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

LUCILLE F. STICKEL

Extracted from a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan

TABLE OF CONTENTS

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

INTRODUCTION

A quantitative field study of a local population of the box turtle, *Terrapene c. 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 animal in the home range, (5) the nature and extent of travels beyond the home range, and (6) the frequency of transients and the causes of them. The study has thrown some light on each of these topics.

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.

I wish to express my gratitude to Dr. Peter O. Okkelberg for his generous encouragement and advice concerning the problem and for his criticism of the manuscript. It is a pleasure to acknowledge my indebtedness to Mr. Arnold L. Nelson of the U. S. Fish and Wildlife Service, without whose encouragement and assistance the project could not have been undertaken. I also wish to thank Dr. George R. LaRue, Dr. Carl D. LaRue, Dr. William H. Burt, Dr. Frederick H. Test, and Dr. Norman E. Hartweg for reviewing and criticizing the manuscript.

The field work benefited greatly from the able assistance of Mr. Clyde Vance on many collecting trips in 1945. Thanks are due Mr. Robert T. Mitchell for assistance in collecting in the latter part of 1944, and to other members of the Patuxent Refuge staff for occasional field records. Mr. Richard W. Stow rendered valuable assistance in the design and construction of the trailing device. Mr. Leon Greenwalt took many of the photographs and did the photographic processing. Mr. William H. Stickel gave much assistance in the review and criticism of the various stages of the manuscript.

HISTORICAL BACKGROUND

Studies of vertebrate population biology have been primarily of birds and mammals. The concepts of home range behavior and territorialism have developed in these fields, and are generally accepted. Home range is defined as the area over which an animal normally travels in the course of its daily activities. Territory is any defended area and may include the entire home range or only a part of it.

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 (Cagle 1942).

Woodbury & 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 (*Terrapene carolina*) 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 carried 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 were also 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.

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 location 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 individual 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.

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, standarized 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 be-

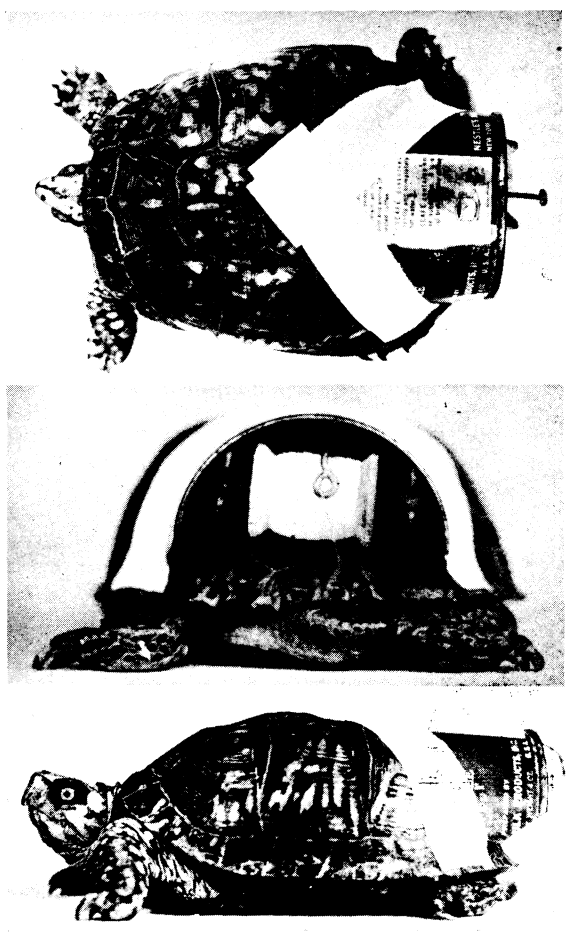

FIG. 1. Box turtle with trail-laying device.

have normally; recorded movements of turtles with and without trailers 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.

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 & 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.

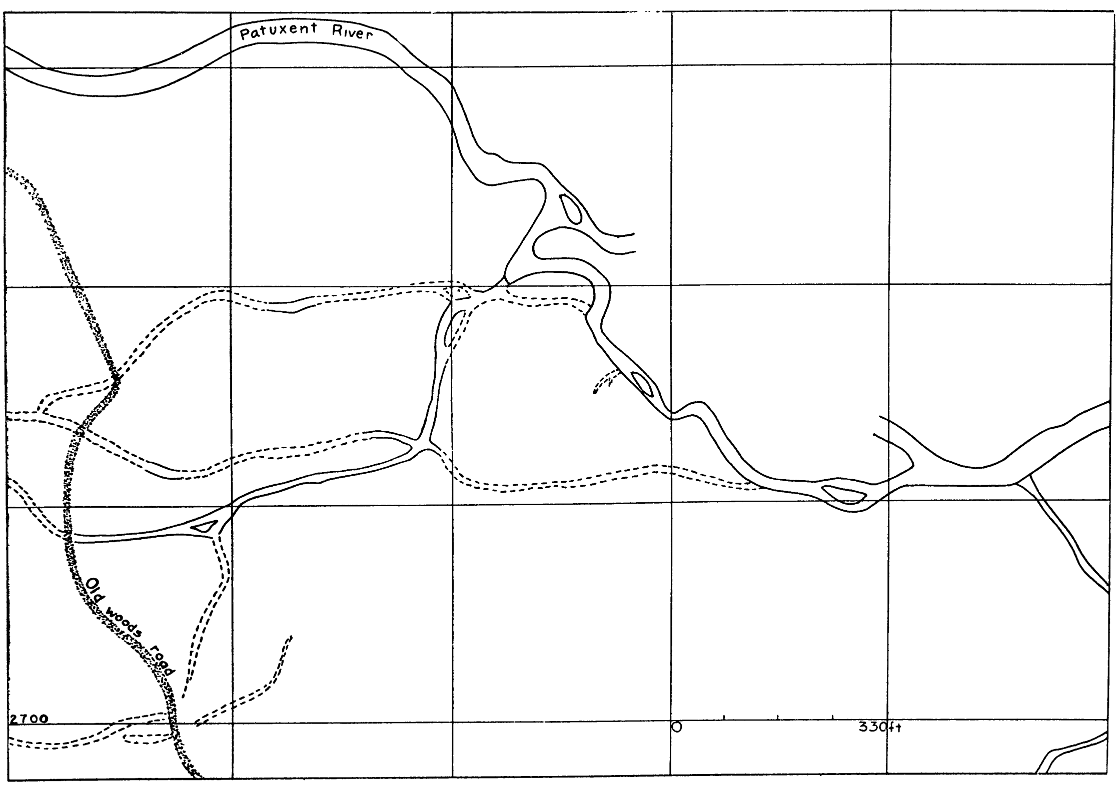

FIG. 2. Map of the box turtle study area, 29.1 acres of bottomland forest along the Patuxent River. The area south of the river represents the study area. The major natural drainage channels are shown as broken and solid lines; the solid lines show the parts that contain water at all seasons.

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 & Stewart (1947) for this plant community include:

TREES

Carpinus caroliniana
Betula nigra
Fagus grandifolia
Quercus palustris
Ulmus americana
Liriodendron tulipifera
Liquidambar styraciflua
Acer rubrum
Fraxinus americana

SHRUBS AND VINES

Lindera benzoin
Toxicodendron radicans
Viburnum prunifolium

HERBS

Arisaema triphyllum
Erythronium americanum
Laportea canadensis
Claytonia virginica
Ranunculus abortivus
Podophyllum peltatum
Impatiens biflora
Viola affinis
Circaea quadrisulcata
Cryptotaenia canadensis
Galium aparine

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 the refuge. Temperature rarely exceeds 85° F. 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. Most of them appear to be formed where stumps have rotted away, the process speeded by the honeycombing burrows of small mammals. 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. Trees and tree branches

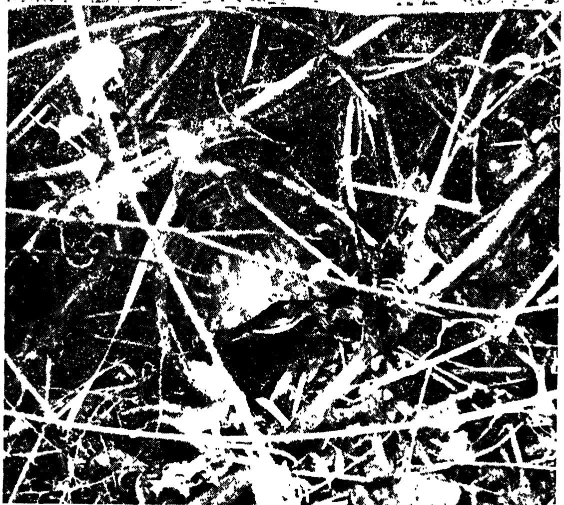

FIG. 3. Wooded bottomlands near the center of the study area.

