Population Structure and Survivorship in the Painted Turtle, *Chrysemys picta*[1]

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The population structure and survivorship were determined for the painted turtle, *Chrysemys picta,* in a southwestern Michigan marsh. More than 1000 turtles were marked and released during the study. Age of older individuals was estimated on the basis of age-length relationships. Slightly more than half of the population was estimated to be comprised of immature individuals. The adult sex ratio was not significantly different from 1 : 1. The survivorship curve for the study population is a combination of Slobodkin's Types IV and III, with egg mortality being close to 100%, juvenile mortality being close to 0, and adult mortality being constant and independent of age. Contrary to popular belief, juvenile *Chrysemys* recruited into the population have an extremely high survival rate and will usually live to reach maturity.

Introduction

In recent years, increased interest in population ecology has placed an emphasis upon studies of natural populations of animals. Numerous animal species have been investigated in attempts to analyze their population dynamics and to relate these changes to the ecology of the species.

Cagle (1953) pointed out that most ecological studies on reptile populations have not met the "critical standards" necessary for formulating ecological principles and advancing ideas. He further indicated that the numerous facts concerned with reptile ecology are of such a diverse nature that they can seldom be integrated satisfactorily. The same is true today, particularly in regard to freshwater turtles.

The objective of the present study was to analyze the population dynamics of the painted turtle, *Chrysemys picta,* as an approach towards determining some of the factors which control or regulate population size and structure in a natural population of animals. The part of the study reported herein is primarily concerned with juvenile and adult survivorship. Reproductive aspects are presented elsewhere (Gibbons, 1968).

C. picta has many attributes which make it a favorable study species in investigations of the dynamics of natural populations. *Chrysemys* is usually found in distinct, well defined populations. Aging is possible to a much greater extent than is true of most other animals and size can be defined accurately by measuring plastron lengths. Information on mortality can be gained because of the durability of turtle shells after death of the individual. *Chrysemys* can be permanently marked for individual identification without injuring the animals or disturbing the population. The sexes can be distinguished externally.

The Study Area

The study was conducted from July 1964 to October 1966 at Sherriff's Marsh (Fig. 1), located in the northwest corner of Kalamazoo County, Michigan, in Sections 2, 3, and 11, T1S, R9W. The marsh is comprised of more than 75 acres of a grass-sedge association and approximately 14 acres of open water. The open water in the marsh consists of approximately a mile of winding channel and its extensions, a 5.5-acre lake, a one-acre pond, and the entrance of a small stream from the north. A more complete description is given by Gibbons (1967b).

Methods

Five techniques were used in capturing turtles. The relative merits for each of these will be discussed separately.

The most successful collecting method throughout the study was simply looking for turtles in the water and then catching them either by hand or by the use of a dip net. A wooden-handled net with ½-inch mesh near the rim grading into ¼-inch mesh at the tip was found to be suitable for

[1] Contribution No. 144 from the W. K. Kellogg Biological Station of Michigan State University.

capturing turtles of all sizes. Collecting was usually done from a rowboat.

Traps constructed of three-inch wire mesh also were successful in collecting turtles. The body of the trap consisted of a three-ft diameter, five-ft high cylinder standing on end. The bottom was of wire mesh but the top was open. A one-ft square was cut out of the cylinder about six inches from the bottom. The square was bordered by wire mesh extending six inches into the trap. Traps were placed along shore in shallow water. Accompanying each tray was a wire drift fence six ft long and two ft high. One end was placed at the side of the door away from shore, and the fence extended away at a 45° angle to the shore. The result was a funnel formed by the shore and the fence. Turtles traveling parallel to shore entered the trap through the open door. Thirteen of these traps were used in the marsh. Most were never moved from their original locations. The traps have the advantage of not requiring any maintenance, such as baiting, yet they are always operative. The major disadvantage of these traps is that they are restricted to use in shallow water near shore, and also, the use of three-inch mesh undoubtedly allows smaller turtles to escape.

