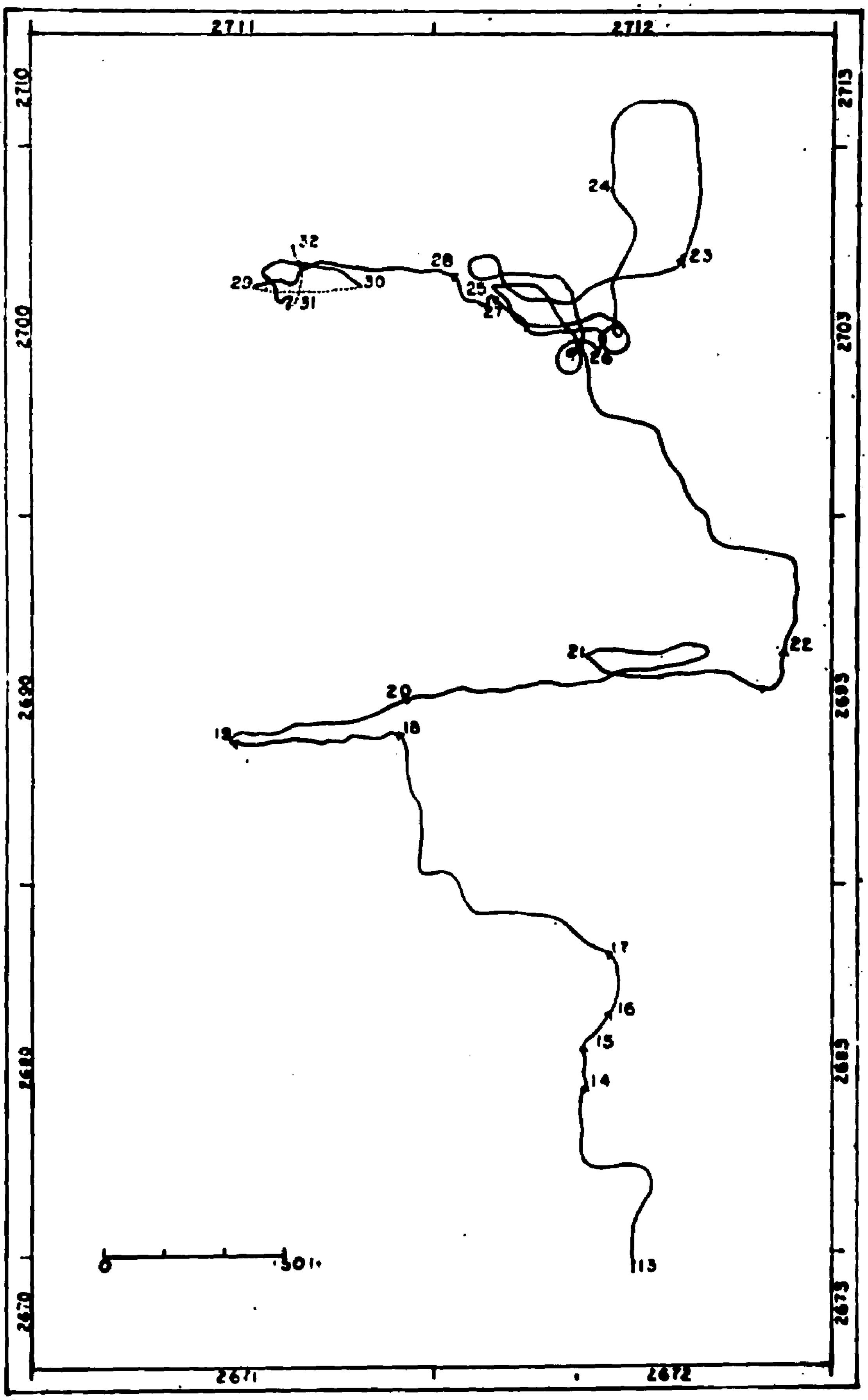


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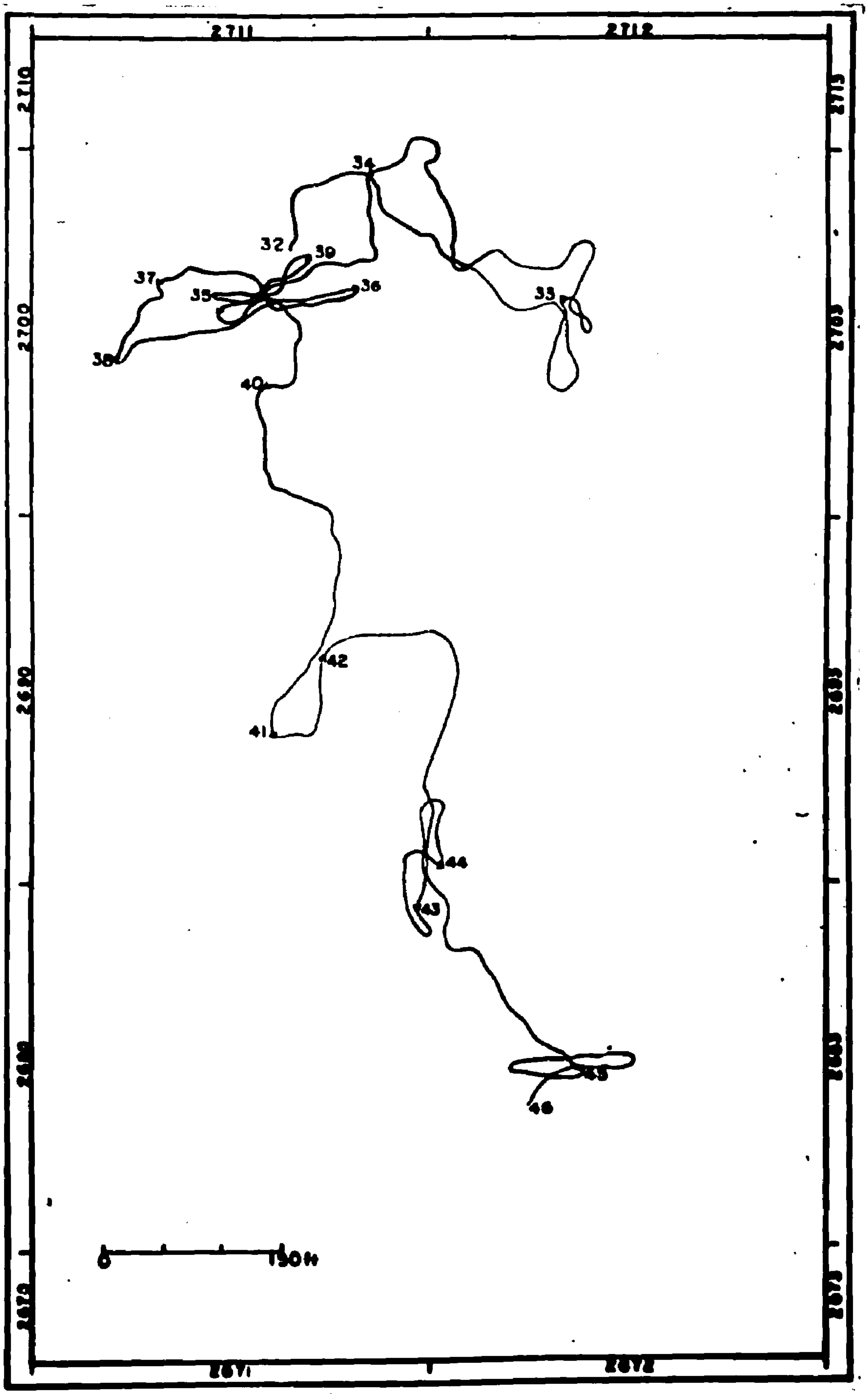
Figure 28

Figure 29. On August 17 she started southward, and in three days traveled a straight line distance of 480 feet to arrive at a place where her movements again took on the typical home range pattern (40-43). She stayed in this vicinity for