FIG. 4. Box turtle coming out of a dense viny tangle where it had spent the night.

FIG. 5. Juvenile turtle leaving a "form" in leaves, sticks, and earth.

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. Heaps of wood and debris are piled around bush clumps and tree bases at times of high water. 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 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. 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 several 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.

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. 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.

A dense thicket near the center of the study plot is one of the most intensively used areas. At some times of the year 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. 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 5 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.

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 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

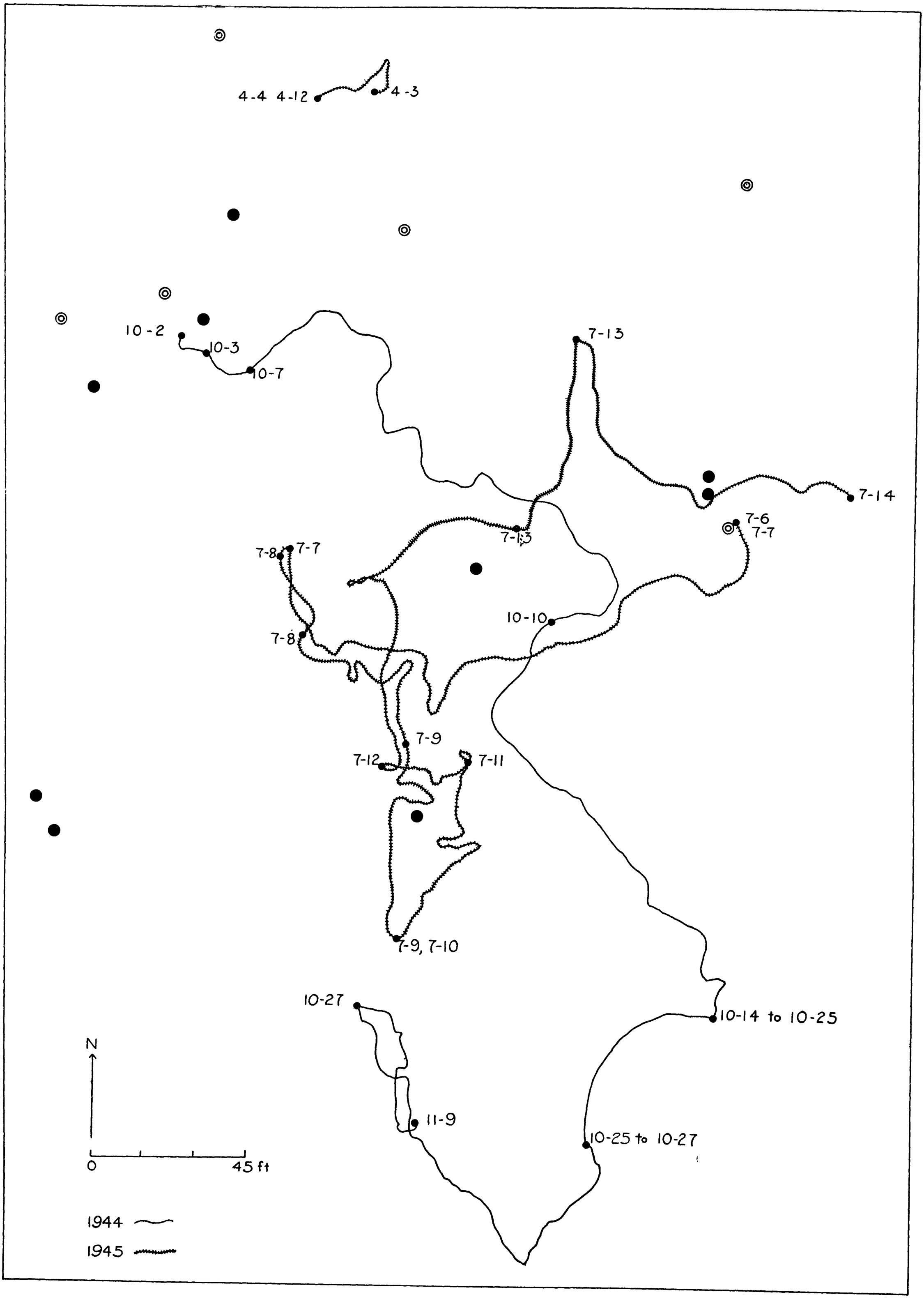

FIG. 6. Trailer records of summer and fall travels, and collection records for male 629. Numerals show dates. Symbols as in Fig. 7.

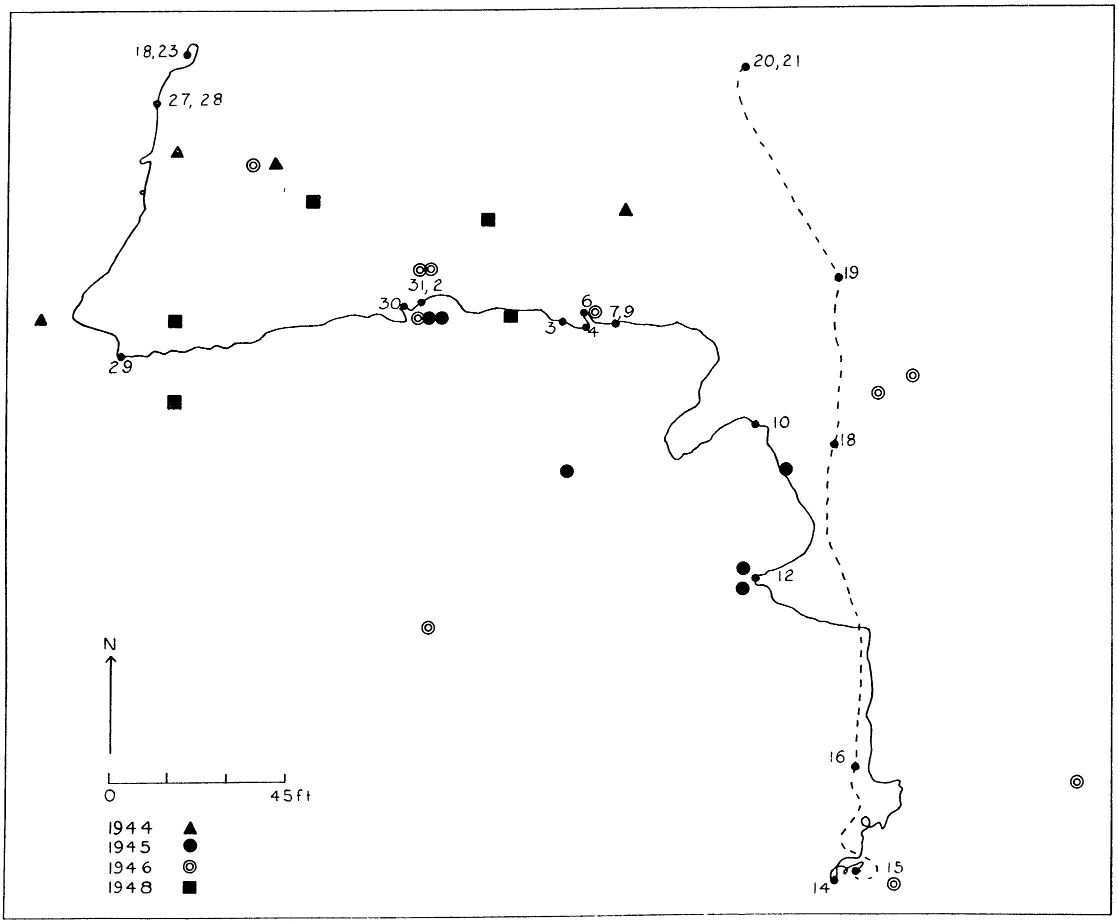

FIG. 7. Trailer record of spring travels of male 515. Numerals show dates in May and June 1945.