Several bait traps constructed of ½-inch mesh galvanized hardware cloth were used at the marsh. The traps were two ft long and one ft square with funnels at each end. Sash cord was tied at the top so that the trap could be lowered to any depth and the cord tied to some object along shore. Dead fish or chicken necks placed in a hardware cloth bait container served as bait. These traps were effective in early spring but captured few turtles during other parts of the year.

Underwater diving was extremely successful under certain conditions. A rubber dry suit, fins, and underwater face mask, and a snorkel (or SCUBA) were used during certain times of the year for capturing turtles. By this method the investigator could swim along until a turtle was seen. The fins enabled one to swim faster than most *Chrysemys*. This technique was used to best advantage in the spring and fall when the water was clear and vegetation at a minimum. It was also found to be an excellent method of approaching basking turtles and catching them before they entered the water.

Muddling, employed by most turtle investigators at one time or another, consists of feeling by hand through mucky areas until a turtle is found. Attempts at muddling in the marsh were seldom rewarding.

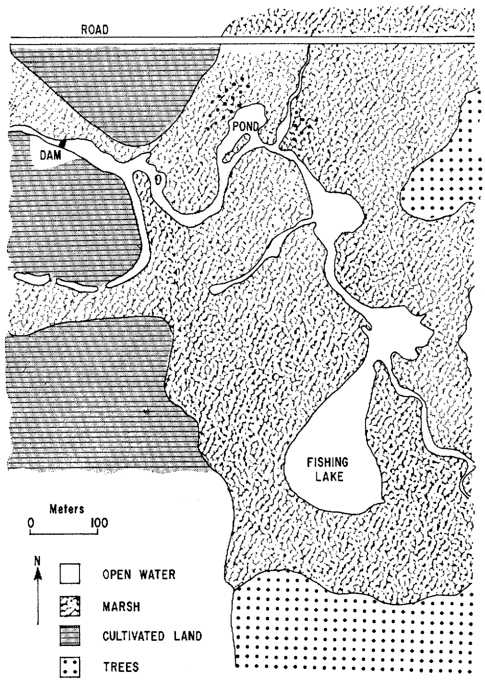

Fig. 1. Sherriff's Marsh, Kalamazoo County, Michigan.

Marking, Measuring, and Aging

Turtles in Sheriff's Marsh were marked for individual identification and usually released a few minutes after capture. Notching the marginal scutes with a small rectangular file was found to be an adequate method of marking adult *Chrysemys*. Cutting v-shaped notches with fingernail clippers was most effective on the flexible shell of juveniles. Though marked marginals occasionally bled, no permanent damage was known to occur as a result of marking. The notches on turtles marked in 1964 and recaptured in 1966 were not noticeably different from notches on turtles that had been marked for less than a month. It was not necessary, therefore, to remark individuals and it is assumed that all previously marked turtles were recognized as such when they were recaptured.

Plastron length of each captured turtle was taken to the nearest mm with a plastic ruler. Age was determined by the number

TABLE 1. GROWTH OF *Chrysemys picta* IN SHERRIFF'S MARSH BASED ON INDIVIDUALS RECAPTURED AFTER MORE THAN 75 DAYS OF GROWING SEASON.

	Plastron Length Range (mm)	No. Recaptured	No. Showing Growth	Cumulative Growth (mm)	Cumulative No. of Growing Seasons Between Original Captures and Recaptures	Avg. Increase in Length (mm/Growing Season = Yr)
♀♀						
	110–114	8	7	13	10.8	1.2
	115–119	12	8	17	15.4	1.1
	120–133	17	12	23	23.8	1.0
	Total	37	27	53	50.0	1.1
♂♂						
	80–89	12	12	28	12.4	2.3
	90–99	5	3	5	5.5	0.9
	100–111	12	5	6	13.8	0.4
	Total	29	20	39	31.7	1.2
♂♂ and ♀♀	Total	66	47	92	81.7	1.1

of annuli present on the left pectoral plate. Estimates of age in older individuals were made on the basis of length, after an age-length relationship was established for the population. The method of estimating age by measuring annuli on a given lamina (Sexton, 1959a) was not used, since annuli are seldom visible on older *Chrysemys*.