one month, until September 17 (points 43 through 57 on this map and the following map, which is a continuation of the same route and shows the same area) before starting north again.



2711
2712
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33
34
35
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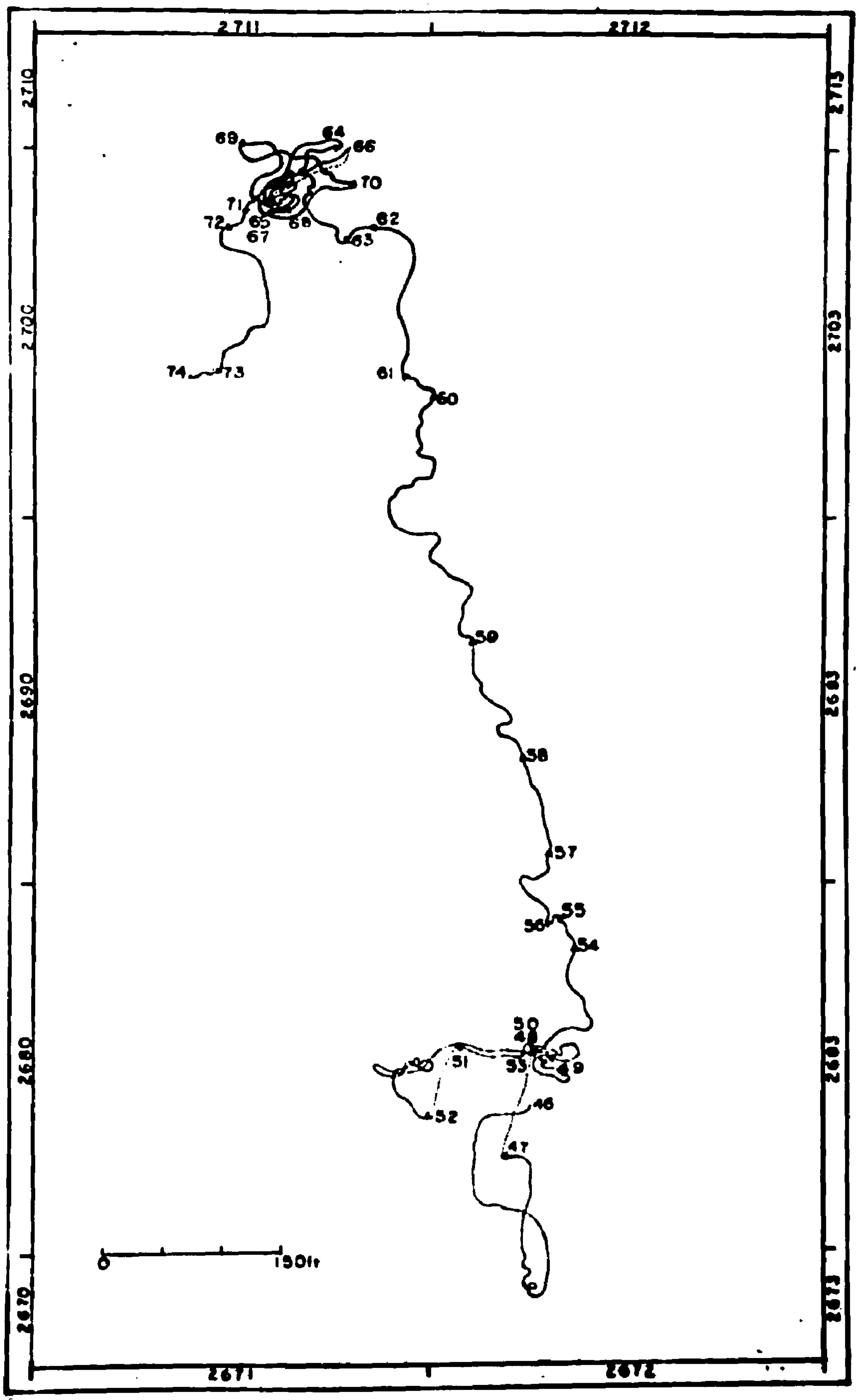
37
38
39
40
41
42
43
44
45
46
150M