TABLE 1. Turtle Activity

FALL 1944

TURTLE		SEPT.			OCTOBER																										
Code No	Sex	28	29	30	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......	♂	...	...	...	...	−	−	−	−	−	+	−	+	+	+	+	+	+	+	−	+	+	−	−	−	+	−	−	+	hiber.	
629......	♂	...	...	...	...	−	−	−	−	−	−	−	−	+	−	−	−	+	−	−	−	−	−	−	−	−	−	−	+	−	+ hiber
593......	♂	+	+	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	+	−	−	−	−	−	−	+	−	−	−		
627...... (subadult)	?♂	...	+	+	+	+	−	−	+	+	+	+	−	+	−	−	+	+													
634......	♀	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	+	−	−	−	+	−	−	+	+	hiber
633...... (subadult)	?♀	...	...	...	...	+	−	−	−	hibernation																					

SUMMER 1945

TURTLE		MAY											JUNE										JULY											
Code Number	Sex	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10	6	7	8	9	10	11	12	13	14	15	16	17
515..........	♂	−	−	+	−	−	−	+	+	−	+	−	−	−	+	+	−	−	−	−	+	+												
424..........	♂	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	+	+	+	+	+	+	?	+	+	+		
629..........	♂	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	+	+	+	+	+	−	+	+	+			
192..........	♂	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	+	+	+	+	+	+	+	+	+	+	+	
476..........	♀	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	+	+	?	+	+	+	−	+	+	+	+	
492..........	♀	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	+	+	+	+	+							

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. Seasonal differences in activity also show in distances traveled. In Figure 6 the travels of ♂ 629 for a month in late fall are contrasted with the travels during a week in July. Activity in a spring month is shown in Figure 7, and behavior in midsummer is shown in the other trailer maps.

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 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 common at the right 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.

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. The findings of the present study concerning home range and territory in box turtles are described in this section.

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 grossly overlap, 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 8. Ranges overlap to an even greater degree in most other parts of the study plot.

Turtles are frequently found near each other, not 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

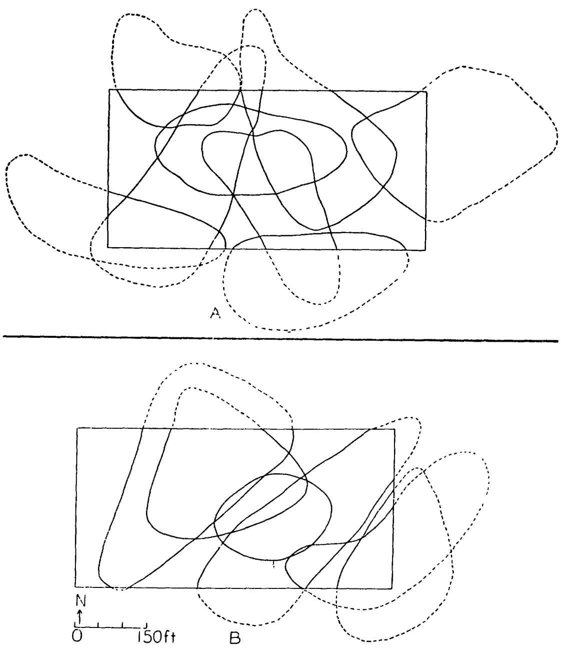

FIG. 8. Ranges of fifteen turtles occupying parts of a five-acre plot in the study area.
A.—males. *B.*—females.

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, 35% of the 48 turtles collected were in the vicinity (within 20 feet) of one or more others. On October 17, 1945, 63% of the 38 turtles collected were near one or more others.

Fighting between box turtles is apparently a very rare occurrence, and is probably not related to territory defense. In the present study no turtles were seen fighting although more than two-thousand collections were made. However, in the summer of 1949 a male turtle was seen facing and biting at the front of the carapace of another. The second turtle, also a male, had the shell closed and showed no resistance. Latham (1917) described a fight between two wild box turtles and Allard (1935) described a fight between two captive individuals. Penn and Pottharst (1940) reported fighting between captive males of another race (*Terrapene c. major*) kept in a fenced enclosure. Most aggressive behavior occurred at the breeding season.

From the records of the present study it appears that fights rarely occur in nature; there is no reason to believe that the turtles defend territories. 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

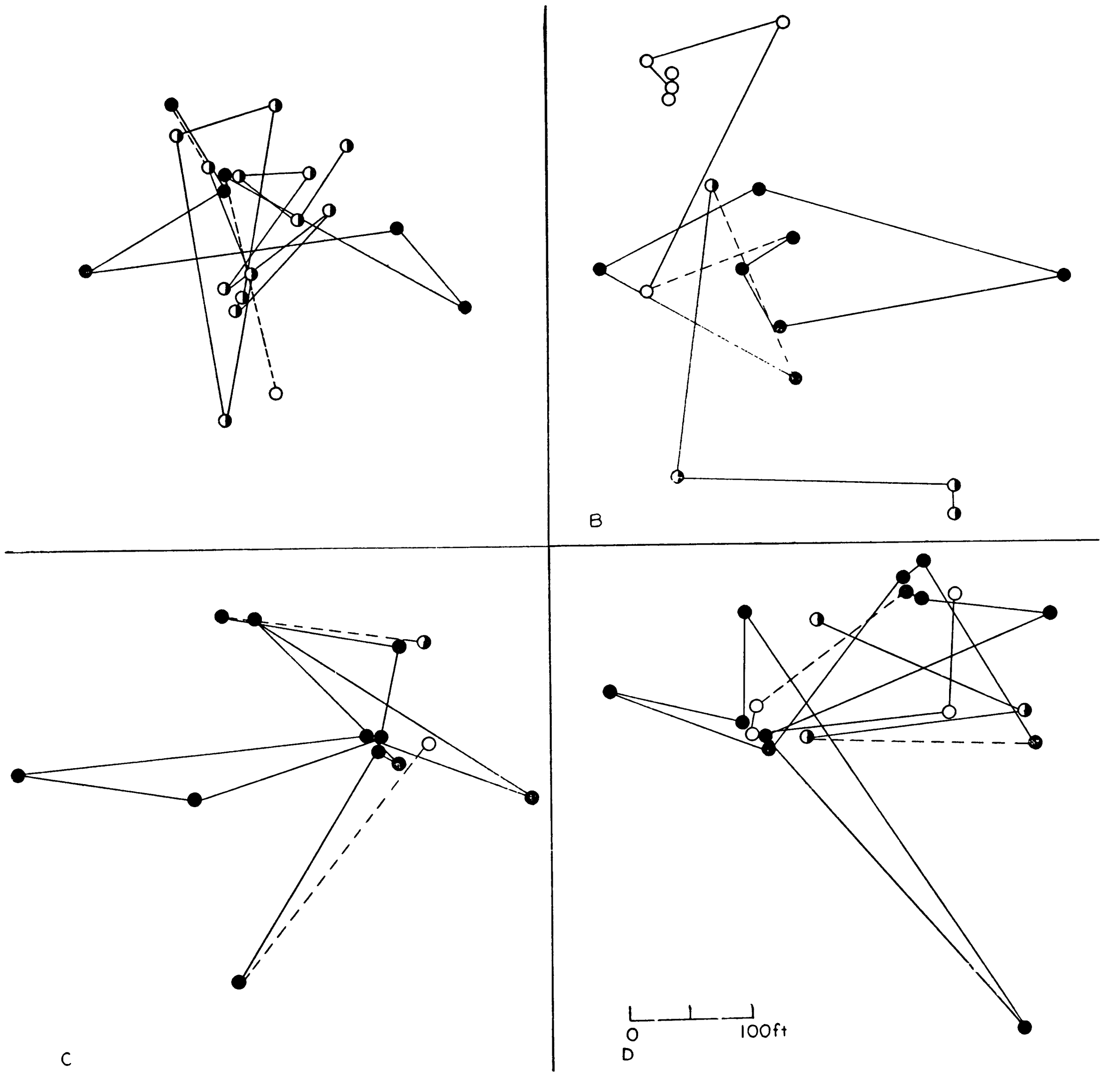

FIG. 9. Sample maps of home ranges based on collection records of adult box turtles. Solid lines connect consecutive collection points in a single season. Broken lines connect the records of different years. Symbols as in Fig. 10. *A.*—female. *B, C, D.*—males