Determination of Population Size

The Lincoln Index (Allee *et al.*, 1949) was used to estimate the number of individuals in the different age, sex, and size classes. Each size-sex category was estimated separately. The final estimate for each category was derived by taking the average of the estimates for six collecting periods. Estimates obtained by this method may be subject to error for a number of reasons, as mentioned below.

Natality.—New turtles were added to the population in the spring of 1965 and 1966. Hatchlings of 1965 were treated as part of the juvenile population in deriving an estimate. Hatchlings of 1966 were not included in making an estimate of the juvenile population. The reason for this is that all estimates prior to the summer of 1966 were based only on the turtles which were in the population at the start of the summer of 1965. Including the 1966 hatchlings which appeared in the final collecting period would have led to an underestimation of the total juvenile population in 1966.

Selection against marked animals.—No marked turtles in the present study were known to be harmed or disabled by being marked. The methods of marking, therefore, are assumed to have had no influence on an individual's chances of remaining in the population.

Growth during the study.—A few turtles passed from immature to adult categories during the census period. Such individuals were classed in their original category for purposes of estimating population size. This caused a small degree of overestimation in the juvenile category and underestimation in the adult categories. The effect on final estimates was negligible.

Mortality.—Death of turtles during the study is assumed to have had little effect on estimation of numbers. Death is not a factor of error in estimating numbers for any given collecting period if marked and unmarked turtles have equal opportunities to die.

Migration.—Migration of turtles to or away from Sherriff's Marsh was probably minimal and had little effect on estimation of population size. Some interchange undoubtedly occurred between turtles in the study area and those in contiguous areas in which no collecting was done. Movement of turtles between these few small areas and the study area would result in a slight overestimation of the population size of the study area.

Behavior of marked turtles.—A possible source of bias was that marked animals may be less likely to be captured than unmarked animals. Evidence that some *Graptemys* and *Pseudemys* become more wary after being captured and released is presented by Tinkle (1958). Sexton (1959b) found that unmarked *Chrysemys* often allowed the collector to get closer in a boat than did previously marked individuals. Behavior of this type was not observed in the present study, but if it did occur, an overestimation of population size would result.

Random redistribution.—One of the assumptions in using the Lincoln Index is that a previously marked individual has as much chance of being collected as any other individual in the population. This assumption cannot be met in a natural population of animals. Although turtles were collected throughout the prescribed study area, certain areas were collected more extensively than others. Hence, a greater proportion of turtles were marked in some zones than in others. However, during each of the six collecting periods on which the estimation was based, some collecting was done in each part of the marsh. The error caused by non-random redistribution was therefore minimized.

Inherent error.—The Lincoln Index is based on chance. Even if it were possible to sample completely at random, the estimation of population size would probably still differ from the true population size. Each estimate therefore must be considered as a general assessment of population size, not as a calculated number of individuals.

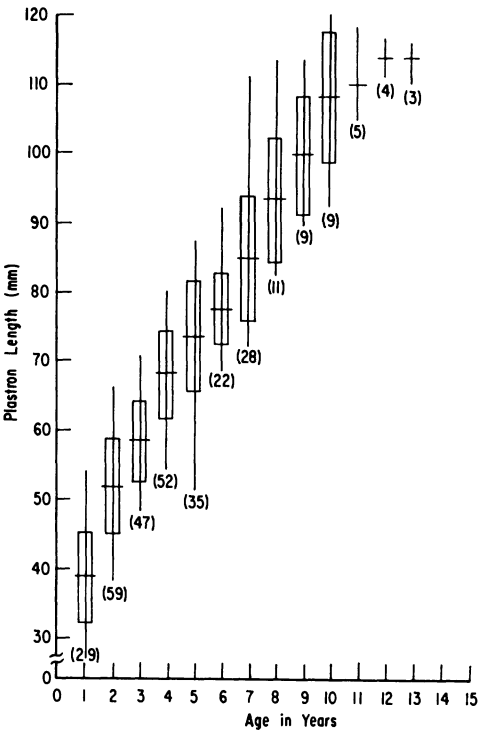

Fig. 2. Age-plastron length relationships of *Chrysemys picta* from Sherriff's Marsh, not including mature males. Vertical lines represent range; horizontal lines represent mean; bars represent standard deviation. Numbers in parentheses are sample sizes.