Figure 29

Figure 30. The northern trip (57-60) took four days. Again in her northern range she showed typical home range behavior, traveling in this region for thirty-three days, until October 23 (60-74). Daily travels were shorter than in midsummer and she did not travel every day. On the night of October 23 she began hibernation (74), thirty feet from the place where she had hibernated in 1944-1945.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74
73
61
60
59
58
57
55
56
54
50
48
51
53
49
52
46
47
0
150ft

Figure 30

CHAPTER VIII

TRAVELS OUTSIDE THE HOME RANGE

Box turtles occasionally leave their normal ranges for more or less extended travels. Females at egg laying time often go long distances from their home areas to deposit their eggs in suitable sites. In the present study it was also found that both males and females occasionally leave their home ranges on trips of unexplained nature.

The length of the egg laying trips probably depends in part on the distance between the home range and suitable egg laying sites. Minimal distances are shown by collections made in June, during the egg laying season, when female turtles are sometimes found far from their normal ranges.

One female, number 426, was collected 1320 feet from her home range on June 15, 1945, and may have gone farther before laying eggs. Later in the summer of 1945 and in 1946 she was collected in her normal home range a number of times. On June 16, 1948, she was collected on the hilltop, 2370 feet from her home range, farther away than the 1945 collection but in the same general direction.

Five other turtles whose study area ranges were well known were collected away from these ranges in June. The

The distances were 2540, 2200, 1550, 850, and 820 feet.

It is not yet known whether turtles return to the same place for egg laying in different years. Three different turtles have been collected in the headquarters area in June or early July of two different years and collected at other distant areas in between times. A number of turtles have been collected in the headquarters area in different years at the egg laying season but not at other times. Some may have been headquarters residents, but others probably had ranges elsewhere. These records suggest that turtles may return to at least the same general locality to lay eggs.

The other travels, made by both sexes, are not so easily understood. These trips have been reported for other animals. Individual Peromyscus are known to make trips away from their normal ranges and then return to them (Blair 1940, Storer, Evans, and Palmer 1944). Travels greater than normal are frequently recorded in population studies. Many of these may indicate trips away from the home range rather than unusually large ranges or random wandering. Some transient behavior may be explainable on the basis of trips away from the home range.

This behavior among box turtles was first suggested by a study of the maps of collection points. Later, trailers were attached to certain turtles suspected of being transients and their travels were followed in an effort to learn more of the nature of these trips.

There is some evidence that the trips outside the home range may not be random in direction, and that travels may be to and from the same area on different occasions. If this is true, the difference between travels away from the home range and the possession of two home ranges is only one of degree, depending on the length of time spent in each area. A female box turtle, number 628, showed this behavior. She was collected in the study area for the first time in late September 1944. She was not retaken in 1945 despite intensive collecting in the vicinity of her capture and in surrounding areas. In the following year, July 8, 1946, she was again collected, near the 1944 locality. A trailer was attached to follow her movements, and she was released July 9. For nine days she showed typical home range behavior, moving around in an area four hundred feet in diameter. Then on July 18, she began moving southeast in a direct line. By July 20 she was several hundred feet outside the borders of the study plot and nearly seven hundred feet from her temporary range in the study plot. The trailer ran out of thread and the record ended at this point. She was not collected again although her temporary range in the study area was searched frequently, and several collecting trips were made in the vicinity of the place where the record ended.

The turtle with two home ranges, discussed above, traveled between the ranges at infrequent intervals. She traversed the same general area each time. If fairly intensive collecting had been done in this intermediate zone and in no other places, it is likely that she would have been collected a time or two in different years. She would have been correctly rated as a transient, but her behavior would not have been understood.

The activities of a male turtle found in the study area once only were recorded by a trailer for a portion of his route. He was collected August 28, 1945, a trailer was attached, and he was released where he was found. He remained in a debris form near this place for four days. On September 1 he began to move, traveling northwest in a nearly straight path for 845 feet. He escaped here near the river several hundred feet west of the study area, and was not collected again.

