

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 2952, 55 pp., 12 figs., 13 tables August 10, 1989

Long-term Ecological Studies on a Population of Painted Turtles, *Chrysemys picta*, on Long Island, New York

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ABSTRACT

A mark-recapture study carried on for 18 consecutive years yielded a variety of ecological information on a population of 21–57 turtles inhabiting a series of small ponds. Adult females were the most stable element of the population, ranging from 9 to 14 individuals and regularly comprising more than half the biomass. Numbers of males fluctuated greatly, in part due to a single large annual brood composed almost wholly of males. Sex ratios of adults and of all turtles averaged close to 1 for the span of years, but fluctuated greatly among years (adults, 0.62 to 1.80 males per female). Different annual cohorts of the same sex differed greatly in growth rate, and males and females of one year class may differ whereas those of another may not. An example is given of males resuming rapid growth well after maturity, and the establishment of growth plateaus in several old females is documented. Known population annual recruit-

ment ranged from 0 to 28 young, with the average of 5 equivalent to less than one successful clutch. Survival of known recruits showed a low rate of loss for both sexes to the end of the fourth growth year, whereupon male losses increased dramatically while female survivorship remained at a high level. The break in the male curve correlates with their attainment of sexual maturity and with an increase in interpond movement. In general, individuals of both sexes were familiar with the three major ponds but spent most of their time in a favored one. Additional topics include immigration and emigration, population density, biomass, productivity, and age structure. Findings are compared with those of other populations of *Chrysemys picta* living in similar and different habitats. A principal conclusion is that with such long-lived animals, extrapolations from fieldwork lasting only a few years are likely to be misleading.

INTRODUCTION

Chrysemys picta is perhaps the most studied freshwater turtle in the world, a situation

reflecting its abundance, availability, and great geographic range. Investigators have report-

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ed at length on its systematics, distribution, and physiology, and especially on diverse aspects of its ecology (Ernst, 1971d and 1988, provided comprehensive bibliographies). In this circumstance, one might question the need for additional ecological studies. A principal reason is that because of its abundance and wide distribution, this is one of the few reptile species yielding comparative information on geographic variation of intraspecific ecological parameters.

Bury (1979: 571), reviewing population ecology of freshwater turtles, commented that most research "consisted of fragmentary, short-term, or descriptive studies." Such studies, while often providing valuable snapshots of population biology, leave questions about variability unanswered. Do different results among studies of the same species imply geographic (racial) variation, or are they within the normal capabilities of a single population? How do populations react to environmental events such as unusual drought? With periods of field research amounting only to a fraction of the average longevity of the turtles, such questions may go unanswered. Happily, since Bury wrote, more long-term studies have begun to appear. The work on *Chrysemys picta* begun by Sexton (1959a) at the George Reserve in Michigan has been continued by Wilbur (1975b) and by Tinkle et al. (1981). At the Savannah River Ecology Laboratory in South Carolina, long-term studies on a variety of freshwater species (but not *C. picta*) are yielding abundant data on growth, survival, responses to environmental perturbations, and other aspects of turtle ecology (e.g., Gibbons, 1987; Gibbons and Coker, 1977; Gibbons et al., 1983; Gibbons and Semlitsch, 1982). These and other works of long duration (e.g., Parker, 1984) usher in a new phase of turtle population ecology.

The present study has certain distinctive, even unique, attributes. It offers data on demography, growth, and movements of a small, isolated population, based on field studies carried on yearly for 18 consecutive years. The size and isolation of the population combined with an intensive capture-recapture program assured that numerical aspects of the study were based on data closely approximating a true census rather than on rough estimates of population size. The long du-

ration of the study provided a better opportunity to observe temporal changes in the population than had been the case in most previous studies.

Following the presentation of my findings in each of the major sections of this work I make comparisons with previously published studies on *Chrysemys picta*. A general review of freshwater turtle biology is beyond the scope of the work, though I refer to work on other species where it seems particularly pertinent.

Over its distribution from Newfoundland to British Columbia and south to Mexico, *Chrysemys picta* exhibits considerable morphological diversity that is formalized in the recognition of four subspecies. The study area is within the range of the eastern painted turtle, *C. p. picta*, as mapped by Conant (1975: map 22), though Pough and Pough (1968) found that turtles in the area showed great variation in characters used to distinguish between that subspecies and the midland painted turtle, *C. p. marginata*.

ACKNOWLEDGMENTS: I extend thanks first to Mr. and Mrs. Horace Havemeyer, Jr., who accorded free access to their estate to me and my student associates. Their tolerance of our incursions at all hours of the day and night and at all times of the year for almost two decades made this and other studies possible. Dr. Wesley Lanyon, Director of the Kalbfleisch Field Research Station, and Mrs. Vernia Lanyon provided an atmosphere that made visits to the Station much like a family gathering. The late Edward Szaly and his successor as Superintendent of the Station, Mr. James Mansky, helped in uncountable ways. Mrs. Frances Zweifel and our children Matthew, Kenneth, and Ellen, responded cheerfully to my frequent requests for assistance. J. Whitfield Gibbons and Joseph C. Mitchell read a late draft of the manuscript and offered many suggestions for improvement, most of which I gladly accepted.

Participants in the American Museum of Natural History's Undergraduate Research Program, sponsored in part by the National Science Foundation, did the vast majority of the fieldwork that provided data for this study while at the same time gathering data for other population ecology projects. The student workers, and the years in which they partic-

ipated, were: 1963, Mr. F. Harvey Pough; 1964, Mr. Erik Kiviat (a volunteer rather than an NSF researcher); 1965–1966, Mr. Thomas Wiewandt; 1967–1968, Mr. Alan M. Brown; 1969, Ms. Charlotte Virzi; 1970, Mr. David J. A. Vleck; 1971, Mr. David C. Deitz; 1972, Mr. Stewart Fefer. It has been my pleasure to see several of these students go on to accomplish significant research in herpetology. No doubt they had long ago given up hope of seeing any published results of their fieldwork, but neither turtles nor senior researchers are easily hurried.

STUDY AREA

The population studied inhabited ponds on the estate of Mr. and Mrs. Horace E. Havemeyer, Jr., located south of and adjacent to the Kalbfleisch Field Research Station on Long Island near Dix Hills, Suffolk County, New York. The site is about halfway between the north and south shores of Long Island on the Ronkonkoma terminal moraine of Wisconsin glacial age. Elevations in the immediate area range from about 70 to 90 m above sea level. Originally covered with deciduous forest, the general area had for more than 100 years been given over to a mixture of cultivated land, pastures, and farm woodlots. When the study commenced, the Havemeyer Estate comprised about 81 ha, mostly in fields, forest, and woodland. Changes in land ownership and use over the 18 years of study affected some study ponds, and a drought had a profound effect. These matters are discussed below in the individual pond descriptions.

Spatial relationships of the ponds and other features of the nearby landscape appear in figure 1, in which the shading pattern indicates deciduous forest, woodland, and hedge-row, whereas open areas represent grassy or brushy fields and, near some of the buildings, lawns. The broken line marks the south and west boundaries of the Research Station, with a permanent pond (C2) near the western edge and a vernal, woodland pond (F6) northeast of it. A road borders the properties on the west. Three ponds, identified on the map as Ponds 1–3, were the ones principally used by the turtles, and two others, Ponds 4 and 6, were less important (fig. 2). Pond 5, a shallow,

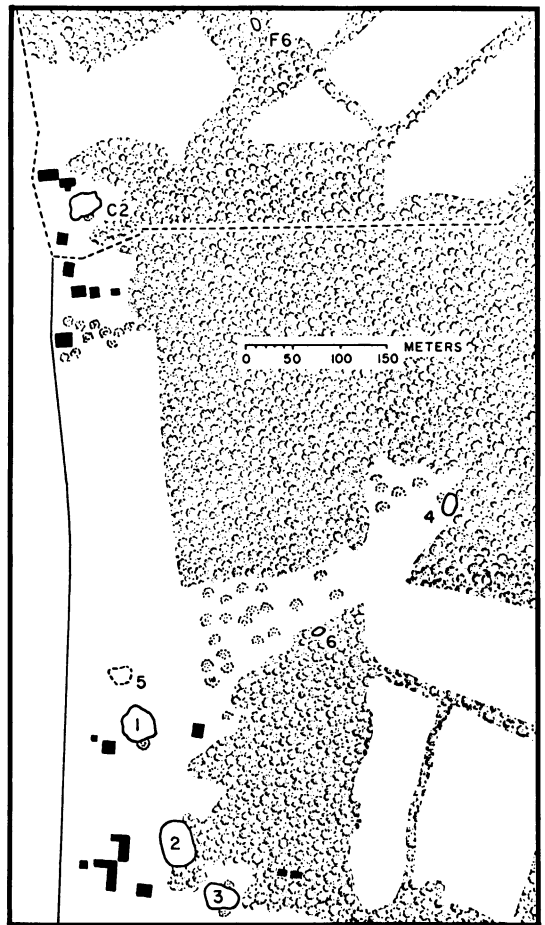


Fig. 1. Map of study area with Ponds 1–6, C2, and F6 numbered and buildings indicated in black. See text for additional details.

marshy area inundated only temporarily in the spring, proved of minimum significance. Descriptions of the other five ponds follow.