Results and Discussion

Growth Rates

A knowledge of individual growth rates permits the use of size as an indicator of age in turtles whose annuli are no longer visible, if it can be shown that size is a function of age. Determination of juvenile growth rates in Sherriff's Marsh was particularly effective because of the large number which could be aged by counting plastral annuli. This method of age determination is considered reliable for the younger age classes of *Pseudemys* (Cagle, 1946) and *Chrysemys* (Sexton, 1959a). Growth rate in older turtles was determined by measuring the increase in plastron length of individuals recaptured during the period of study.

Immature *C. picta* grow at a relatively steady rate which decreases markedly when maturity is reached. The mean plastron length, range, and standard deviation for each age class from one to 11 are given in Fig. 2. Males over 80 mm in plastron length are mature (Gibbons, 1968) and, because of their slower growth rate, are not included. Plastron length increased steadily through the 10th year. The 12 turtles in their 11th–13th years were only slightly larger than those in their 10th year. Excluding turtles in their 11th–13th years, the increase in mean size in successive years varied from 13.0 mm between the first and second years to 4.3 mm between the fifth and sixth. The average increase in mean size in successive years from one to 10 was 7.7 mm/year.

On the basis of recaptures, females 110 mm or more averaged 1.1 mm per year, mature males 1.2 (Table 1). Combining recapture data for both sexes, the average growth rate was 1.1 mm/year. The trend in both sexes was for the larger adult size classes to show less growth than smaller ones over comparable lengths of time. Age-length relation-

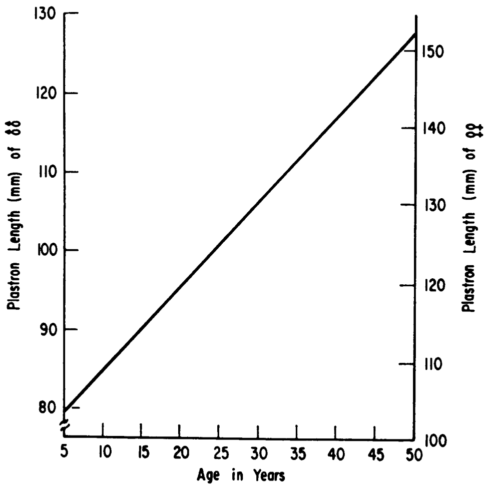

Fig. 3. Age-plastron length relationship of *Chrysemys picta* from Sherriff's Marsh based on an estimated growth rate of 1.1 mm/year.

ships based on the above data are indicated in Fig. 3.

Population Size and Density

From July 1964 to October 1966, 1010 *Chrysemys* were marked at Sherriff's Marsh and 408 recaptures were made on 258 marked individuals. The percentage of recaptures generally increased during successive collecting periods from early 1965 to late 1966 (Table 2).

An estimate was made of the number of *Chrysemys* in each size-sex category (Table 3). More than 1400 immature turtles, composing approximately 59% of the total population, were estimated to be present in Sherriff's Marsh. The estimated number of mature turtles was 925. Actual captures were 521 (52%) immature and 480 (48%) mature.

Chrysemys in Sherriff's Marsh were restricted to the 14 acres of open water. The minimum density, derived from the estimate of 2328 individuals, would therefore be 166 turtles/acre. However, approximately four acres of Fishing Lake were not utilized by turtles and should not be considered in determining density. Excluding these four acres, this results in a density estimate of 233 *Chrysemys*/acre.