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 the 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

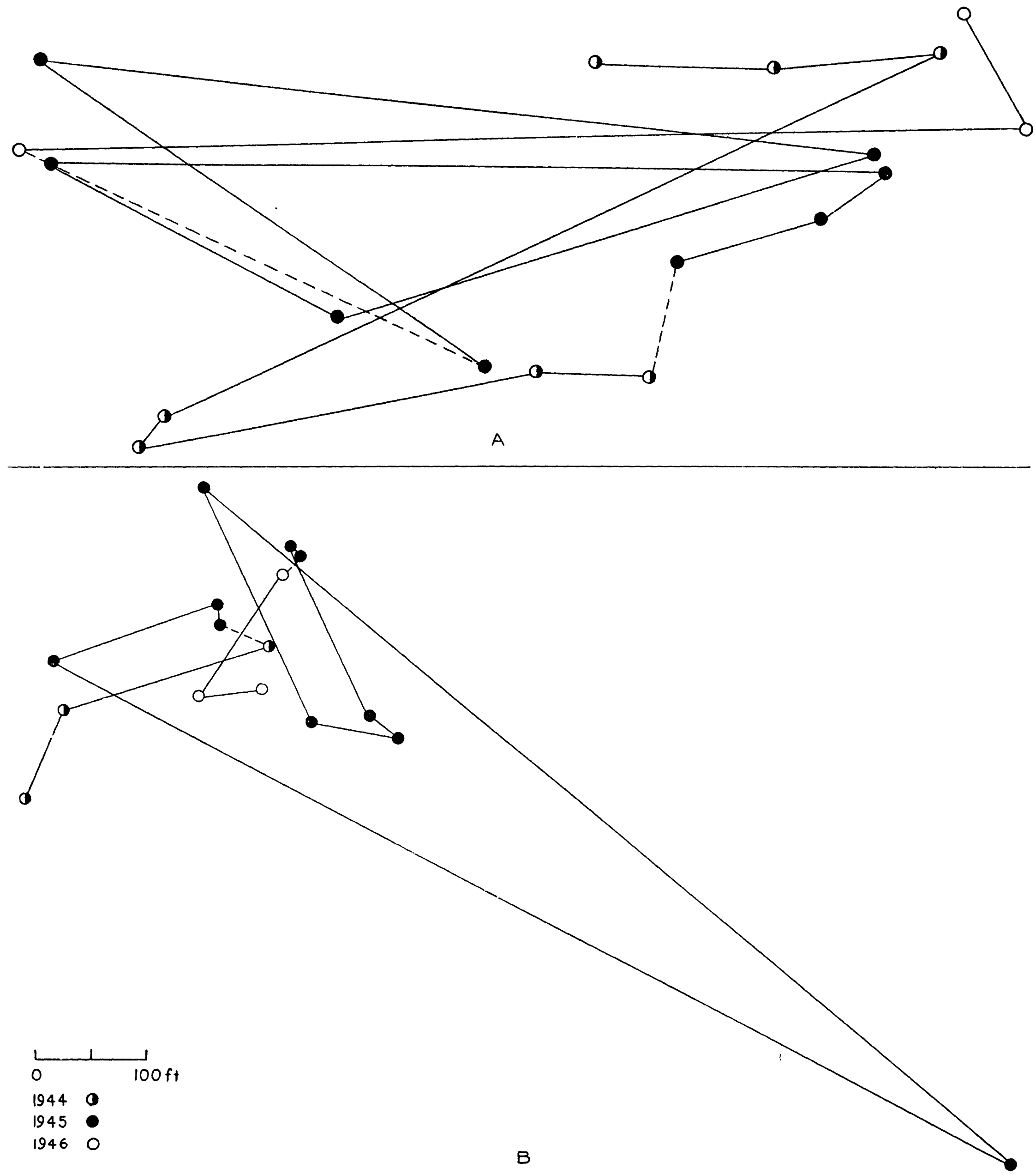

FIG. 10. *A*.—Sample map of home range of a female box turtle based on collection records.
B.—Map of collection records of a turtle displaced from her normal range by a flood in the summer of 1945. Records in the home range both preceded and followed the flood record of July 20.

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 9 and 10.

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 10b). 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 later. They are mentioned here to show that constancy to the home range is not invariable.

The foregoing 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 3. The paucity of data concerning juveniles may be an indication that some turtles of this age behaved differently from those previously described.

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 (L. F. Stickel, 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 simi-

TABLE 2. Box Turtle Ranges and Collections in 1945

Maximum diameter of known range (feet)	Number of Collections in 1945: 2 ♂	2 ♀	3 ♂	3 ♀	4 ♂	4 ♀	5 ♂	5 ♀	6 ♂	6 ♀	7 ♂	7 ♀	8 ♂	8 ♀	9 ♂	9 ♀	10 ♂	10 ♀	11 ♂	11 ♀	12 ♂	12 ♀	13 ♂	13 ♀	14 ♂	14 ♀	15 ♂	15 ♀
0-50	2	4	1	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†	1		....		1									
251-300	1	1	1	2	....		....			1	1		....		1	1↕	1			1								
301-350	1		2			3	2	3*		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‡	....		....		....		....		. ..		....			1
501-550	....			1	....		2		....		1	1	....		....		....		. ..		....		. ..		1			
551-600	....		....		1		1	1	1		....		....			1												
601-650	....																											
651-700	....			1	....		....		. ..		. ..			1§														
701-750	....			1	....		. ..		. ..			1																
751-800	1																											
1000		1																										
1060	....		1																									
1470	....		....		1																							
1540	....		1																									
2310		1																										
2400		1																										

*Increased to 765 ft. on trip away from home range.
†Increased to 770 ft. on trip away from home range.
‡Increased to 855 ft. when carried by flood.
§Increased to 1380 ft. on egg laying trip.
↕Increased to 985 ft. at peak of flood.

larity 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 detemine which turtles have their home ranges completely within the study plot, and which 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. In a season's collecting, the permanent residents of the area will be collected more times than the transients and 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 4, 5, or 6 times were not significantly different from each other. Individuals collected more than six times were too few in each unit group 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 55 turtles, an average of 8 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 known 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 of variation 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 (1939) 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.

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.

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 were made in a straight line from anterior to posterior margin 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.

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.

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 1 to 44 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 patterns (See Figures 6-7, 11-13):

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

(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.

(3) There is a tendency for some routes to be traveled more frequently than others. At intervals