POND 1: This pond is a rounded, shallow depression about 34×30 m, with a maximum surface area of about 800 m^2 . It is a natural pond, presumably a kettle-hole, fed only by direct precipitation and immediate local runoff. In rare periods of overflow it drained north to Pond 5. Rocks around the pond's periphery provided basking sites only for a relatively brief period annually, as they typically were covered during spring high water and were outside the pond margin for much of the rest of the year. When the study commenced in 1963 and into 1966 the pond was open to a small herd of cattle. Conse-

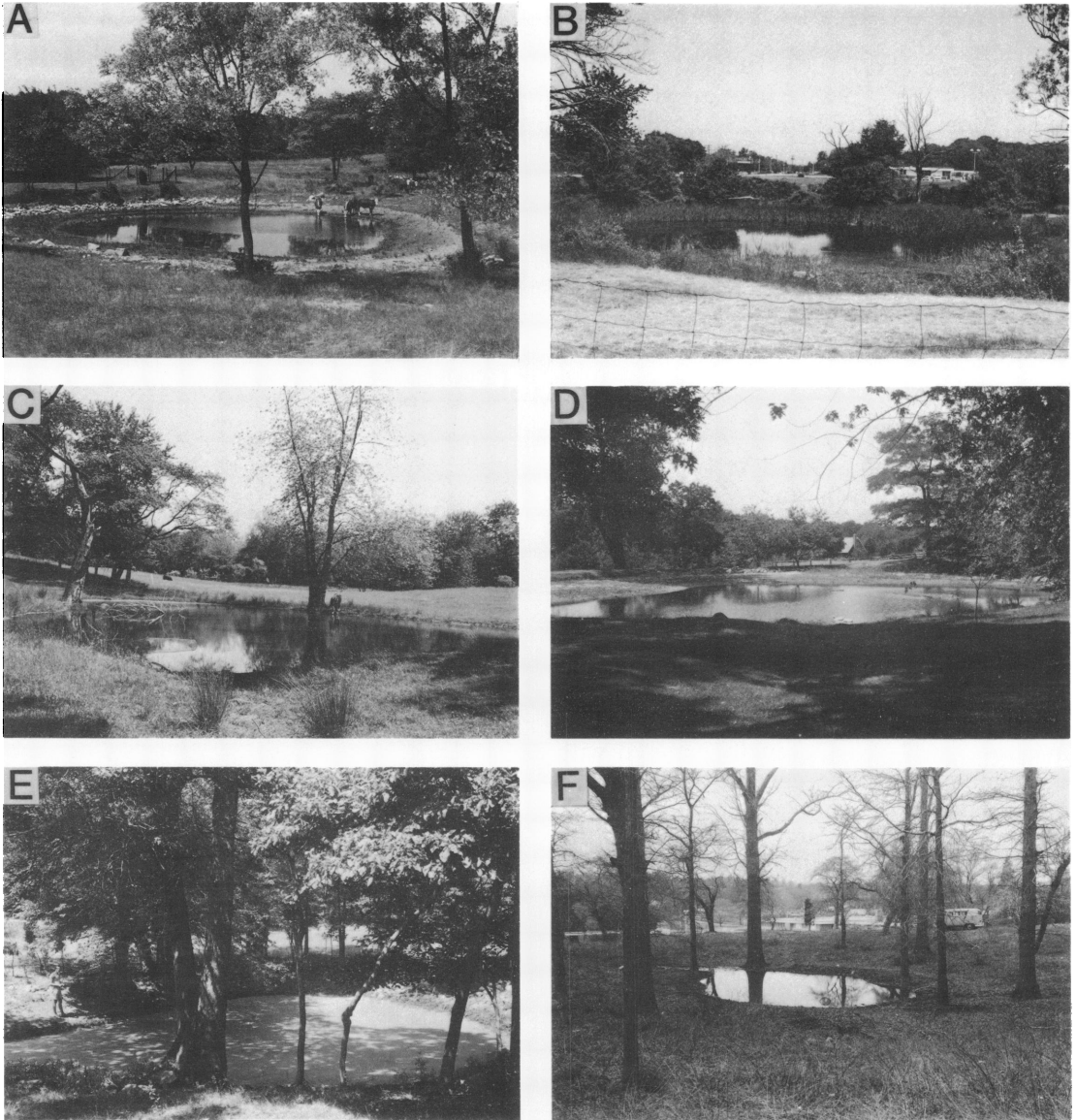


Fig. 2. A. Pond 1 as it appeared in August 1966 during a time of drought before cattle were fenced out. B. Pond 1 at spring high water in April 1976. Cattle had been excluded for several years and a dense growth of cattails crowded the shallows. C. Pond 3 in May 1977; cattle kept the marginal vegetation low. D. Pond 2 in August 1966, bordered largely by mowed grass. Cattle never had access. E. Pond 4 in August 1966, the largely shaded surface covered with duckweed. F. Pond 6 in May 1971.

quently, the area about the pond was heavily grazed, no emergent vegetation grew in the pond, and the water was abundantly fertilized (fig. 2A). In later years the cattle were excluded, except briefly on occasion, and the character of the pond and its surroundings changed. Cattails (*Typha*) came to border

much of the pond and other emergent and submerged vegetation (*Myriophyllum*, *Potamogeton*) flourished. On land, grass grew high and invading shrubs occupied much of a belt around the pond (fig. 2B). The elongate, open area north of Pond 1 (including Pond 5, fig. 1) was taken over as a site for the con-

struction of a school late in the summer of 1969. A high, chain-link fence protected the pond from incursions.

Typically the pond was filled, though not necessarily to overflowing, in the early spring, but the level dropped throughout the summer. Judged from the presence of fish when the study commenced in 1963, the pond had not dried in many years. There was no record of fish having been introduced, and no access from ponds containing fish. The years 1964 and 1965, the latter especially, were noted for one of the most extreme droughts the northeast has experienced, and this profoundly affected this and the other ponds. The long-term average annual rainfall in the study area, 115 cm, was reduced to 100 cm in 1964 and 74 cm in 1965. That the main deficits in rainfall occurred in warm months—May, June, and August 1964; May and following months in 1965—compounded the effect. Total rainfall in 1963 was no greater than in 1964, but approximately average amounts through July and again in September forestalled serious impact on the pond.

By August 3, 1964, Pond 1 had a maximum depth of 18–20 cm above the deep mud bottom, and the fieldnotes for August 11 describe it as “little more than a bovine cesspool,” but the pond did not dry completely in 1964, as fish were present in the spring of 1965. Though the pond was nearly full in the early months of 1965, the water level dropped greatly in late spring and by July 1 the depth was scarcely 15 cm. The pond had dried by mid-September when it was dredged to a depth of about 1.3 m. The year 1966 also had less than average rainfall, but the pond, now deeper, retained at least some water throughout the year, as it did in all subsequent years.

POND 2: Located about 88 m (between high water levels) south-southeast of Pond 1, this pond is both larger (46×40 m, 1300 m²) and deeper. Apparently it originated as a spring-fed, natural pond, but was enlarged in the distant past for use as an ice pond. Mowed lawn borders all but the eastern margin edged in closed woodland (fig. 2D). There was little or no emergent vegetation and little submerged vegetation, a considerable contrast to Pond 1, especially in the post-drought years. The pond drains westward from its north end, having no connection with Pond 1. Drainage

into the pond is from Pond 3 to the southeast. Pond 2 lost most of its water in the severe drought year of 1965, having a depth of no more than about 20 cm when dredged in mid-September to a depth of about 2 m. No land use changes affected the pond during the study years.