One female turtle traveled away from her normal range in the fall, hibernated in the new area, and returned to the original range in the spring. The records of this turtle are of particular interest because her normal range was so small. She was collected more times than any other turtle in the study area, so the record of her behavior is relatively complete. She lived on the riverbank in the northern part of the study area. She was collected thirty-three different times from 1944 through 1946. Twenty-five of these collections were within an area 170 feet in diameter. In the fall of 1944 she moved from this range to a place

220 feet away. For most turtles this distance would not be significant, but it was an appreciable trip for this unusually sedentary turtle. She hibernated in the new location. On March 29, 1945, she was found emerging from the hibernating hole, a cavity dug in the ground in the midst of logs and brush. She mated near this same place April 26. On May 31 she was retaken in her home range on the river bank. The hibernating area was searched in the spring and fall of other years, but she was not again found away from the riverbank (Figure 31).

Some turtles were collected in the study area once only in each of two or more different years, often near the same place each time. Others were collected only once. Some of these visitors to the area were also collected outside the borders of the plot often enough to show that their ranges adjoined or partially entered the plot and it was entirely reasonable to expect that they would be collected in the study area occasionally. The river bordered one side of the study area and formed a partial barrier that was crossed by an occasional turtle. Five females and one male were each collected in the study plot near the river and later collected on a river island opposite.

Some of the visitors were re-collected far from the study plot, and others were never taken again. Nothing is known of the status of these turtles. Probably some of them had home ranges elsewhere and returned to them. Some may have been wanderers, without established ranges, although there is no evidence of this.

It may be said in summary that turtles occasionally travel away from their established ranges. Sometimes on successive trips nearly the same paths are followed to a particular destination. It is not known how often this is true, for the destination and frequency of trips are poorly known. There was one record of a turtle traveling to a new area, hibernating there, and then returning to her normal range. Female turtles regularly undertake long travels for egg laying purposes.

Figure 31. Travel outside the home range. A female turtle, number 416, lived on the river bank in the northern part of the study area. She was collected thirty-three different times from 1944 through 1946. Twenty-five of these collections were within an area 170 feet in diameter. In the fall of 1944 she moved from her normal range to a place 220 feet away (9-6 to 3-29 on map). On March 29, 1945 she was found emerging from a hibernating hole in the new location, and she mated near this same place April 26. On May 31 she was retaken in her range on the riverbank. She was collected there many times again that year and in 1946.