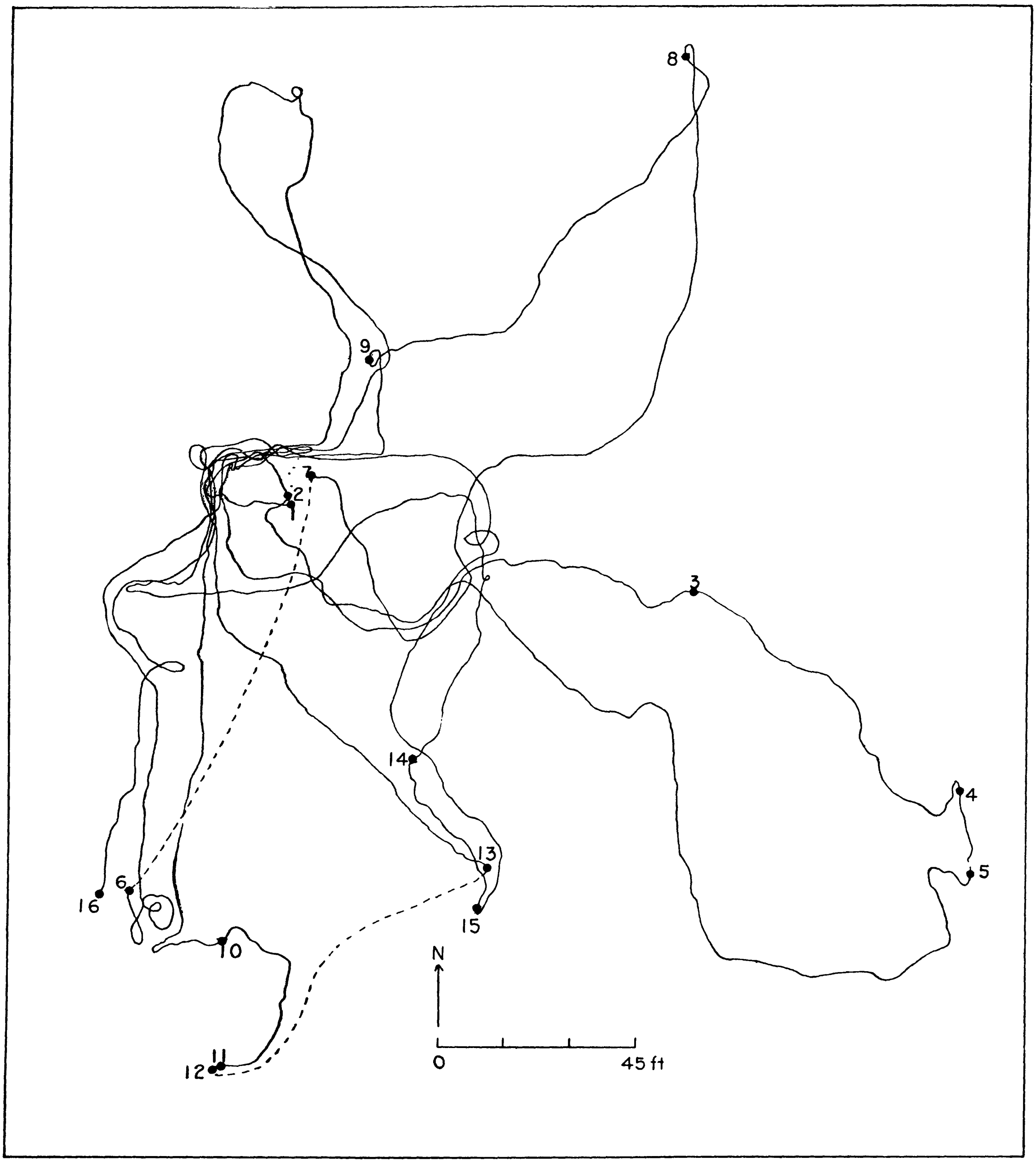

FIG. 11. Travels of adult male 424 during eight days of midsummer, July 7 through July 14, 1945. (1) released July 6 at 7:00 p.m. (2-4) July 7, (5) July 8, (6-8) July 9, (9-11) July 10, (12-13) July 11, (14-15) July 13, (16) July 14.

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 11.

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 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,

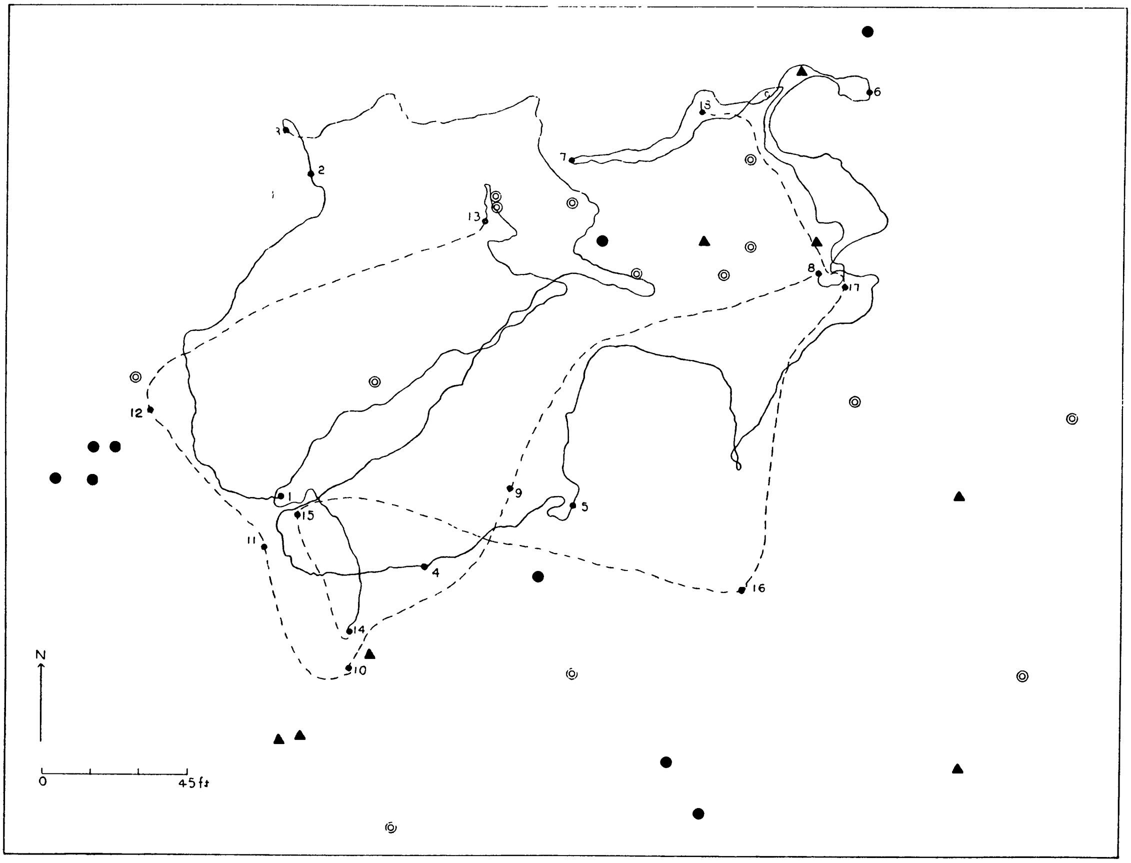

FIG. 12. Collections and trailer records for male 192. Symbols as in Fig. 7. Trailer records, 1945: (1-2) July 6, (3-5) July 7, (6-7) July 9, (8) July 10, (9-10) July 11, (11-12) July 12, (13) July 13, (14) July 14, (15) July 15, (16-17) July 16, (18) July 17.

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 it 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 Male 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 12.

Example 2.—Trailer records for Female 476 covered an area 390 feet in greatest diameter during a two-week period in July. Seven collections during the year showed a maximum range of 355 feet. This record is shown in Figure 13.

Example 3.—The home range of Male 629 was determined by collecting records to be about 235 feet in diameter. During five days in July, while carrying a trailer, he covered an area 185 feet in diameter. Trailer records for four additional days did not increase the distance. These and other records for this turtle are shown in Figure 6.

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

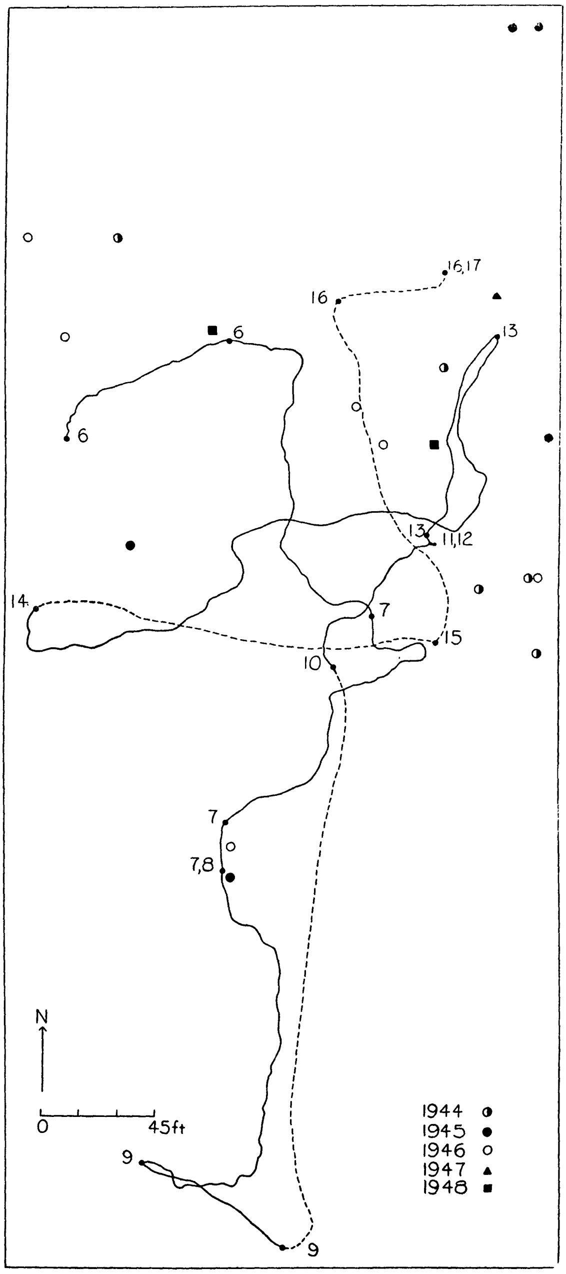

FIG. 13. Collections and trailer records for female 476. Trailer record numbers show dates in July, 1945.