POND 3: With dimensions of about 32×23 m at high water and a maximum surface area of 560 m², Pond 3 was the smallest of the principal ponds (fig. 2C). A shallow drainage about 30 m long joined Pond 3 with Pond 2 to the northwest during spring high water. In contrast to the other ponds used by the turtles, it was not natural but was dug in 1960 in a marshy area in which runoff gathered. (Turtles were not slow to take advantage of the new resource, as they were using the pond at least by 1963.) The pond was deeper than the others prior to their being dredged and held water through the drought years. Pond 3 was not dredged and so provided a refuge from drying and disturbance, though it became quite shallow by late 1965. Cattle used the pond for watering in all years of the study. No emergent vegetation survived their feeding and trampling, and little but algae grew in the fetid water.

POND 4: This was a woodland pond, smaller than Ponds 1–3 and different in other respects as well. The small size (25×16 m, 300 m²) and shading by trees made it suboptimal for *Chrysemys*, but a few turtles used it regularly or even exclusively (fig. 2E). It apparently was a kettle-hole and in the infrequent instances when overflowing, drained southwestward in the direction of Pond 6, a distance of about 170 m. Though the general direction of drainage was toward Pond 1, 370 m away, the two did not connect. Thick leaf litter covered the bottom of the pond, and in late summer the surface developed a continuous cover of duckweed (*Lemna*). Pond 4 held water throughout normal years though when dredged to a depth of 1.5 m in mid-September 1965 it almost was dry. Cattle had access to the pond but, except in the drought, disturbed it less than they did the others.

In the winter of 1971–1972, accompanying a change in land ownership, Pond 4 became accessible to the public. Accompanying disturbance and even loss of traps made it impractical to continue regular trapping there.

The pond and its immediate surroundings were not altered until the summer of 1973, when road construction caused some silting. By the early spring of 1974 houses surrounded the pond, though it was allowed to remain intact.

POND 6: Pond 6 was a woodland pond even smaller than Pond 4 (exact size not recorded, fig. 2F). Probably it was perennial only in wetter years—it dried before the end of June in 1964, when the other ponds maintained at least a little water through the summer, and also dried in 1965. There were no resident *Chrysemys* here, though one turtle used it frequently. The pond was heavily used by cattle and was destroyed in August 1972 in the course of housing construction.

VERTEBRATE FAUNA: *Chrysemys picta* was the only aquatic species of turtle resident in the ponds. A snapping turtle (*Chelydra serpentina*) trapped in Pond 2 escaped from confinement at the Research Station and 20 days later was trapped in Pond 3, having traveled at least 1 km overland. Released there, it was never seen again. Only one other *Chelydra* was captured (in Pond 3), and then only once. Undoubtedly these turtles were transients. The only other aquatic turtle captured was a musk turtle (*Sternotherus odoratus*) found once in Pond 1 to which it had moved from its place of introduction in the C2 Pond on the Research Station.

Bullfrogs (*Rana catesbeiana*) and green frogs (*R. clamitans*) were breeding residents, often abundant, in Ponds 1–3. Both species sometimes were present in Ponds 4 and 6, but usually as young, dispersing individuals. No breeding was detected there. Fowler's toads (*Bufo woodhousii fowleri*) and spring peepers (*Hyla crucifer*) bred in Ponds 1–3 in the spring and the latter together with woodfrogs (*Rana sylvatica*) bred in Ponds 4 and 6. Spotted salamanders (*Ambystoma maculatum*) were abundant in Pond 4 during their brief breeding period in early spring and much less so in the impermanent Pond 6. A few marbled salamanders (*Ambystoma opacum*) bred annually at Pond 4, and larval newts (*Notophthalmus viridescens*) were found there once. No salamanders occurred in the larger Ponds 1–3.

Prior to the 1964–1965 drought, bullheads (*Ictalurus nebulosus*) and goldfish (*Carassius*

auratus) were abundant in Ponds 1–3 but no fish ever were found in Ponds 4 or 6. The drying of Pond 1 in 1965 eliminated the fish there and none became reestablished. Probably they were extirpated from Pond 2 also in 1965, but reinvaded after 1966, presumably from the refuge of Pond 3. Mosquito fish (*Gambusia affinis*) and ricefish (*Oryzias latipes*) were present at one time or another in Ponds 1–3, but these introduced populations seldom persisted for more than a few months to a year.

Raccoons (*Procyon lotor*), potentially important predators on turtle nests as well as on the turtles themselves, frequented the grounds of the Research Station and no doubt used the Havemeyer ponds too. Among the birds, only the green heron (*Butorides virescens*), by virtue of its possible predation on hatchling *Chrysemys*, is likely to have been of any significance in the turtles' economy.

METHODS OF CAPTURE AND RELATED TOPICS

EQUIPMENT: Most captures were made with baited hoop-net traps of the sort described and illustrated by Ream and Ream (1966: 327, fig. 2): a tube of welded wire fencing about 60 cm in diameter and 120 cm long with funnel ends of nylon netting and a bait container suspended between the openings of the funnels. Traps generally were set in water slightly shallower than their own diameter (to allow trapped turtles to breathe) and were staked in place to prevent rolling into deeper water. Traps provided with floats and set in open water and basking traps also received trial, but no obvious improvement in trapping success resulted so these techniques were discontinued. Canned sardines were the usual bait; Ernst (1965) also found this to be the best bait among several alternatives tested.

During periods of drought it was difficult to find water deep enough to cover the mouths of the funnels of standard traps. Flattened, rectangular wire traps with net funnels at one or both ends were useful under these circumstances, as they could be set where the water was as little as 15 cm deep. They also served for use in shallows under more normal conditions.

In addition to trapping, we took turtles by

dip net and by hand whenever possible. These methods were especially important early in the year when turtles basked but were disinclined to enter traps.

TRAPPING PROTOCOL: During the summers with a student worker in residence, trapping was done on a rotating basis. Several traps would be set in one pond for a number of days—generally until no new captures were forthcoming—and then the traps were shifted to another pond. Several cycles of trapping could thus be accomplished in one summer. This was not a rigid schedule, and often there were traps in two or more ponds at one time. In the years following 1972 when there was no resident student, trapping was much less intensive, rarely with as many as three consecutive days of trapping and with the total trapping time greatly reduced. Trapping in the spring and fall of all years was limited to occasional periods of one or two days duration.

SELECTIVITY IN COLLECTING: That particular collecting methods may be biased as regards the size (age) or sex of turtles is a legitimate concern. Ream and Ream (1966) investigated the matter methodically and established that hoop-nets, basking traps, and hand capture each yielded significantly different proportions of young, old, male, and female *Chrysemys*. Vogt (1979) investigated the possibility that male *Chrysemys* may be attracted to traps containing females, thereby giving a biased sex ratio. Bider and Hoek (1971) combined a floating blind with hand (dip net) capture and felt that this method furnished a sample more nearly approximating the true proportions of age and sex in the population.

The two principal biases associated with hoop-nets are that small turtles (in their first year in the pond) are much under-represented, and that adult males may be more prone to capture than their female counterparts, especially in the mating season. With respect to sampling the whole population, the latter bias is effectively negated if trapping is sufficiently intensive and continues over a long period of time, as was the case in the present study. Only rarely did an adult turtle avoid capture in a year when it was known on the basis of earlier and later captures to be in the population. Turtles in their first year in the

ponds began to be captured in the traps with some regularity late in the summer. Most of our captures of such small turtles earlier in the year were by hand (literally, or by dip net). As it was not possible to collect intensively by this method in the spring before student workers took up residence, it is virtually certain that some young turtles that reached the water died before ever being captured.

CATCHABILITY: The use of a proportional index means of estimating population size requires a number of assumptions, not the least of which is that individuals do not differ significantly in their susceptibility to being captured. Although it was not necessary to use a proportionality method in the present research, some observations on individual variation in tendency to enter traps are worth putting forth for their possible pertinence to other studies.

It became apparent early that some turtles were captured much more frequently than others, and this impression grew as more years of experience accumulated. I have selected data from one trapping session to illustrate the point. The data cover a six-day period in July 1971 when seven traps were continuously deployed in Pond 1 for a total of 42 trap-days. Records for this and the other ponds before and after this trapping session indicate that at this time probably 44 turtles were present in Pond 1. There were 143 captures of 41 turtles, which on the basis of a population of 44 gives a mean of 3.25 captures per turtle over six days. The range was from zero captures for three turtles to 11 for one, with the mode being two captures for 11 turtles (fig. 3).