Sexton (1959b) estimated density in his population further east in Michigan to be 166 *Chrysemys*/acre during a dry period, 40/acre during a period of high water. The similarity in the density estimates of these

TABLE 2. RECAPTURE RATIOS OF *Chrysemys picta* FROM SHERRIFF'S MARSH.

Size-Sex Category	Collecting Period	Total No. Captured	Recapture %
Juveniles < 80 mm in plastron length	Apr–May 1965	34	0
	Jun–July	71	6
	Aug–Oct	56	9
	Mar–May 1966	21	17
	Jun–July	108	28
	Aug–Oct	85	30
Immature ♀♀ 80–114 mm in plastron length	Apr–May 1965	22	5
	Jun–July	44	23
	Aug–Oct	32	15
	Mar–May 1966	45	13
	Jun–July	59	21
	Aug–Oct	39	23
Mature ♂♂	Apr–May 1965	46	4
	Jun–July	54	17
	Aug–Oct	43	22
	Mar–May 1966	86	22
	Jun–July	67	33
	Aug–Oct	34	29
Mature ♀♀	Apr–May 1965	54	7
	Jun–July	41	22
	Aug–Oct	36	36
	Mar–May 1966	36	22
	Jun–July	57	23
	Aug–Oct	29	55

two populations is striking and suggests a relatively narrow range at which population size is optimum. However, to establish this, density determinations of other *Chrysemys* populations will be necessary.

Sex Ratio

The sex ratio of mature individuals, males more than 80 mm and females more than 115 mm in plastron length (Gibbons, 1968), was close to 1 : 1. This was true on the basis of actual captures and upon Lincoln Index estimates (Table 3).

Aberrant sex ratios have been reported for some species of turtles (Hildebrand, 1929; Risley, 1933; Cagle, 1942). Sexton (1959b) reported that the *C. picta* of known sex in his population were in a ratio of 1.49♀♀/1.0♂, but that if only mature animals were considered, the ratio was 0.76♀♀/1.0♂. The slightly greater apparent abundance of mature males at Sherriff's Marsh is probably only a result of the method of determining maturity in females. Based upon dissection

TABLE 3. POPULATION SIZE OF *Chrysemys picta* IN SHERRIFF'S MARSH.

Size-Sex Category	No. Estimated	% of All Estimated Individuals	No. Actually Captured	% of All Captured Individuals
Juveniles < 80 mm in plastron length	862	37	305	31
Immature ♀♀ 80–114 mm in plastron length	541	23	216	22
Mature ♂♂	490	21	265	27
Mature ♀♀	435	19	215	22
Total	2328		1001	

of females of different lengths, a plastron length of 115 mm was chosen to represent the size at which most females reach maturity. The length was arbitrarily picked from a relatively narrow size range. A length of 113 or 114 mm could just as easily have been used as a standard length for the size at which maturity is reached. In reality, then, the sex ratio of mature *C. picta* in Sherriff's Marsh probably does not vary significantly from 1 : 1.

Age Structure and Survivorship

An estimate was made of the number of individuals in each of the first four age classes by using 1965 as a precensus period and 1966 as a census period (Table 4). There was no trend towards reduction in numbers during successive years. One cohort (hatchlings from 1964) had fewer individuals than any of the others. Presumably before their second year this cohort suffered from a source of mortality which did not affect older juveniles to the same extent.

Due to difficulties in aging and complications brought about by the changes in growth rates as males neared 80 mm, a satisfactory estimate of the number of individuals in the 1961 age class was not made.

Age could not be determined by counting annuli in many of the immature females over 80 mm in length. However, a general age-length relationship is indicated in Fig. 2. Most females between 80 and 89 mm were in their 7th year, although this size range also included some individuals in older and younger age classes. The 90–99 mm size range was composed mostly of eight and nine-year-old animals. The 100–109 mm size range primarily included individuals 9–11 years old. Essentially, then, the immature females which were 80–109 mm in length included almost all females eight or nine years old, more than half of those 10 or 11 years old, about two-thirds of those that were seven years old, and about one-fifth of those five or six years old.