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. The eleven day route is shown in Figure 11.

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 the hour at the same place. The first part of her route 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 (Figs. 14a & b).

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 (Fig. 14b, c).

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 mid-summer 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 30 ft. from the spot where she had hibernated in the winter of 1944-45 (Fig. 14c).

She left the place of hibernation on May 1, 1947 and traveled about 10 ft. 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

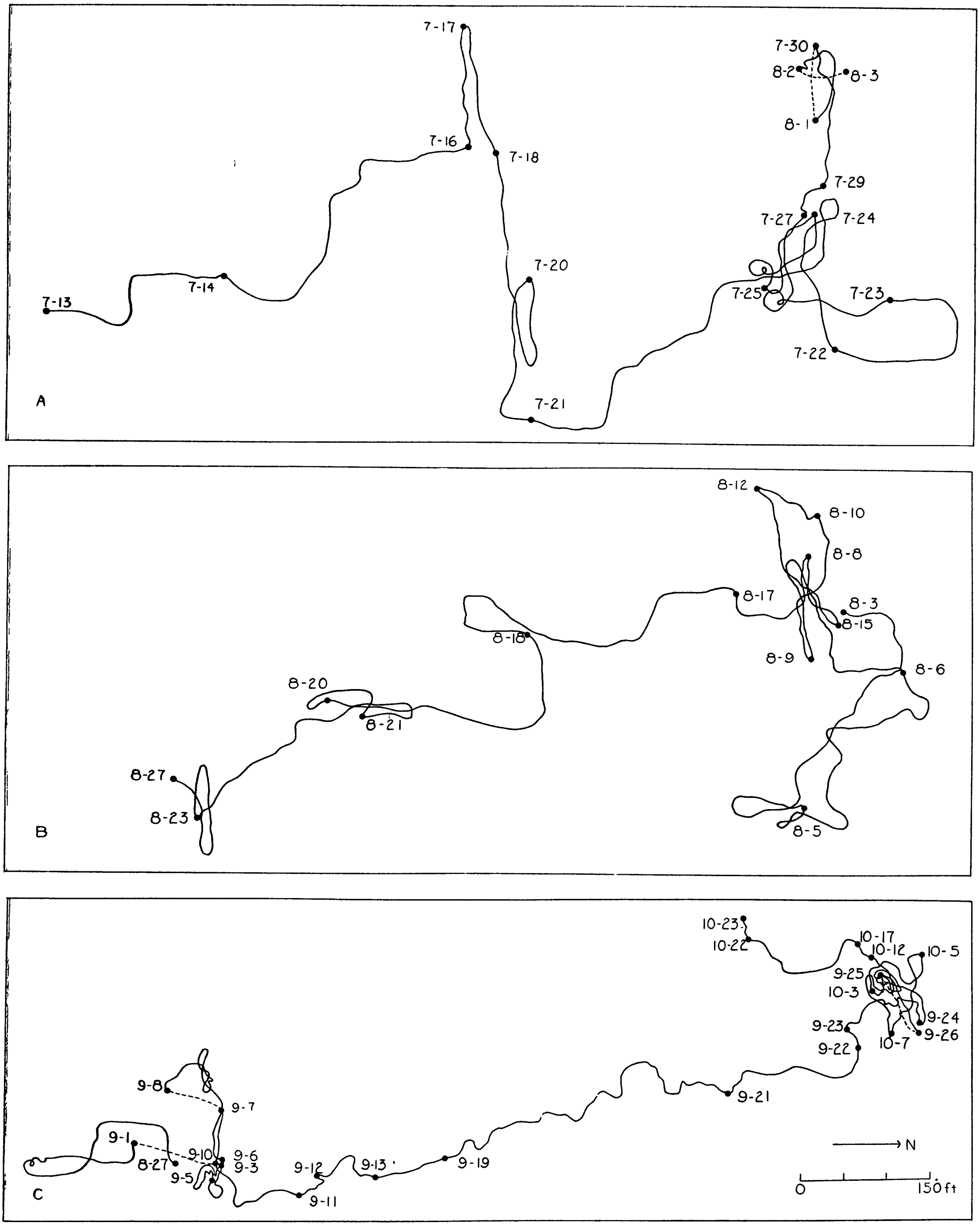

FIG. 14. Maps of the travels of female 539 from July 13, 1946 until hibernation October 23. The three maps show the same area and give a continuous record. Orientation from map to map can be made from the dates marked along the route.

Returning from an egg-laying trip, she entered the bottomlands July 13 and traveled some each day. On July 22 she was found in the home range where she had been collected several times in the previous year. 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.

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. She stayed in this vicinity for one month, until September 17 before starting north again.

The northern trip 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. Daily travels were shorter than in midsummer and she did not travel every day. On the night of October 23 she began hibernation thirty feet from the place where she had hibernated in 1944-1945.