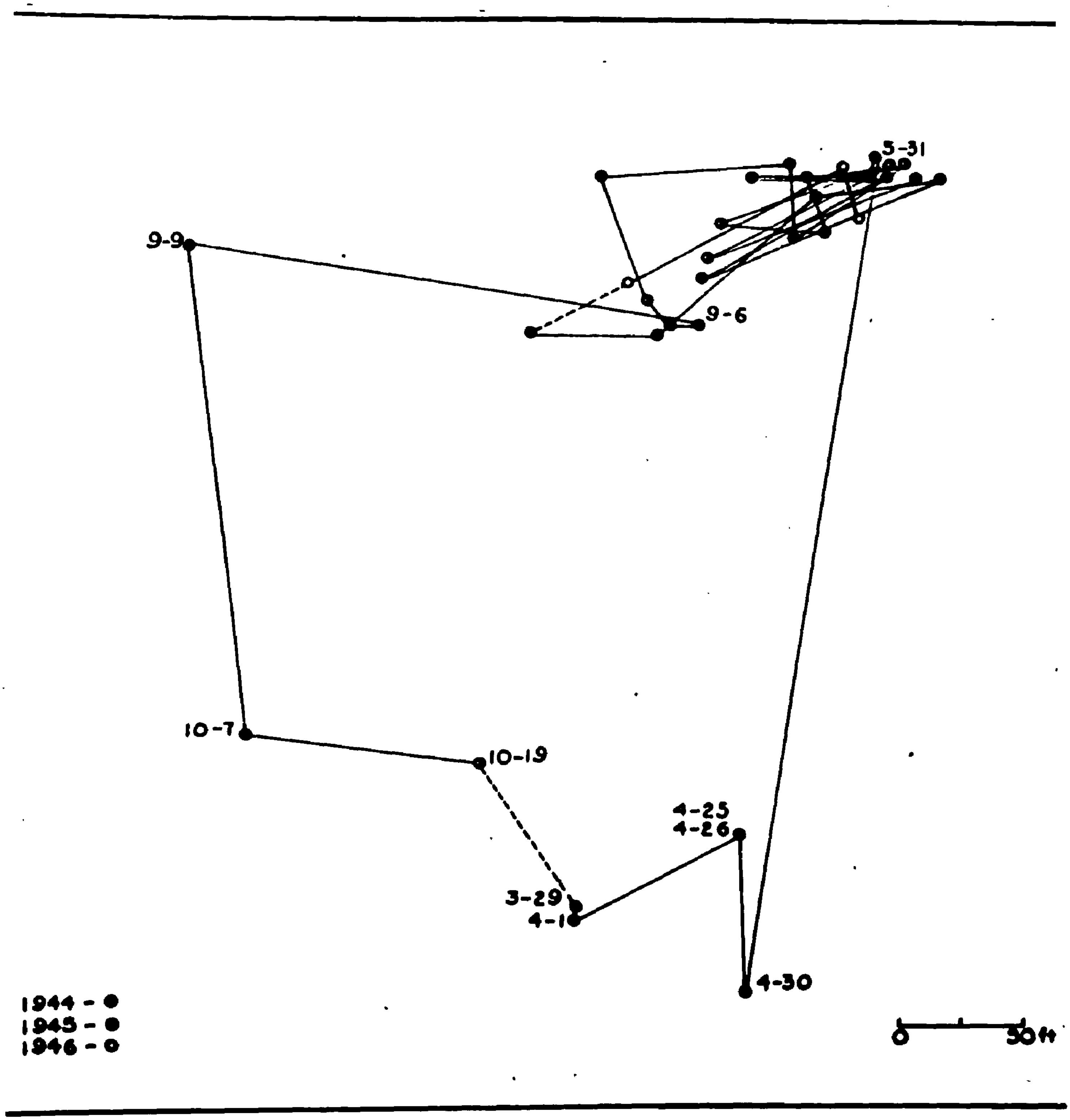

Figure 31

CHAPTER IX

POPULATION SIZE

Collection ratio. - The number of box turtles in the study area was estimated by sampling the population at different times and comparing the samples by a collection ratio. This ratio may be expressed in general terms as follows:

$$\frac{\text{Total number of animals in the population}}{\text{Total number of marked animals in the population (marked when the first sample was taken)}} = \frac{\text{Number of animals in the second sample}}{\text{Number of marked animals in the second sample}}$$

Pearse (1923) and Cagle (1942) used this method to estimate numbers of turtles. Various workers have used it to estimate numbers of birds and mammals. The equation has frequently been referred to as the Lincoln Index, following its use by Lincoln (1930) in estimating waterfowl abundance. A complex elaboration of the method, taking both death and migration into account, was made by Jackson (1939) in estimating numbers of tsetse flies. Several modifications of the method have been used in fisheries research. Although methods of making the estimates have varied with individual problems, the most thorough mathematical analyses have applied to large populations where, as in fisheries problems, the proportion of marked animals was very small in relation to the size of the population being sampled. The discussion that follows applies primarily to estimates of small population units.

Assumptions inherent in the ratio. - In collecting the data for population estimates it is necessary to give particular attention to the sampling criteria that are implicit in the equation. If the above equation is used it is assumed that:

(1) All animals in the population are equally likely to be collected. In other words, collection is not selective. The marked animals in the population are neither more nor less likely to be collected than are unmarked animals. Methods of collecting, marking, and handling should not adversely affect the animals, nor should they make them easier to collect. Any periodic behavior of individuals or groups that would alter availability should be considered.

In the present study, locations and code numbers were recorded in the field, and the turtles were released where they were found. The handling and marking did not affect the behavior or condition of the turtles, insofar as could be determined. Late summer collections were used for census calculations so the data would not be influenced by the absence of females on egg laying trips, by early hibernation of some turtles, or by the ease of collecting others at sunning areas in the fall. The collections were spaced to allow free movement of turtles over their ranges between collections and assure the more nearly equal availability of all turtles.

(2) Collecting is either geographically random or systematically thorough in each sample. In other words, it is assumed that there is no prejudice in collecting and that certain areas do not receive particular attention to the neglect of other areas. If the animals moved at random, the collecting method might not be so important. But since most animals have finite ranges, collecting should either be randomized or equally distributed geographically.

Samples for estimating the size of the box turtle population were taken by systematic collecting trips. During these census trips an effort was made to cover the study plot as thoroughly as possible. The length of the collecting periods was standardized and collections were made by the same two persons.

(3) The balance between marked and unmarked animals is assumed to remain undisturbed between the two sampling periods. That is, marked animals in the area do not leave it to be replaced by unmarked animals, and so reduce the proportion of marked animals. There is no influx of unmarked animals into the area and there is no differential loss to the population among marked animals as against unmarked animals.

This assumption is not apt to be true in any natural population. A large influx of unmarked animals would not be expected unless a breeding season intervened between the two samples. However, there is a steady stream of transients in many populations and if they are numerous some of them will be marked in the first sample. Before the second sample is taken they will move on and be replaced by other, unmarked transients. The ratio of marked to unmarked animals in the area will then be different at the time of taking the second sample than it was immediately following the first sample. This disturbance is not likely to be large enough to be significant except under unusual circumstances, when there is a very large transient population.

The box turtle population always included a small proportion of transients. The method of taking their numbers into account in the population estimate is described below.

(4) All animals that have any part of their range in the sampling area are assumed to have an equal chance of being collected in either sample. This could be true only under certain special conditions.

(a) If all animals living in the area are confined to it, as in island populations, ecologically isolated populations, or populations in securely fenced areas.

(b) If all the animals whose ranges are partly inside and partly outside the area are within the area and subject to collection in both periods. This might be true for some animals, for example mice, where the sample is taken by a uniform set of traps. Mice move freely over their ranges in short time periods, and are likely to be caught if there are enough traps available. Mice resident within the trapped plot and those whose ranges overlap its borders would have nearly equal chances of being taken. The estimate would represent the population of an area larger than actually covered by traps, because of the outside area normally occupied by the border residents. For turtles or for most of the larger mammals, a single sample is not likely to include comparable proportions of border residents and regular residents. An increase in the length of the sampling period will increase the captures of border residents but will also increase the capture of transients and so introduce another error.

(c) If the individual members of the border population are distributed in the same way in both periods. The ones that are outside the borders at the first sample are also outside it at the second sample, and the others are inside the area both times. It is highly improbable that this identical distribution will occur at two separate sampling periods. It is probable that some of the same individuals will be inside at both samples, but that others will be inside the study area at one sample and outside it at the other. Error from this source will be small if the study area is large enough that there are a great many more animals with ranges confined to the area than there are animals with ranges overlapping the borders. The error may be very great if the sampling area is relatively small in comparison with the ranges of the animals. In practical field problems it is almost always necessary to use relatively small study plots, so the error introduced is often significant.