The tendency of some individuals to enter traps more frequently than others is not merely a matter of their being situated more favorably in the pond relative to traps. On more than one occasion a turtle, when released from a trap, swam completely across the pond and entered another trap in the few minutes that it took the trapper to walk around the pond and service two or three intervening traps.

In the sample trapping period discussed here, three of the seven turtles with the most captures (6–11) were old adult females, two were large subadult females, one was a small-

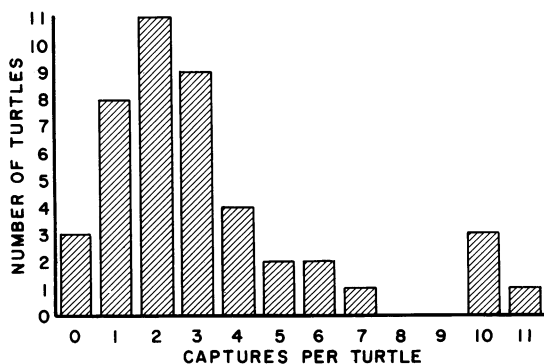


Fig. 3. Captures of turtles in Pond 1 during a six-day period when probably 44 turtles were present. Three individuals escaped capture, another was taken 11 times, and the mean was 3.25 captures per turtle.

er subadult (probably female), and one was a subadult male. This suggests trapping bias favoring the larger and older females, especially as adult females only slightly outnumbered adult males, and subadults were far more numerous than adults at the time. However, there were adult females with low frequencies of capture and an adult male (resident in Pond 2 at this particular census) was as prone to capture as any of the females.

My experience with adult painted turtles suggests that there are both sexual and individual differences in behavior that may influence success in trapping. Adults cannot be assumed to comprise a group uniformly susceptible to baited traps. Sufficiently intensive trapping of small populations can overcome this potential handicap, but it remains a consideration under other conditions. Wilbur and Landwehr (1974) discuss some statistical aspects of the problem.

MARKING: Notching or drilling two marginal shields of the carapace provided an adequate series of reliable, long lasting, and unique marks. The shells of small turtles were notched with toe-nail clippers whereas larger turtles were drilled with an electric drill. The shields of the thickened bridge region—fourth, fifth, and sixth from the anterior end—were not used. When a turtle that had been notched at a small size was recaptured at a sufficiently large size, holes were drilled medial to the notches.

Notching alone does not provide a permanent mark in young, rapidly growing in-

dividuals. If the mark is not renewed (or holes drilled in the same shields), the turtle's identity as a marked individual can become questionable in a few years. Wilbur and Landwehr (1974: 1344) noted: "In turtles marked during their first growing season the marks become obscured by regenerating bone; otherwise marks last for the life of the turtle." The problem may extend beyond cessation of the first year's growth, however. For example, a turtle notched at the end of its first growth year was recaptured at the beginning of its fourth year, before any of that year's growth had taken place. In this period of two years of growth the notches had filled in to such an extent that they easily could have been overlooked, or if noticed could not without other evidence have been accepted as proof of identification. In this case a photograph of the turtle's plastron provided confirmation through unique aspects of the color pattern. This was a turtle that grew at an unusually rapid rate, and I do not think that undetected loss of notches caused any misidentifications in this study. However, in studies where individuals are not captured so frequently, failure to take this factor into account ignores a potentially serious source of error. Even drilled holes may break through at the margin of the shield and with wear and growth become less distinct, but this did not cause any problems of identification in this study.

RESULTS

ACTIVITY

SEASONAL ACTIVITY

I visited the study ponds only infrequently early and late in the year, so have few observations that might provide information on the extent of the activity season. However, persons resident at the Research Station made note of early and late sightings of *Chrysemys* in the C2 pond, and activity in the principal study ponds is unlikely to have been significantly different. The earliest record of a turtle seen basking was on March 16, and other records ranged from mid to late March. On many occasions turtles basked in April though attempts to catch them in baited traps achieved little success until May. Trapping generally was successful into early October

and turtles often basked later than that, with the latest sighting being on November 4. A record for November 24 from the same general area (Burnley and Schlauch, 1968) extends the period somewhat.

Seasonal changes in trapping success undoubtedly reflect reluctance of turtles to feed at low temperatures. Sexton (1959a: 125) noted that "*Chrysemys* begins to feed when the temperature of the water rises above 15°C." Kepenis and McManus (1974), studying the relationship of temperature to food intake, egestion, and assimilation of young *C. picta*, found that at 15°C the turtles did not feed. As temperature is lowered and approaches 15°C, there is an abrupt increase in digestive turnover time, reflecting a deviation from linearity seen at higher temperatures (Parmenter, 1981). Conditions in the study ponds no doubt were similar to those in the C2 pond at the Kalbfleisch Field Research Station, where shallow temperatures in the pond generally were not above 15°C for even part of the day until the third week in April and dropped below 15° in mid-October. The bottom temperature (about 1 m) was 15° or higher from June through September.

The painted turtle's yearly activity cycle as reported for other populations is generally as given above, with differences in the length of the period of greatest activity attributable to temperature. Typically adult turtles become active in late winter or early spring—weeks before feeding commences. The early activity of adults is correlated with mating (Gibbons, 1968b), whereas juveniles generally delay their emergence somewhat. Turtles in a far northern, river dwelling population in Saskatchewan did not become active in the spring until late April at the earliest, with larger individuals preceding the smaller (MacCulloch and Secoy, 1983b). Latest records of activity in two years were September 23 and October 2. Evidently most individuals in populations studied in Michigan (Sexton, 1959a; Gibbons, 1968b) and Pennsylvania (Ernst, 1971b, 1972) are active by mid-March or early April. Activity decreases considerably after mid-October, as is best documented by Sexton (1959a). Cagle (1954) supposed that the growing season (significantly shorter than the activity season where best known) of painted

turtles in Louisiana might be five months longer than in Illinois. This is perhaps reasonable, but is inferred from air and water temperatures rather than on the turtles' activity.

Chrysemys may be active on occasion during winter. Ernst (1971b, 1972) had records for every month except February, and Sexton (1959a) mentioned turtles swimming beneath the ice. *Chrysemys* hibernates in mud or sand at the bottoms of ponds or marsh channels (Cahn, 1937; Ernst, 1972), a habitat likely to have a severe oxygen deficiency. However, these turtles can endure weeks, even months of submergence at temperatures near freezing, even in the virtual absence of dissolved oxygen (Ultsch et al., 1985, and references therein). Turtles active in the winter, at temperatures too cold for mating or feeding, may be taking advantage of favorable opportunities to reverse physiological stress due to anaerobic metabolism.

OVERWINTERING OF HATCHLINGS: It is well established that hatchlings of *Chrysemys picta* may overwinter in the nest cavity and not emerge above ground until the spring (Bleakney, 1963; Cagle, 1954; Christens and Bider, 1987; DePari, 1988; Hartweg, 1944, 1946; Mitchell, 1988; Nichols, 1933; Sexton, 1957). Gibbons and Nelson (1978) discussed aspects of this behavior, including geographic variation and facultative local variation. Storey et al. (1988) reported that hatchlings of *Chrysemys* have the remarkable ability to survive freezing of extracellular body fluids, an adaptation well suited to overwintering in a shallow nest site. Among other reasons, it is important to know when hatchlings emerge in order to estimate when individuals start feeding and growing and to know when to treat them as members of the free-living population for demographic purposes.