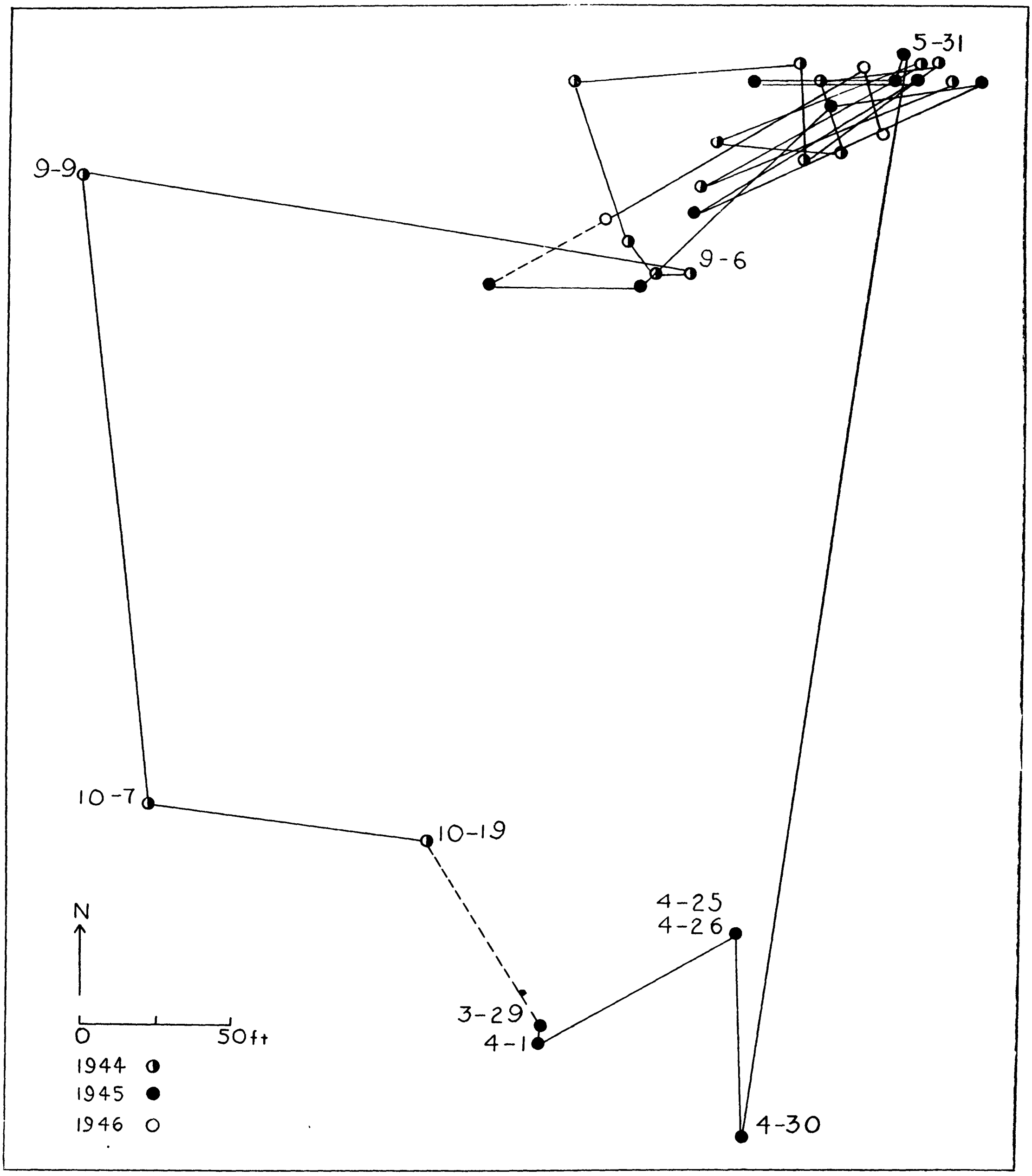

FIG. 15. Collection records for female 416, showing restricted summer range on riverbank, and travels to hibernating area south of there in 1944, with return to riverbank range the following spring.

eggs. On June 18 she was at the edge of the field, not more than 50 ft. 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 400 ft. 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 28 days. The two ranges were more than 400 ft. 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.

One female turtle traveled away from her usual 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 summer 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 33 different times from 1944 through 1946. Twenty-five of these collections were within an area 170 ft. in diameter. In the fall of 1944 she moved from this range to a place 220 ft. away. For most turtles this distance would not be significant, but was an appreciable distance 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 where she was frequently collected thereafter. The hibernating area was searched in the spring and fall of other years to see if she would return to the same area. On October 15, 1948 she was again found near her 1944 hibernating place. In the spring of 1949, on March 29, she was found emerging from a hibernating hole about 50 ft. east of the place used in the winter of 1944-45 (Fig. 15).

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.

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 ft. 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 ft. 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 distances were 2540, 2200, 1550, 850, and 820 ft.

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 400 ft. 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 700 ft. 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, female No. 539, 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 ft. He escaped here near the river several hundred feet west of the study area, and was not collected again.

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.

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. Female turtles regularly undertake long travels for egg laying purposes.

POPULATION SIZE

Estimate from season's collecting.—During the summer of 1945, 245 adult box turtles were collected on the 29.1 acre study plot. Recapture records showed that some of these turtles had ranges entirely within the study plot, while others ranged both outside and inside the area. Still others apparently visited the plot briefly or passed through on the way to other areas.

The number of turtles collected on the study area is therefore greater than the actual population. Dice (1938) stated that on the average it is statistically correct to assume that when all the animals using a plot of ground are collected, they will represent the population of that area plus the population of an area around its borders equal in width to one-half the average home range. The home range diameter of the turtles averaged 350 ft. Adding a border strip of one half this width (175 ft) around the study plot increases the area to 42.6 acres. The residents and border residents can then be considered to represent the population of a 42.6 acre area.

The number of visitors or transients through the area will also increase the number of turtles collected. The behavior of these turtles is discussed in a previous section. Their numbers are difficult to determine exactly, but a reasonable estimate can be based on the number of times individual turtles were collected during the season (Table 4). Resident turtles will be captured a number of times, border residents less frequently, and transients even less often.

TABLE 4. Repeat Collections in 1945

Number of Collections	Number of Individuals		Cumulative Totals	
	Male	Female	Male	Female
1	26	36	117	128
2	19	19	91	92
3	16	23	72	73
4	16	11	56	50
5	12	11	40	39
6	5	12	28	28
7	10	4	23	16
8	4	2	13	12
9	3	4	9	10
10	2	2	6	6
11	2	2	4	4
12	1	0	2	2
13	0	0	1	2
14	1	1	1	2
15	0	1	0	1

It is believed that most turtles collected only once were transients, although some transient turtles were collected two or even three times on their way through the area. On the other hand there were probably 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, but is probably true for the great majority of individuals, and satisfactory for use in generalizations. Trailer studies of transient turtles support this view. It is also of interest that the sex ratio is equalized if one-capture individuals are disregarded (Table 4).

There were 183 turtles collected two or more times and 62 others collected only once in 1945. In all there were 928 collections, with 62 (6.7%) being 1-capture individuals. These occasional visitors were fairly evenly distributed in collections through the season. The population can then be estimated at 4.3 adult residents and border residents per acre (183/42.6 A) plus a transient population comprising about 6.7% of the total at any one time. This brings the total to 4.6 per acre. The population of adult turtles is therefore estimated to be between 4 and 5 adult turtles per acre on the study plot.

Estimate from special census trips.—The number of box turtles was also 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, and it was used in fisheries work at least as long ago as 1895 (Peterson 1895). The equation has frequently been referred to as the Lincoln Index, following its use by Lincoln (1930) in estimating waterfowl abundance. An elaboration of the method, taking both death and migration into account, was made by Jackson (1939) in estimating numbers of tsetse flies. Schnabel (1938), Schumacher & Eschmeyer (1943), Underhill (1941) and others have also presented methods for obtaining estimates from collections when several successive samples were taken from the same population.

Assumptions concerning the sampling.—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 principle of the above equation is to be applied in making estimates it is assumed that:

(1) All animals in the population have equal chances of being 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 of the turtles so far 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) There is no prejudice in collecting. 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 (See also below).

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 period 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 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.

Another factor affecting the balance between unmarked and marked animals is the behavior of animals living on the borders of the area, with part of their range inside and part of it outside. These animals will have less chance to be collected than will strictly resident animals. Some individuals marked in the first period will be outside the area at the next collection and be replaced by unmarked individuals from outside. 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.

Modifications of the box turtle data to allow for the behavior of border residents is now discussed.

Effect of random sampling.—Even though the sampling itself is carefully done, 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 for this reason alone.

Several workers have concerned themselves with this problem and have developed methods to give the best results from available data. Reference is made particularly to the papers of Jackson (1933, 1936, 1939, 1944), Ricker (1948) Schnabel (1938), Schumacher & Eschmeyer (1943), and Underhill (1941).

In general these methods provide suitable methods for combining the data from successive sampling of the same population. Schnabel's fourth method, which she recommends for use when the size of the sample is relatively large in proportion to the size of the population seems most applicable to the present problem. The formula is

$$\left[\frac{\Sigma\ Mt}{\Sigma\left(\frac{r^2}{Mt}\right)}\right]^{1/2}$$

where M = the number of animals collected and marked in the first sample; t = the total number of animals taken in the second sample; r = the number of repeats (marked animals) taken in the second sample.

A simpler procedure used by Underhill (1941), adapted from one of Schnabel's methods gives essentially the same results in the present study. The formula is

$$\frac{\Sigma Mt}{\Sigma r}$$

with the symbols having the meanings just given.

The relatively small number of turtle repeats (8 to 18) will decrease the reliability of estimates from these formulas, tending to give estimates that are slightly high.

In the census collecting, each turtle could be collected only once in a given period, and 40 collections means 40 different individuals. In truly random sampling (as assumed by the collecting ratio and the equations above) each individual would have an equal chance of being taken at each of the 40 collections in the sample. In a population that is very large in proportion to the size of the sample being drawn this would make no essential difference in results. In the present instance it will tend to slightly increase the number of repeats, and slightly decrease the final estimate.

Despite its difficulties the collecting ratio is a method that can be used to give a fair estimate of population size by sampling over a limited time period, and so has much usefulness.

Field data and modifications.—Data to be used in the formulas of Schnabel & Underhill were obtained from five collection trips made in the late summer by the methods described. The field data were modified as follows to offset the effect of 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.

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 random samples, the turtles that are collected can be assumed to average 39% (11.2/29.1) border residents and 61% 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 to 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. For calculations it is probably best to assume that one-half the previously collected border residents remain in or return to 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.

Turtles collected only once during the entire season were considered transients. The basis of this rating is discussed in the previous section. The transients taken in the five census trips represented 6.7% of the collections. They are subtracted from the totals before application of the formulas.