Modification of the box turtle data to allow for the behavior of border residents is discussed below.

<u>Effect of random sampling</u>. - Although the assumptions inherent in the equation may be fulfilled, the error of random sampling will in practice produce variations in the estimates. An estimate based on one pair of samples will often be seriously in error. When many samples are drawn and estimates are made separately by pairs, the estimates will fall on a normal distribution curve and the arithmetic mean will represent the most nearly correct figure. In actual sampling an infinite number of samples cannot be drawn. There have been various methods proposed to make the best use of limited data.

The least squares method of Schumacher and Eschmeyer (1943) was used by them in fisheries studies where collecting data were cumulative; numbers of fish collected in the first period were compared with numbers collected in the second period, first and second samples were combined for comparison with the third, the first three samples were combined for comparison with the fourth, and so on. Their statistical procedures for obtaining an estimate from their total data served to weight the value of the samples according to their size. The larger samples, where the error of random sampling would be smaller, were thus given more weight than the small samples where this error might be very large. Underhill (1941), adapting a procedure discussed by Schnabel (1938) adopted a simpler procedure which also weighted the data according to size of sample. In both studies the samples drawn were very small in relation to the size of the population being sampled.

In a more direct procedure, the data from one sample can be compared in the equation with data from a second sample, and all the samples available can be handled in this way by pairs. The average of these estimates can then be considered the closest to the true population size. The disadvantage of this procedure is that small and large samples will receive equal weight and a stable population size during the time of the sampling is assumed. An advantage is that corrections for the behavior of border residents and transients can be made on each sample before its use in the equation.

Comparisons of the results of these methods applied to data similar to that available in the box turtle collections (but with no "transients" or "border residents") were made on populations of one hundred and of fifty beans. Random samples of twenty-eight to thirty-eight beans were drawn, and repeats between samples were tabulated. Sets of five samples were drawn and the data arranged in the ten pairs possible in comparing each sample with each succeeding sample. The results of using these ten pairs of data independently in the equation and averaging the results were very nearly the same as when the data were handled by the least squares method. In every set of five the results were very close by the two methods, although sometimes one and sometimes the other method would be slightly closer to the true population size.

When the same data were cumulated (sample 1 compared with 2, samples 1 and 2 combined and compared with 3, and so on) and an estimate made by the least squares method, the results were also essentially the same.

Estimates made on the smaller population of fifty beans were individually more reliable than those made on the larger population of one hundred beans, since in the former the samples of twenty-eight to thirty-eight made up a larger proportion of the population.

In the present study the behavior of the border residents and transients make corrections of the raw data desirable. Since the population was stable within the sampling period and the samples all essentially the same size, it was concluded that the direct procedure of using each pair of samples in the equation and averaging the results would be most suitable.

Corrections for border residents and transients. - When all animals using a plot of ground are collected, their numbers will represent, on the average, the population of the plot plus the population of an area around its borders equal in width to one-half the diameter of an average home range (Dice 1938). It follows that the animals whose ranges overlap the borders of the plot represent the population of an area that is equal in width to the diameter of the average home range. The width of this marginal strip will be one-half home range diameter inside the study plot and one-half home range diameter outside its borders. These statements can be used as a basis for corrections of population calculations, with the understanding that their reliability is general or average in nature.

The 350 foot average range of the box turtles was used to determine the acreage of the marginal strip. The area of this strip was calculated to be 24.7 acres, with 11.2 acres inside the study plot and 13.5 acres outside its borders. No marginal area was allowed on the side where the study plot bordered the river.

If the population is distributed uniformly over the study plot and the surrounding area, the border residents present in the 29.1 acre study area at any one time will equal the population of 11.2 of these acres. In a random sample, the turtles that are collected can be assumed to be 39 per cent (11.2 ÷ 29.1) border residents and 61 per cent regular residents. At a subsequent collection the marginal residents collected at the first period may have moved to other parts of their ranges, outside the study plot, where they are not available for collection. Other border residents, not present in the area in the first period, may be there at the second collection. At one extreme, no border residents that were collected the first period would be available the second period. At the other extreme, all would still be available in the study area the second period. On the average it would be expected that one-half of the border residents present in the study area at the first collection will have been replaced by other border residents by the time of another collection. Thus, for a single set of calculations it is best to assume that one-half the previously collected border residents remain in the study area, and to make corrections on this basis. To make no correction is to assume the unlikely condition that all the previously collected border residents remain in the study area. An exaggerated population estimate would follow.

Some of the turtles collected were transients. An estimate of the number of transients was based on the number of collections per turtle during the entire season. By intensive collecting, resident turtles were each collected a number of times. It is believed that most turtles collected only once were transients. A few transient turtles may have been collected two or even three times on their way through the area. On the other hand there may have been some turtles that were collected only once because their ranges barely entered the plot. The criterion of a single collection to indicate a transient individual is therefore not infallible. Nevertheless the ratings on this basis are probably true for the great majority of the individuals, and can be satisfactorily used for generalizations. On this basis, in the five census trips used for the population estimates, seven per cent of the collections were of transient individuals.