Overwintering in the nest appears to be the usual habit on Long Island and nearby areas. Nichols (1933: 41) cited a number of instances of hatchling young found at Mastic, Long Island, between April 18 and June 1 that "apparently had not yet reached the water." Finneran (1948: 126) mentioned "two newly emerged turtles" found away from water in April and another "immature specimen with a very small yolk sac" in May, all in coastal Connecticut. A tiny hatchling found

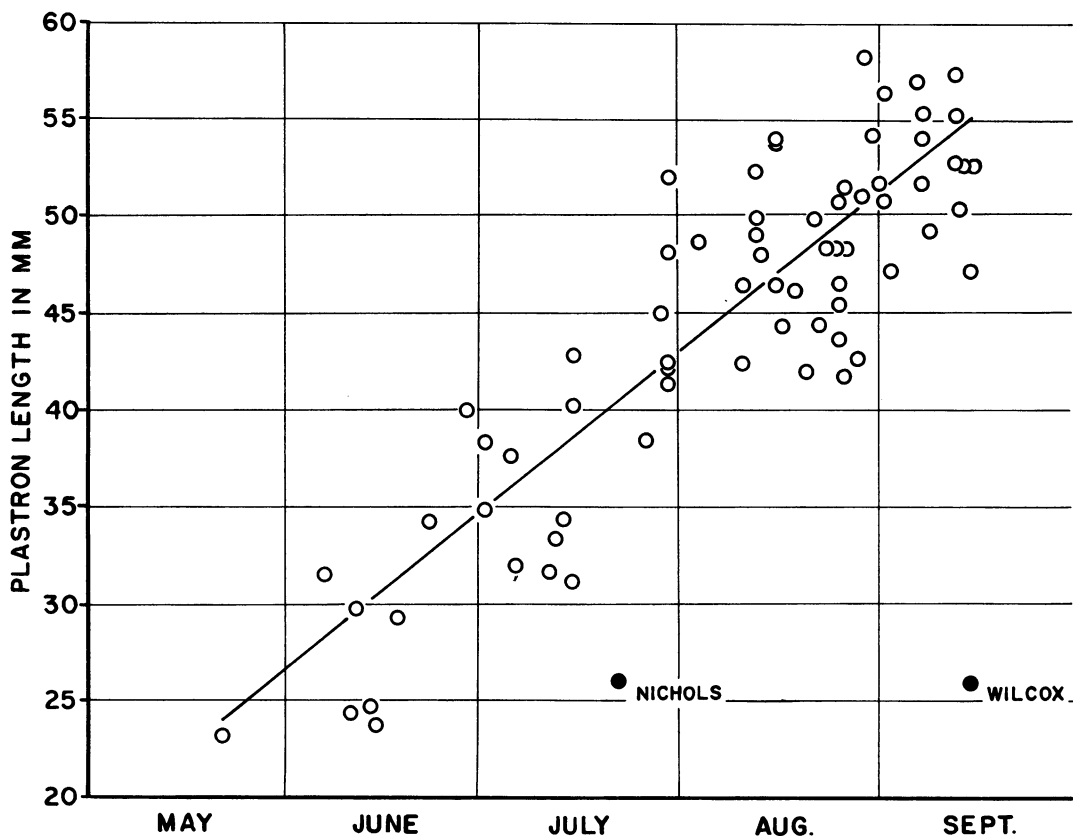


Fig. 4. Open circles show sizes of 69 *Chrysemys* turtles at their initial capture in the first year of growth (May record represents two individuals). Closed circles are literature records for Long Island *Chrysemys* that may have (Nichols) or almost certainly (Wilcox) left the nest without overwintering. The regression formula (open circles only) is $Y = 0.26X + 23.95$, $r = 0.887$.

growing turtle. Wilcox (1933) reported a in May in the pine barrens of New Jersey (House, 1970) also is indicative of overwintering without growth.

Evidence for summer or fall emergence of hatchlings in the Long Island region is meager. Nichols (1933: 41) found a turtle with a shell length of " $1\frac{1}{16}$ inches [27 mm] . . . away from water . . . on July 23." For this individual to be a hatchling of the same year's brood it would have had to come from an unusually early clutch (late May compared to Nichols' earliest record of June 8) and had exceptionally rapid development (ca. 60 days to emergence). Yet its size is well below the minimum in my records for animals in late July in their first growth season, so if it had overwintered it was an exceptionally slowly

hatchling found on September 15 on Long Island. There can be little doubt that this represents development and emergence in the same year (fig. 4).

Bayless (1975) studied *Chrysemys* in Albany County, New York, about 200 km north-northwest of my study area, and inferred that hatchlings emerged from the nest in late summer rather than overwintering there. At my request, Dr. Bayless kindly reviewed his data on the sizes of young taken late in May that were the basis for his conclusion. These measured 41–50 mm PL, so were much too large to have left the nest only late the previous summer. Turtles of this size, however, are within the size range of young after their first full season of growth (figs. 4, 5), so it is likely that they had overwintered in the nest as

hatchlings the previous year and were commencing their second year of growth when first captured.

There is nothing in my data to confirm emergence of hatchlings from the nest in the same calendar year the eggs were deposited and much to refute this. Among 69 records of initial capture of turtles in their first season of growth (as indicated by annular rings), no turtle was of a size clearly appropriate to summer emergence (fig. 4). All 27 individuals in August were more than 41 mm PL (hatchlings are less than 30 mm), and all 16 in September were more than 47 mm PL. The only possibly suspect individual had a plastron length of 31.6 mm when first captured on June 7. Conceivably it could have grown briefly the previous fall before entering hibernation, but early emergence from the nest in the spring and rapid growth could account as well for its relatively large size. Examples of hatchlings that almost certainly overwintered in the nest are two taken on May 22 measuring 23 mm PL and three taken June 11–15 at less than 25 mm PL.

I question whether hatchlings emerging in late summer or fall would be able to grow much if any that year. Known dates of oviposition in the Long Island region range from June 3 to July 12 and incubation periods from 61 to 81 days (Finneran, 1948; Nichols, 1933; Schlauch, 1971; Wilcox, 1933). Only under the exceptional circumstances of earliest oviposition, most rapid development, and a late termination of the growth season would a hatchling have as much as five weeks of growth time. A more nearly average situation with oviposition in mid-June or later and 70 or more days until hatching would place the hatchlings at or past the time of the year when turtles show any significant growth. I conclude that fall emergence of hatchlings in my study area occurs infrequently if at all and for practical purposes can be ignored when determining growth rates and when tabulating hatchlings as members of the population.

MOVEMENTS

Movements may be classified in three general categories: 1) those associated with nesting (to and from the nest site by the female;

dispersal by the young leaving the nest); 2) those within the non-nesting home range (within or among ponds); 3) greater movements involving more lasting changes of home range (immigration and emigration). I have no information to offer on the first of these categories, quite a bit on the second, and a little on the third. I use the term "home range" in a broad sense to include the area intensively used on a day-to-day basis, as well as areas only occasionally visited but obviously with which the animals evidently are familiar.

INTRAPOND MOVEMENTS. Although I gathered no data specifically directed to studying intrapond movements, I saw no indication that the turtles restricted their movements within these small ponds. Adult turtles could swim the length of any of the ponds within a few minutes and are known to have done this on several occasions, being captured in two different traps within a short time. Very small turtles might be less inclined to wander if impeded in their movements by the mass of submerged vegetation in late summer in the shallowest pond, but I have no evidence for or against this suggestion.

INTERPOND MOVEMENTS. Almost 2000 captures of 118 turtles over a period of 18 years provide abundant data on the extent and frequency of movements of individuals among the ponds that constituted the home range of the population. Some bias is present in that Pond 1 was trapped more intensively than the others. In any one trapping session traps were usually placed in Ponds 1, 2, and 3, but Pond 1, which had the greatest concentration of turtles except in the peak drought years, normally had more traps. Ponds 4 and 6 received even less attention than the others and neither was trapped after 1972, when Pond 4 became inaccessible and Pond 6 was destroyed. Since only seven different turtles ever were found in Pond 4 and only three in Pond 6, these ponds are of little consequence in the broad picture, though their records provide data on movements.

In order to estimate the amount of movement among ponds and the relationship of movement to age and sex, I assembled the following data for turtles of known ages 1 (the turtle's first year in the pond) through 15 years:

total years in which a turtle was captured two or more times in only one pond; total years in which a turtle captured two or more times moved between Ponds 1 and 2 or farther (Ponds 4 and 6). The sexes are pooled for years 1 to 3 and treated separately for the balance.

Turtles in their first year in the ponds rarely were captured until late in the season, so the sample that might show movement is small—13 individuals—but none of these had moved. Juveniles in their second and third years were almost as sedentary: only 10 percent (3 of 30 and 5 of 50) had moved, and some of these few movements were influenced by the 1964–1965 drought. Young turtles are capable of substantial overland movement, however. A yearling found in Pond 6 in June was taken next in Pond 1, minimum distance 190 m, in August.

The statistics for male turtles in their fourth year are similar to those of young turtles—only 7 of 46 (15%) moved. But the amount of movement increased markedly in the fifth and sixth years, with 13 of 32 (41%) moving in the fifth year and 9 of 15 (60%) in the sixth. This increase in movement follows attainment of sexual maturity. Ten turtles in the seventh year included three movers (30%). The balance of the sample of males (8–13 years, 1–5 individuals per year) is too small for confidence, but none of the turtles is known to have moved.