For example: 44 turtles were collected on July 31 and 43 on August 10. Subtracting transients (4 on 7-31 and 3 on 8-10) leaves 40 for each date. Marginal residents collected on the first date are assumed to be .39 x 40. Half of these, 7.7, subtracted from 40 leaves 32.3 to represent the number of marked turtles from the first period assumed present in the area at the second period.

Calculations.—Since the turtles were individually identifiable the returns between the different census trips could be independently determined. Comparing each sample with each succeeding sample in the set of five provides ten sets of data (Table 5). The ten sets of data are not strictly independent of each other, even though the repeats are in each case independently determined. Nevertheless it seems certain that a more reliable estimate will be obtained by utilizing the whole of the data than by restricting comparisons to the strictly independent pairs.

When the field data are modified as described above and estimates are made using Schnabel's formula, the population of the 29.1 acre area is 130 (121 plus 9 transients) or 4.5 per acre. Underhill's formula gives 129 or 4.4 per acre. If account is taken of

TABLE 5. Collection Data for Population Estimate

FIRST SAMPLE		SECOND SAMPLE		Recaptures
Date	Number	Date	Number	
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 border residents.

border residents but not of transients, the estimate becomes 140 or 4.8 per acre.

If no corrections are made in the field data the estimate can be expected to represent the population of an area greater than the 29.1 acre study area, but less than the "system" (the 42.6 acre area including one-half home range diameter around the borders of the plot). Using Schnabel's formula, the estimated number is 173, which would represent a population more than 4.1 but less than 5.9 per acre. A very large transient population would bring the estimate nearer to the population of the larger area, and conceivably even beyond it.

There is a close correspondence between estimates made by the collection ratio from special census data and the estimate based on the entire season's collecting. Both are between 4 and 5 adult turtles per acre.

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.

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 4.6 per acre, the estimate for juveniles by this method will be 7/225 of 4.6 or .14 per acre. For the intermediate group, 6/225 of 4.6 is .12 per acre.

(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 4.6 or .49 per acre. For the intermediate group this will be 12/245 of 4.6 or .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 turtle per acre, and the estimated number of turtles in the intermediate size group is between .1 and .2 turtle per acre.

These numbers are small in comparison with the number af 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 c. 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.

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.

Maximum home range diameters were determined by measurements of the mapped ranges of individual turtles. The average range of adult males was 330 feet, adult females 370 feet. The difference between male and female ranges was not statistically significant.

There was no evidence of defense of territory. Ranges of turtles of all ages and both sexes overlapped grossly. Turtles were frequently found near each other and no antagonistic behavior was observed.

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.

The size of the population was estimated on the basis of collections during one complete season. Allowance was made for behavior of transient individuals and those whose ranges overlapped the borders of the plot.

Systematic census trips, standarized for time and procedure, provided the data for a second method of esimating population size. 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. The estimate by this method was the same as by the first method.

The population of the study area was estimated to be between four and five turtles per acre, with juveniles constituting less than 10% of the total.

LITERATURE CITED

Allard, H. A. 1935. The natural history of the box turtle. Scientific Monthly **41**: 325-338.

Blair, W. F. 1940. A study of prairie deer-mouse populations in southern Michigan. Amer. Midl. Nat. **24(2)**: 273-305.

Bogert, C. M. 1937. Note on the growth rate of the desert tortoise, Gopherus agassizii. Copeia **1937 (3)**: 191-192.

Breder, R. B. 1927. Turtle trailing: a new technique for studying the life habits of certain Testudinata. Zoologica **9(4)**: 231-243.

Burt, W. H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. Misc. Publ. Mus. Zool. Univ. Mich. **45**: 1-58.

Cagle, F. R. 1939. A system of marking turtles for future identification. Copeia **1939(3)**: 170-173.

1942. Turtle populations in southern Illinois. Copeia **1942(3)**: 155-162.

1944. Home range, homing behavior, and migration in turtles. Misc. Publ. Mus. Zool. Univ. Mich. **61**: 1-34.

Dice, L. R. 1938. Some census methods for mammals. Jour. Wildl. Mgt. **2(3)**: 119-130.

Engelhardt, G. P. 1916. Burrowing habits of the box turtle. Copeia No. **31**: 42-43.

Fenneman, N. M. 1938. Physiography of eastern United States. McGraw-Hill, N. Y. xii + 714 pp.

Grant, Chapman. 1936. The southwestern desert tortoise, Gopherus agassizii. Zoologica **21(19)**: 225-229.

Harper, R. M. 1918. A phytogeographical sketch of southern Maryland. Jour. Wash. Acad. Sci. **8**: 581-589.

Hotchkiss, Neil & R. E. Stewart. 1947. Vegetation of the Patuxent Research Refuge, Maryland. Amer. Midl. Nat. **38(1)**: 1-75.

Hurter, Julius, Sr. 1911. Herpetology of Missouri. Trans. Acad. Sci. St. Louis. **20(5)**: 59-274.

Jackson, C. H. N. 1933. On the true density of tsetse flies. Jour. Anim. Ecol. **2(2)**: 204-209.
1936. Some new methods in the study of Glossina morsitans. Proc. Zool. Soc. London (1936): 811-896.
1939. The analysis of an animal population. Jour. Anim. Ecol. **8(2)**: 238-246.
1944. The analysis of a tsetse-fly population II. Ann. Eugenics. **12(3)**: 176-205.

Latham, R. 1917. Studying the box turtle. Copeia No. **40**: 15-16.

Leopold, Aldo. 1933. Game management. Charles Scribner's Sons, N. Y. xxi + 481 pp.

Lincoln, F. C. 1930. Calculating waterfowl abundance on the basis of banding returns. U. S. Dept. Agric. Circ. **118**: 1-4.

Medsger, O. P. 1919. Notes on the first turtle I ever saw. Copeia No. **69**: 29.

Nichols, J. T. 1939. Range and homing of individual box turtles. Copeia **1939(3)**: 125-127.

Overton, F. 1916. Aquatic habits of the box turtle. Copeia No. **26**: 4-5.

Pearse, A. S. 1923. The abundance and migration of turtles. Ecology **4(1)**: 24-28.

Penn, G. H. & K. E. Pottharst. 1940. Reproduction and dormancy of Terrapene major in New Orleans. Herpetologica **2(2)**: 25-29.

Peterson, C. G. J. 1895. Rept. Dansk Biol. Sta., **6**: 21. (From Borror, D. J. 1948. Analysis of repeat records of banded white-throated sparrows. Ecol. Monogr. **18(3)**: 420.)

Pope, C. H. 1939. Turtles of the United States and Canada. Alfred A. Knopf, N. Y. xviii + 343 pp.

Ricker, William E. 1948. Methods of estimating vital statistics of fish populations. Indiana Univ. Publ. Sci. Ser. No. **15**: 1-101.

Schmidt, Johs. 1916. Marking experiments with turtles in the Danish West Indies. Meddelelser Komm. Havundersögelser Ser. Fiskeri **5(1)**: 1-26 (from Cagle 1944).

Schnabel, Z. E. 1938. The estimation of the total fish population of a lake. Amer. Math. Mo. **45(6)**: 348-352.

Schneck, J. 1886. Longevity of turtles. Amer. Nat. **20(9)**: 897.

Schumacher, F. X. & R. W. Eschmeyer. 1943. The estimate of fish population in lakes or ponds. Jour. Tenn. Acad. Sci. **18(3)**: 228-249.

Stickel, L. F. 1948. A study of the trap line as a measure of small mammal populations. Jour. Wildl. Mgt. **12(2)**: 153-161.

Storer, T. I., F. C. Evans & F. G. Palmer. 1944. Some rodent populations in the Sierra Nevada of California. Ecol. Monogr. **14(2)**: 165-192.

Surface, H. A. 1908. First report on the economic features of turtles of Pennsylvania. Zool. Bull. Div. Zool. Penna. Dept. Agric. **6(4-5)**: 105-195.

Underhill, A. H. 1941. Estimation of a breeding population of chub suckers. Trans. Fifth N. Amer. Wildl. Conf. pp. 251-256.

Woodbury, A. M. & Ross Hardy. 1948. Studies of the desert tortoise, Gopherus agassizii. Ecol. Monogr. **18(2)**: 145-200.