The details of making the corrections for border residents and transients is given below to show the procedure that was followed:

Example. The comparison between the collections of July 31 and August 10 will be used. This is the first item in Table 4. As shown in the table, 44 turtles were collected on the first date and 43 were collected on the second date. Eleven collected on the first date were retaken on the second. Examination of the season's collecting data showed that 4 turtles collected on the first date and 3 turtles collected on the second date were collected at no other time. For correction purposes these were considered to represent the number of transients. These numbers were subtracted from the respective collections, leaving 40 turtles for each date. Correction was next made for border residents. As described above, about 39 per cent of the first collection would be expected to be border residents, and one-half of these were considered to be outside the study area by the time of the second collection. This number, 7.7, is subtracted from the first collection to obtain the number of marked turtles available for collection at the second date. This is 32.3. The data were then used to solve the equation as follows: $x:32.3 :: 40:11$ and $x = 117.45$

Estimate of box turtle numbers. - Corrections were made for transients and border residents by the methods described above. Ten estimates were made from the data of the five collections by comparing each sample with each succeeding sample. The ten estimates from five samples were possible because the turtles were recognizable as individuals, and the returns between any two census trips could be independently determined.

TABLE 4

COLLECTION DATA FOR POPULATION ESTIMATE

First Sample		Second Sample		
Date	Number	Date	Number	Recaptures
7-31	44(4)*	8-10	43(3)	11
8-10	43(3)	8-29	40(2)	8
8-29	40(2)	9-13	42(4)	13
9-13	42(4)	9-26	56(2)	15
7-31	44(4)	8-29	40(2)	9
8-10	43(3)	9-13	42(4)	11
8-29	40(2)	9-26	56(2)	9
7-31	44(4)	9-13	42(4)	10
8-10	43(3)	9-26	56(2)	14
7-31	44(4)	9-26	56(2)	18

*Numbers in parenthesis represent transients. See text for explanation, and for methods of making corrections for transients and for border residents.

The average of these estimates, 124.7, is considered the best approximation to the actual size of the resident population. The number of transients increases the population estimate to 133.6 or 4.6 per acre on the 29.1 acre plot.

The population of adult turtles is thus estimated between 4 and 5 turtles per acre.

Statistical constants can be calculated to show the error of the estimate. However, these calculations may be affected by the fact that the ten sets of data were based on only five samples. Hence, I do not know that standard procedures are entirely valid. They nevertheless give an approximate measure of margins of error. The mean (estimated size of population) is 124.7. The standard error of the mean is 8.25, the standard deviation 26.4. These calculated constants can be interpreted to mean that other sets of samples taken by the same methods and used in similar calculations would have mean values within the range indicated by the standard error of the mean. Also, single additional estimates would vary within the range indicated by the calculated standard deviation. Uncorrected data from these same census trips would give an average figure about 33 per cent greater than the corrected estimate. If the study plot had been smaller in relation to the size of the animals' home ranges, the difference in estimates would have been greater. A greater number of transients would also have increased the difference.

Population estimate by a second method. - The size of the turtle population as estimated above can be compared with an estimate based on the entire season's collecting. The population as considered here includes all the resident turtles whose ranges are normally confined to the study plot; one-half the border residents, whose ranges overlap the margins of the plot; and the transients present in the area at one time. In the course of the entire season's collecting it is presumed that the regular residents will be collected more frequently than the border residents, but that eventually all individuals in both groups will be taken. The total number of turtles collected will then be greater than the population of the area, because all rather than half of the border residents will be included. Transients through the area at different times will also increase the total.

When collecting is continued through the season, the numbers collected should approach the population of the 29.1 acre study area plus the population of the 13.5 acre marginal area outside (See pages 124-125), a total of 42.6 acres. In the preceding section the population was estimated at 4.3 residents and border residents per acre. The theoretical expectation for the entire season would be 183.2 residents and border residents plus an additional unknown number of transients.

The actual records for the entire season showed that 183 turtles were collected two or more times and 62 others were collected only once. In the estimates made in the previous section, turtles that were collected only once were considered transients. Using the same criterion here, the results of the two methods correspond. The very close correspondence is purely coincidence, but the similarity in results from the two sets of data does show that the estimates approximate the true population size.

Juvenile population. - The number of juveniles in the population was relatively small in comparison with the number of adults. The problem of estimating their numbers was complicated by several factors: (1) Small turtles were not numerous and this made it difficult to get adequate samples, (2) Small turtles were not as easy to see as larger turtles, and (3) Small turtles may have more tendency to wander than adults. This is not an established fact, but is a possibility that must be considered (See page 86).

Turtles with carapace length 107 mm. and smaller were classed as juveniles. Turtles of this size had the secondary sex characters poorly or not at all developed and were presumably immature. Turtles greater than 118 mm. in carapace length were mature and had the secondary sex characters well developed. However, some individuals in this group had probably not reached maximum size and were still growing. The intermediate group, 108-117 mm. carapace length contained some immature and some fully grown mature turtles. It seemed most satisfactory to treat the three groups separately because of the difference in collectability of large and small turtles, and because a separation into two groups only, juvenile and adult, would have been quite arbitrary.

The number of turtles in the smaller size groups was estimated by two methods, one designed to give a minimum figure and the other a maximum figure, with the supposition that the actual population size would lie between the limits.

(1) The actual number of juvenile collections on the census trips is compared with the number of collections of adults on these same trips. The juvenile estimate is made by proportional comparison with the estimated adult population. Error caused by transients is avoided by this method. However, it assumes that young and adults are equally visible and available to collecting. Since this is not true, the estimate will be too low.