Three of 10 females of age 4 (30%), 4 of 12 (33%) of age 5, and 3 of 8 (37%) of age 6 moved. The sample size in years 7 through 15 is only one to seven individuals. Only three movements were recorded in all nine years, so while these meager data suggest that older males and females are similarly sedentary, they do not indicate a spurt of activity following maturity such as appears to take place with males.

In addition to the turtles of known age, there were several in the population at initiation of the study that were too old for accurate age estimation but could conservatively be aged by size at a minimum of five to eight years in 1963. Data for these in the years 1966–1980 (avoiding the drought years 1964–1965 with their forced movements) involve nine females followed for up to 15 years and four males up to 6 years. The females showed only 32 turtle-years (39%) with no

movement against 49 (61%) with movement, and the males had similar proportions—4 turtle-years without movement (36%) and 7 (64%) with. Thus, the data from these older turtles contrast somewhat with that of the turtles of known age.

The fact of considerable movement between ponds does not necessarily imply a lack of fidelity to a particular pond. In order to estimate the extent to which turtles utilized different ponds, I have analyzed the records of the 34 individuals (17 of each sex) presumably native to the ponds (not known to be immigrants) and with capture records extending over 7 to 18 years. This subset provides abundant data while reducing the chance element of missing turtles in the less heavily trapped ponds due to a shorter time span in the data. At one time or another the vast majority of these turtles used more than one pond: 29 (85%) were taken both in Ponds 1 and 2, and 15 (44%) had captures in Ponds 1, 2, and 3. The use of the three ponds was strikingly unequal, however, more so than is explicable by trapping bias. Nineteen turtles (56%) had more than 80 percent of their captures in Pond 1, and 27 (80%) had more than 60 percent there. Five turtles with records ranging from 7 to 13 years and an aggregate of 108 captures were taken only in Pond 1. No turtle with seven or more years of captures was taken only in Pond 2 or Pond 3 or in these two ponds to the exclusion of others.

If records for all turtles are considered, the picture does not change significantly. There were 1361 captures of 108 turtles in Pond 1, 390 captures of 61 turtles in Pond 2, and 141 captures of 34 turtles in Pond 3. It appears that the majority of turtles that survive for more than a few years become familiar with two or more ponds but spend most of their active season in the favored Pond 1.

Movement between Ponds 1 and 2 involved a minimum of 88 m of travel on dry land, partly through high grass and brush and partly over mowed lawn. The shorter direct route between Ponds 2 and 3 (30 m) followed an overflow channel through grass either cropped by cattle or mowed. Travel between Pond 1 and Ponds 4 or 6 presented more formidable challenges. Minimum distances (370 and 190 m, respectively) were much greater and the terrain rougher, with high grass and weeds, rocks, logs, and other potential

obstacles. Nevertheless, two turtles journeyed between the ponds too frequently for the trips to be considered immigration and emigration.

An adult female captured several times in Pond 1 and once in Pond 2 between August 1963 and June 1965 appeared in Pond 4 in April 1966 (probably having gone there in 1965), was in Pond 1 again in June and back in Pond 4 in July and August. Records for 1967 through the last capture in May 1973 include two years in which it was taken only in Pond 4, three with captures only in Pond 1, and one with captures in Pond 1 bracketing a capture in Pond 4. Clearly this turtle was utilizing these widely separated ponds as part of its normal home range.

Another adult female included Pond 6 as well as Ponds 1, 2, and 3 within its home range. It was found many times in Pond 1 from 1963 to 1969 and much less often in Ponds 2 and 3. In 1970, 1971, and 1972 it was captured in Ponds 1 and 6, and in both 1970 and 1971 went from Pond 1 to Pond 6 and back again. Possibly it may have used Pond 6 before this, as the pond was not trapped in the earlier years.

One turtle normally resident in Ponds 1 and 2 is known to have used Pond 4 temporarily. This adult male was captured in Pond 4 in April 1966, presumably having moved there in 1965 when Pond 1 dried up. It was back in Pond 1 in May 1966 and was taken only there or in Pond 2 through its last capture early in 1968.

The data suggest declining frequency of movement through the year. Among 146 turtles captured in May and again in the following June, 22 (15.1%) had moved between Ponds 1 and 2 or a greater distance. Corresponding figures for later months are: June–July, 203 captured, 28 moved (13.8%); July–August, 175 captured, 21 moved (12.0%); August–September, 116 captured, 9 moved, (7.8%). There is a strong negative correlation ($r = -0.962$) between capture periods and percent of recaptured turtles that had moved. These data exclude the drought years which compelled considerable mid- and late summer movement but are not corrected for the conspicuously low amount of movement of juveniles.

I suspect that the pattern of population movement changed over the years in re-

sponse to changes in the habitat. Although Pond 1 evidently did not dry up in the years preceding the 1964–1965 drought (see Description of Study Area), it was shallow, polluted, and lacking in vegetation—altogether an unsavory habitat in the summer period of heat and low water. When the first trapping was done in July 1963, only 5 of 16 turtles taken were in Pond 1. In June 1964, 13 of 19 were in Pond 1, but six of these had already moved out by the end of the month. By mid-August all 19 adults (and an immigrant) were in Ponds 2 and 3, while only three juveniles remained in the vestige of Pond 1. (One of these juveniles, PL less than 50 mm, was still in Pond 1 late in August but was in Pond 3 the following April.) Pond 1 was repopulated again by June 1965 (at least 13 of the adults present), but drying again drove them to the other ponds.

With the amelioration of the drought in 1966 and deepening of the pond by dredging, the exodus from Pond 1 lessened and some turtles remained throughout the summer. In later years with cattle almost completely excluded, enough rainfall to maintain the pond, and abundant aquatic vegetation enhancing the habitat, many fewer turtles moved to the other ponds and Pond 1 held the bulk of the population year-round.

I infer that prior to the drought the turtles may have used Pond 1 mostly in the spring and early summer when its basking sites and shallower, warmer water provided better conditions than in Ponds 2 and 3. The exodus in the drought years was an exaggeration of a usual annual pattern of movement. In the later post-drought years Pond 1 was a superior environment at all times of the year and turtles were more inclined to remain there.

EMIGRATION: Opportunities to verify instances of emigration were extremely limited. Many turtles that disappeared from the ponds may have emigrated rather than died within the home range, but there is no way of knowing. There were few ponds within the vicinity of the study area where one might have found emigrants. The pond on the land of the Kalbfleisch Field Research Station (530 m from Pond 1 and 450 m from Pond 4) was trapped every year and provided only one instance of movement from the study area (discussed under Immigration). A pond on an estate 2 km from the study area was trapped

in the summers of 1970 and 1972 yielding 19 turtles, none from the study population.

One apparently valid instance of emigration involved a male turtle about seven years of age that had been in the population at least since the study began in 1963. It was in Pond 2 at least as late as June 4, 1967, and next was caught by a child at a pond about 1.6 km away one month later. Released in Pond 2, it was never recaptured. In view of its fairly frequent captures in previous years, it is likely that it again emigrated.

IMMIGRATION: Verifiable immigrants into the study area all were marked turtles either introduced into the pond on the Research Station in 1963 or were descendants of introduced turtles. These are sufficiently few that they may be discussed individually.

An introduced male, probably in its fourth year, moved from the Research Station to Pond 2 (minimum distance about 600 m) between July 15 and August 20, 1964, at the height of the drought. It was captured several times in Ponds 1, 2, and 3 until found dead, apparently due to predation, in June 1966.

Another introduced male (of indeterminate age, but at least in its sixth year when it first moved) had a complicated history of movements. Captured at the Research Station on August 6, 1965, it was in Pond 4 (minimum distance, 450 m) by September 18. It was present in Pond 4 to at least April 1969, but reappeared in the Research Station pond in June 1969. The peripatetic beast was back in Pond 4 in May 1970 and was captured there as late as August 1972, when trapping there became impractical. Surprisingly, it survived the difficulties of life in a pond surrounded by houses and moved (presumably without assistance) to Pond 1 (minimum distance, 370 m), being captured there in 1978 to 1980. This turtle evidently had three successive home ranges: 1963 to 1965 in the Research Station pond; 1965 to 1978 in Pond 4 (with at least part of 1969 back at the Research Station), and from 1978 on in Pond 1. As was the case with the first turtle, the initial movement out of the Research Station pond was in a drought year.