TABLE 4. NUMBER OF JUVENILE *Chrysemys picta* IN SHERRIFF'S MARSH.

Age Class	Age in 1965	No. Marked and Released in 1965	No. Originally Captured in 1966	No. Recaptured in 1966	Total Captured in 1966	No. Estimated to Be in Population
1965	1	20	41	6	47	157
1964	2	17	19	6	25	70
1963	3	38	39	15	54	137
1962	4	33	30	6	36	198

The 80–109 mm size range was thereby composed of immature females from the equivalent of approximately four age classes. Since 358 females were estimated to be 80–109 mm in length, (Table 5), this size range would average about 90 individuals/age class. This estimate is in accord with the estimates for the younger juveniles. There is no evidence, therefore, to indicate that mortality increases with age in immature *Chrysemys*. Apparently, then, once a juvenile has completed his first year his chances of reaching maturity are extremely high.

The survival pattern from the egg stage until maturity assumes that of a Type IV survivorship curve (Slobodkin, 1963). Approximately 6000 eggs are laid each year at Sherriff's Marsh, based upon the annual reproductive potential (Gibbons, 1968) and the number of mature females. Around 2% of the eggs develop into juveniles which become recruited into the population. Most of these juveniles reach maturity.

There are at least three possible causes of mortality in the nest. (1) Non-hatching of *Chrysemys* eggs, observed both in the field and laboratory, may be due in some part to infertility, as has been observed for *Malaclemys* (Hildebrand, 1929). (2) Extreme

TABLE 5. POPULATION SIZE STRUCTURE OF *Chrysemys picta* IN SHERRIFF'S MARSH.

	Size Range (Plastron Length in mm)							
Mature ♂♂								
	80–84	85–89	90–94	95–99	100–104	105–109	110–116	Total
No. captured	38	59	54	46	35	28	5	265
% of total	14.3	22.2	20.4	17.4	13.2	10.6	1.9	
Estimated No. based on % of 490	70	109	100	85	65	52	9	490
Immature ♀♀								
	80–89	90–99	100–109	110–114				Total
No. captured	42	42	59	73				216
% of total	19.5	19.5	27.3	33.8				
Estimated No. based on % of 541	105	105	148	183				541
Mature ♀♀								
	115–119	120–124	125–129	130–134	135–140			Total
No. captured	83	69	43	15	4			215
% of total	38.6	32.1	20.2	7.0	1.9			
Estimated No. based on % of 435	168	140	88	30	8			435

environmental conditions such as excessive heat, cold, moisture, or dryness seem likely sources of mortality, although insufficient field data were collected to support this position. (3) Predation is a major mortality factor at the egg stage, although an attempt at quantitative assessment was unsatisfactory. The amount of predation is no doubt excessive under some circumstances, since numerous destroyed nests were observed.

Adults of both sexes experience a much higher mortality rate than is true of immature turtles. There appears to be a sudden reduction in the number of individuals per age class when maturity is reached. This phenomenon may be a result of the method of age determination. Growth rate was assumed to be 1.1 mm/year for all ages of both sexes. The ages in Table 6 are based upon this age-length relationship. However, old adults probably grow more slowly than young ones. If differential growth rates are taken into account, the smaller size ranges in Table 6 would include fewer age classes than the larger ones. The effect of this would be to raise the number of individuals per age class in the younger adults. The number of individuals per age class would be reduced for older turtles. The resulting survivorship curves for both sexes would then approach a Type III, as defined by Slobodkin (1963). Such a curve is characterized by a constant mortality rate for individuals of all ages.