On the census trips used for estimating the size of the adult population, 225 collections were made. On these same trips there were 7 juvenile collections and 6 collections of turtles of intermediate size. Since the adult population was estimated at 133.6 or 4.6 per acre, the estimate for juveniles by this method will be 7/225 of 133.6, which is 4.2 or .14 per acre. For the intermediate group, 6/225 of 133.6 is 3.6 or .12 per acre.

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(2) The total number of juveniles collected in the entire season is compared with the total number of adults. This assumes that in the course of the season the proportion of the resident juvenile population that is collected will be the same as the proportion of the resident adult population that is collected; that the handicap of low visibility is overcome with increased numbers of collections. It also assumes that juveniles are no more transient than adults. If the latter is untrue, the estimate will favor juveniles and be too high.

In the 1945 season, 245 individual adults were collected in the study area, plus 26 juveniles and 12 of the intermediate group. The estimate for juveniles by this method will be 26/245 of 133.6 or 14.2, which is .49 per acre. For the intermediate group this will be 12/245 of 133.6 or 6.5, which is .22 per acre.

The intermediate group is more likely to resemble the adults in visibility and habits than the truly juvenile group. The expectation that minimum and maximum values by the two methods would be closer together for the intermediate group than for juveniles proved to be true.

The estimated number of juveniles is between .1 and .5 turtles per acre, and the estimated number of turtles in the intermediate size group is between .1 and .2 turtles per acre.

These numbers are small in comparison with the number of adults in the population. Their addition to the adult figures does not change the total estimate of between 4 and 5 turtles per acre.

SUMMARY

A population study of the box turtle (*Terrapene carolina* Linnaeus) was made during the years 1944 to 1947 at the Patuxent Research Refuge, Maryland.

A thirty acre area in well drained bottomland forest on the flood plain of the Patuxent River was selected for intensive study. Similarly forested land extended in all directions from the study plot.

Markers were established at eighty-three foot intervals over the study plot for reference in recording locality data. Individuals were marked by filing notches in the marginal scutes according to a code system. There were 2109 collections of study area turtles.

Records of collecting sites and turtle behavior showed that in the bottomlands habitat cover is utilized extensively during the day as well as at night. Turtles not actively moving about are almost always found in or around brush piles, heaps of debris, and tangles of vines and briars. Gully banks and woods openings are used for sunning. Turtles are occasionally found in the mud or water of the gullies.

The commonest type of night retreat is a cavity constructed by the turtle in leaves, debris, or earth. These cavities, termed "forms", may be used only once,

but are sometimes used repeatedly, often at intervals of several days or more. Different turtles sometimes use the same form on successive nights.

Weather conditions most favorable to turtle activity are high humidity, warm sunny days, and frequent rains. The most unfavorable influences are low temperatures and drought. On most summer days there are some active turtles but individual turtles are not active every day. Periods of activity are alternated with periods of quiet even in favorable weather. This behavior is most pronounced in early spring and late fall when inactive days are often more numerous than active ones.

Maximum home range diameters were determined by measurements of the mapped ranges of individual turtles. The average range of adult males was 330 feet in diameter (standard error of mean, 26 feet; standard deviation, 137 feet). The average range size for adult females was 370 feet (standard error of mean, 29 feet; standard deviation, 149 feet). The difference between male and female ranges is not significant; the difference between the means contains its standard error 1.04 times.

Locality maps were prepared for all turtles. There was no evidence of territorialism. Ranges of turtles of all ages and both sexes overlapped grossly. Turtles were frequently found near each other and no antagonistic behavior was observed.

Adult turtles occupy specific home ranges which they maintain from year to year. The turtles living in the study plot retained their ranges even through a flood that completely covered the area.

A trail-laying device was developed in order to follow individual travel routes. The trailer consists of a light weight housing fastened to the turtle's back. It contains a spool of white thread that unwinds as the turtle moves, thus marking its exact route.

Turtles selected for this more detailed study were followed with trailers for a total of 456 turtle days. Maps illustrating their travels are shown. Normal movements within the home range are characterized by, (1) turns, doublings, detours, and criss-crossing paths completely covering the area, (2) interspersion of fairly direct traverses of the home range, (3) frequently repeated travels over certain paths or routes.

Trailer records and mapped collection records both show that the maximum limits of the home range are ordinarily reached within a few days or weeks. This general procedure is varied by some turtles to include intensive coverage of only one portion of the range at a time.

Some turtles have two home ranges and travel between them at infrequent intervals. One turtle showing this behavior was followed with a trailer for 161 days during 1946 and 1947.

Trips outside the home range are made by some turtles. These include egg laying trips by females as well as trips of unexplained nature made by both males and females. Turtles from other areas occasionally occur as transients in the study plot.

Systematic census trips, standardized for time and procedure, provided the data for estimating the size of the population. Census data used in the estimates were those taken in late summer after females had returned from egg laying. The samples were spaced at intervals of a week or more to allow free movement of turtles over their ranges between collections, and so assure the more nearly equal availability of all turtles.

The population size was estimated by comparing the standard samples by a collection ratio. Assumptions involved in the use of this ratio are discussed. Correction factors were applied to the raw data to make allowance for turtles whose ranges were partly inside and partly outside the study area. Corrections were also made for transient turtles. A second estimate, on the basis of the entire season's collecting, gave closely comparable results.

The population of the study area was estimated to be between four and five turtles per acre, with juveniles constituting less than ten per cent of the total.

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