A female turtle that spent its first two years (1967–1968) in a small pond of uncertain permanency on the Research Station and was last taken there in April 1969, was in Pond

4 (minimum distance, 520 m) in April 1970. It remained there at least into August 1970.

A male turtle in its fourth year when trapped in the Research Station pond in May 1976 was next taken in April 1977 in Pond 1 (minimum distance, 530 m). It was still in Pond 1 at its last capture in September 1979.

Another male trapped several times in the Research Station pond, the last time on July 9, 1979, was in Pond 1 on September 8, 1979 and was in that pond a year later when the study terminated. It was in its fifth year when it moved.

The last of the immigrants of known immediate origin may have immigrated to the Research Station pond before moving on. It was at least in its fifth year (PL 99.7 mm) at its only capture at the Research Station (July 16, 1977). The second and only subsequent capture was in Pond 2 on September 2, 1977. The probability of a turtle evading capture for four years is small, leading to the conclusion that it was a recent immigrant to the Research Station before moving on to Pond 2, and then apparently continuing its wandering.

On four occasions unmarked turtles were captured in the study ponds that on the basis of their size and apparent age when first taken almost certainly were immigrants. Two adult males at least seven years of age were taken on July 20, 1970, one in Pond 1, the other in Pond 2. One had additional captures that year but was sick at the last and dead when found the next year. The other had numerous captures in Ponds 1, 2, and 3 up to the end of the study.

A very old female found in Pond 2 in October 1971 remained until found dead two years later. Another female, possibly in its fourth year when taken in Pond 3 in September 1969, was in Pond 1 when last captured in August 1970.

COMPARISONS WITH PREVIOUS STUDIES

MOVEMENT WITHIN A HOME RANGE: The potential size of a turtle's home range may be constrained by local conditions that promote or impede movement. Populations in rivers or lakes may have ready access to large

areas without recourse to overland travel. Turtles living in small ponds may necessarily include terrestrial interpond corridors in even small home ranges. Age, sex, and quality of habitat also may influence the amount and extent of movement. Comparison of movements of *Chrysemys* reported in several publications emphasizes the great adaptability of the species to habitats as different as large rivers and small ponds.

Adult *Chrysemys* are capable of rapid movement in water over long distances. MacCulloch and Secoy (1983a) reported a male that traveled 6.5 km (in a river) in one day and a female that moved 6.5 km in four days. Williams (1952) studied homing in a lake-dwelling population and found that displaced turtles often returned rapidly and repeatedly to their capture site, the fastest covering a minimum distance of 640 m in no more than 18 to 23 hours. This potential for movement must be kept in mind when considering size of home ranges.

The maximum distance of movement reported for painted turtles is in a river in Saskatchewan, where MacCulloch and Secoy (1983a) used a minimum unit of 500 m in assessing individual movements. The majority of adult turtles moved at least 500 m between their first and last captures in one season: the average male moved about 5–6 km, the average female about 2–3 km. Movement was not correlated with direction of the current. These authors felt that individuals appeared to be familiar with large segments of the river but showed no fidelity to a restricted home range. The movements evidently do not represent random wandering in unlimited habitat. The turtles in this river are wholly carnivorous, and prey items are concentrated within 1 m of the bank (MacCulloch and Secoy, 1983b). Just covering enough area to acquire sufficient food may require considerable travel (e.g., a 10 km strip of river is equivalent in area to a 1 ha pond).

A pond or lake offering potential for considerable unencumbered movement may nevertheless be patchy with respect to preferred habitat. Turtles may choose to confine themselves largely to relatively small areas but may make extensive movements when circumstances dictate. Sexton (1959a) described a situation where the majority of tur-

tles hibernating in a 5 acre pond, adults especially, undertook an early spring emigration (part of it overland) into adjacent marshy areas. Some turtles moved as much as 1000 m. Return to the pond contrasted in being a gradual process, with some emigrants moving back in late spring and others prolonging their return into the summer. Repopulation of the pond appeared to correlate with the development of surface vegetation there, and the local distribution of turtles in the pond then varied with changes in vegetation due to growth and fluctuation in water level.

Gibbons (1968b) found that fewer than 15 percent of *Chrysemys* recaptured in a marsh in a single summer had traveled more than 100 m, though the proportion went up for female turtles captured in successive summers. Pearse (1923a) reported similar results for a lake population: 166 turtles had moved an average of 112 m in an average recapture period of 5 months and 12 days. Williams (1952) studied the movements of turtles captured at several points around a lake and released at a common point, whereupon the majority returned quickly to their capture sites.

Home ranges may include disjunct bodies of water. This is noted above in Sexton's work, and Cagle (1944) also observed that *Chrysemys* traveled between a large reservoir and nearby ponds. These overland movements covered perhaps 100–200 m; because of discrepancies in Cagle's text and among his maps (1944: fig. 1 and map 1), a more precise statement is not possible.

The findings in my study fit into the rather broad picture painted by earlier work. Living in an area with little suitable habitat, and that distributed among disjunct parts, these turtles behaved like those studied in more generous habitats but on a smaller scale. All but the younger turtles moved about enough to have been captured in at least two of the three principal ponds, though they concentrated their activity in the most favorable site or sites. In the early years of the study, when one pond provided the best conditions in the spring, the turtles moved to that pond in the spring (as did Sexton's turtles), leaving it in the summer as conditions deteriorated. In later years changes in the pond permitted permanent residence and the turtles modified

their behavior, becoming more "faithful" to this pond.

It does not seem possible to define a typical home range of *Chrysemys*. Clearly, painted turtles have the ability and live long enough to become familiar with extensive areas. Home ranges may include different seasonal centers of activity or may change from year to year, and may vary greatly in size according to local circumstances. In the case of my study population, most turtles probably spent their entire lives in two or three ponds or walking between them or to nesting sites. This amounts to an area of less than 1 ha, of which no more than 0.27 ha is aquatic habitat. At the other extreme, the turtles studied by MacCulloch and Secoy (1983a) ranged over several kilometers of river.

Other freshwater emydine turtles evidently show movement patterns within the home range similar in variety and extent to those of *Chrysemys picta*. Map turtles (*Graptemys geographica*) living in a river had lengthy ranges—means about 2 km for males, 1 km for females—as do *Chrysemys* (Pluto and Bellis, 1988).

HOMING: Homing may be defined as the ability to return to an area with which one is familiar from outside that area. Homing ability has been tested experimentally in two principal ways: by displacing turtles and seeing how successful they are at returning to their capture sites, and by observing the directions taken by turtles when released at a distance from their capture sites.

Examples of the former method of study include Cagle (1944), Williams (1952), and Ernst (1970). Cagle mentioned several instances of *Chrysemys* that returned after being displaced from one part of a lake to another, evidently having moved several hundred meters (details are sparse). Williams' account cites numerous examples of turtles returning, sometimes repeatedly, to capture sites as much as 620 m away in a lake. The difficulty with these studies as examples of homing is that there is no assurance that the turtles were displaced into unfamiliar territory. The baseline information on the extent of the turtles' home ranges was rather scanty.

Ernst (1970) removed turtles from a pond and released 50 1 mi up the stream flowing through the pond, 50 more 1 mi downstream,

and 60 2 mi downstream. Eventually, 25 of the upstream turtles (5–763 days later), 22 of those released 1 mi downstream (59–739 days), and 12 of those released 2 mi downstream (20–409 days) were recaptured in the pond. Ernst could reasonably assume that the turtles were released in unfamiliar territory, as trapping revealed turtles downstream only just below the pond dam, and for only 150 m upstream from the pond. Though he did not specifically say so, Ernst presumably felt that the returning turtles had homed. He did not discuss the possibility that random movements of the released turtles (confined to the stream) might result eventually in some of them returning to familiar territory. As it was, 47 percent of the turtles released 1 mi away returned as did 20 percent of those released 2 mi downstream. Too much significance should not be attributed to the difference in percent returns between the 1 and 2 mi groups, as the latter group was released a year later and apparently had less time in which to be recaptured.

Considering the demonstrated ability of painted turtles to move rapidly for hundreds of meters from release points to previous sites of capture (Williams, 1952), the long periods of time taken by most of Ernst's turtles to return (mean 295 days from 1 mi upstream, 384 days from 1 mi downstream) suggest to me that random movement rather than homing is a more reasonable explanation. Indeed, Ernst pointed out that according to his estimates of potential speed of travel, a turtle might return from 1 mi away in as little as two hours!