Once a *Chrysemys* reaches maturity at Sherriff's Marsh, its chances of survival presumably remain the same regardless of age. Many physiological and behavioral changes accompany maturity. Some of the more obvious effects are increased activity in the spring, expenditure of energy for reproductive functions, and a greater likelihood of terrestrial activity (Gibbons, 1968). These and other changes associated with adulthood make mature *Chrysemys* susceptible to environmental hazards that do not confront immature individuals. The result is a much higher adult mortality rate.

Emigration and Immigration

The effect on the population of *Chrysemys* entering, or leaving, the study area appeared to be minimal. A statement that migrations to, or from, any unenclosed area do not occur can hardly be made. However, indirect evidence supports the view that the population of *C. picta* at Sherriff's Marsh is relatively uninfluenced by migration.

More than 100 collecting trips were made to Sherriff's Marsh during the study. On many of these trips the roads encircling the marsh were traveled by car. The only turtles, dead or alive, were found on the road north of the marsh, between two aquatic areas. Also, other than females laying eggs, no turtles were found on land around the marsh during the entire study.

More than 1000 turtles were marked in Sheriff's Marsh. In 1965–66 almost 400 turtles were captured two miles away in

TABLE 6. AGE STRUCTURE OF *Chrysemys picta* POPULATION AT SHERRIFF'S MARSH. Estimates for years 1–4 are based on a Lincoln Index of turtles in which age was known. A 1 : 1 sex ratio is assumed. The collective estimate for immature females 6–11 years old was derived from the age-length relationships (Fig. 2) and the estimated number in each size class (Table 5). Estimates of mature turtles were based on a growth rate of 1.1 mm/yr for both sexes and on the number estimated to be in each size class.

♂♂			♀♀		
Plastron Length in mm	Age in 1965	Estimated No. in Age Class	Plastron Length in mm	Age in 1965	Estimated No. in Age Class
	1	79		1	79
	2	35		2	35
	3	69		3	69
	4	99		4	99
80–84	6.0–10.0	15.6		6–11	90
85–89	10.5–14.5	24.2	110–114	12.0–16.0	40.7
90–94	15.0–19.0	22.2	115–119	16.5–20.5	37.3
95–99	19.5–23.5	18.9	120–124	21.0–25.0	31.1
100–104	24.0–28.0	14.4	125–129	25.5–29.5	19.6
105–109	28.5–32.5	11.6	130–134	30.0–34.0	6.7
110–116	33.0–37.0	1.4	135–140	34.5–39.5	1.5

Wintergreen Lake, the nearest sizable population of *Chrysemys*. None of these was a marked turtle from Sherriff's Marsh. Also, 266 *Chrysemys* from Wintergreen Lake were marked and released by Dr. M. M. Hensley in 1957. Although several of these were recaptured in Wintergreen Lake during the present study, none was seen in Sherriff's Marsh. There is no evidence of interchange between the Sherriff's Marsh and Wintergreen Lake populations.

Longevity

Turtles are usually considered to be long-lived animals. Carr (1952) stated that the age attained by turtles is "perhaps the greatest of any living vertebrate." Hildebrand (1929) gave a "conservative estimate" that *Malaclemys* live 25–40+ years. Cagle (1950) stated that *Pseudemys* under natural conditions may have a life span "possibly within the range of 50–75 years." Nichols (1939) estimated that *Terrapene carolina* were fully grown in about 20 years but that some of the older ones were probably as much as 80 years old. Schneck (1886) reported an individual *Terrapene* which was marked in 1824 and recaptured several times during the next 60 years. Turtles are always among the oldest vertebrates in zoos (Flower, 1944; Conant and Hudson, 1949).

Once a *Chrysemys* hatchling is incorporated into the Sherriff's Marsh population the chances of reaching maturity appear to be excellent. Therefore, most males live at least six years, females at least 12. In spite of the increased mortality of adults at least 50% of each sex probably reach an age of 15 years or more (Table 6). A few individuals were estimated to be close to 40 years old. Due to the difficulty of aging old individuals, this is very likely a minimum estimate. There is no indication that *Chrysemys* at Sherriff's Marsh approach the "maximum life span" for the species (Deevey, 1947).

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