Emlen (1969) worked with the same population of *Chrysemys* as Sexton (1959a). Hence, areas the turtles might be expected to be familiar with were known. A large proportion of 98 turtles released on land 100 m north, south, or east of the pond (west was within the assumed home area) headed pondward. Such orientation disappeared when the release distance was increased to 1 mi. These and additional experiments suggested to Emlen that visual recognition of local topographic landmarks may be important in enabling *Chrysemys* to home. The turtles released within 100 m of the pond presumably were not on familiar terrain though within sight of familiar landmarks.

I made no effort to study homing in my population, but the data on movements that bear on home range are pertinent to any future attempts to experiment on homing in a similar situation. Most important, one must appreciate that even years of study may not reveal the extent of the area over which turtles may travel or may have traveled. In the section on movements I discussed a turtle that over several years was resident in Ponds 1 and 2 (88 m apart), but just once was found in Pond 4, 370 m from Pond 1. Given only the captures in Ponds 1 and 2, it might have been considered reasonable to test this animal's homing ability by moving it to Pond 4.

IMMIGRATION AND EMIGRATION: Deleterious changes in habitat coincident with long-term population studies have provided opportunities for gathering information on migratory movements of several species of turtles. Drought in South Carolina enabled Gibbons et al. (1983) to compare the responses of five sympatric species. *Pseudemys scripta* and *P. floridana*, relatives of *C. picta*, abandoned their drying ponds in greater numbers than usual, while another emydine, *Deirochelys reticularia*, and two kinosternid species either moved no more than usual or stayed put. Parker (1984) found a modest amount of emigration and immigration in pond-dwelling *Pseudemys scripta* in Mississippi, but in years following treatment of a pond with algicide (interfering with the food supply), emigration increased to a peak of 61 percent of the population.

Little is known of the extent to which *Chrysemys* may travel over unfamiliar terrain. Sexton (1959a) recorded movements of up to 1000 m within a pond-ditch-marsh system (presumably within the home range), but in a limited amount of trapping did not find marked individuals among turtles caught in outlying ponds about 450 to 600 m away (distances estimated from Sexton's fig. 1). These ponds had at best tenuous aquatic connection with the principal habitat. Cahn (1937: 134) "frequently found specimens . . . nearly half a mile [800 m] from water . . . their wanderings having no connection with age, sex, breeding, or hibernation."

Several instances of emigration from a pond on the Kalbfleisch Research Station to my

study ponds (see Movements) provide verified examples of dispersal over 450 to 600 m of presumably unfamiliar territory (the turtles were established residents at the Station and never before had been taken in the study ponds). The record of a turtle taken in a pond 1.6 km from its earlier capture sites in the study ponds represents the greatest apparent distance traveled. I have no reason to question the data (see Movements), though with turtles especially there is the possibility that someone picked it up on the road, carried it for awhile, and then dropped it in a pond. Additional instances confirming overland movement of this magnitude are needed. The unquestioned movements of up to 800 m (Cahn, 1937) are not surprising, considering that females may nest 620 m from water (Christens and Bider, 1987) or even farther (Finneran, 1948, mentioned a hatchling found about one-half mile from water).

MOVEMENT IN RELATION TO SEX AND AGE: There are few data in the literature providing detailed information on movements in relation to sex and age, except those pertaining to nesting females. Sexton (1959a) compared relative numbers of juveniles, subadult females, and adults of both sexes moving in an annual spring emigration from a pond to a marsh. Relative to their estimated proportions in the pond prior to emigration, many fewer juveniles moved, but subadult females moved about in relation to their numbers. More adults emigrated than expected, with seemingly more females moving than males.

Gibbons (1968b) found no significant differences in distances moved among males, females, and juveniles that had moved more than 100 m in a marsh in one summer. Females captured in two successive summers showed greater movement than males with similar records of capture. He suggested that lack of incentive to leave a suitable habitat could explain the sedentary nature of males and juveniles, and attributed the greater movement of females over two seasons to a possible change of area following nesting.

Adult male *Chrysemys* recaptured by MacCulloch and Secoy (1983a) in a river had moved farther on the average than adult females, though the difference lacked statistical significance. Juveniles moved considerably less than either class of adults.

Juveniles up to their third or fourth year in my study were much less mobile than adults. Males became increasingly active at sexual maturity but many apparently reduced their level of interpond movement in later years. Adult females showed no peak of activity but maintained at least a moderate amount of movement throughout life. Among turtles that moved, there was clearly a decline in the incidence of travel through the annual season of activity.

It should be apparent that these several studies are not closely comparable because of the various conditions under which the turtles lived. Gibbons' turtles may, as he suggested, have had little cause to move. Sexton's had good reason to emigrate in spring and, later having returned, to shift their centers of activity to accommodate to changes in aquatic vegetation. The river turtles of MacCulloch and Secoy commonly traveled so far that these authors used half a kilometer as their minimum unit of movement. In the early years of the study, my turtles exhibited a population movement not unlike Sexton's, but in later years they more closely resembled Gibbons' in being more sedentary. The other studies were not sufficiently detailed to detect the spurt in activity of newly mature males if it existed.

GROWTH

A number of aspects of growth deserve consideration, among them individual and sexual differences in rate, changes of rate with age, and differences among seasons, years, and localities. Information from this study addresses all of these aspects, some more thoroughly than others.

METHODS: The first time a turtle was captured during a trapping session it was taken to the laboratory, weighed on a triple-beam balance, and measured. In the early years of the study measurements included the width and length of both carapace and plastron, but over most of the period of fieldwork only plastron length (measured along the midline) was recorded. This last measurement is routinely used in studies of emydid turtle population ecology, making different data sets readily comparable. Carapace length may be estimated from plastron length or the reverse

if necessary.² Measurements of turtles up to about 120 mm plastron length were made with dial calipers read to the nearest 0.1 mm. Larger turtles were measured with dividers read against a metric scale to the nearest millimeter. With the largest, variation of a millimeter or rarely more sometimes occurred in successive measurements when there was no reason to suppose that an actual change of size had taken place. However, captures were usually sufficiently frequent that such spurious variation could be recognized and taken into account. Weight was recorded to the nearest 0.1 g.

For some aspects of this study it was necessary to estimate the length and weight of a turtle at the beginning and end of the growing season although the individual may not have been captured at exactly the appropriate times. Turtles are active in the late summer and fall after growth has ceased and again in the spring before growth has resumed. Thus, for a turtle captured at only one of these times it is possible to estimate the length and weight at the other with a high degree of accuracy. Even for turtles captured slightly within the growing season adequate estimates can be made.

AGE DETERMINATION: I have made the simplifying assumption that all hatchling turtles in my study population overwinter in the nest (see Seasonal Activity). Therefore, the first growth year is actually the turtles' second calendar year of life. A turtle that emerges from the nest in the spring is almost a year from the time of conception and possibly eight months from hatching. I discuss growth in terms of growth years, commencing at time zero when the young turtle emerges from the nest and begins its first season of growth.

Within limits, the age of a *Chrysemys* can be determined by counting rings on the scutes of the shell. Commonly one of the paired plastral scutes is employed for this purpose. At the point where the growth of one season ends and that of the subsequent season begins, a distinct line forms. So long as these

² Male $PL = 0.951CL - 3.513$; $CL = 1.048PL + 3.91$ ($N = 82$, $r = 0.998$, sample ranges CL 27.5–136 mm, PL 24.3–124 mm). Female $PL = 0.986CL - 6.009$; $CL = 1.017PL + 5.453$ ($N = 70$, $r = 0.997$, sample ranges CL 46.1–150 mm; PL 40.0–139 mm).

lines are distinct, the number of seasons of growth is simply the number of such lines, counting the edge of the original hatching scute as zero. (The size of the original abdominal scute at hatching remains the same as the turtle grows—Cagle, 1954.) A minor complication is that accessory lines may form when the turtle undergoes its annual ecdysis. Such lines are usually conspicuously weaker than seasonal lines and are readily differentiated with a little experience.

A more serious problem is that the annual lines themselves are transitory and disappear with growth, the older lines first. This limits the assignment of known age to turtles first captured while young enough to show the hatching annulus. We measured the width of growth annuli on turtles of known age and later noted when the line separating the hatching scute from the first year's growth, or when lines dividing later years' growth, became obscure or disappeared. In most instances, the division between the hatching scute and the first year's growth (the "zero annulus") was gone before the third year's growth commenced. In no instance did a turtle that had completed three seasons of growth exhibit a zero annulus. This meant that with rare exceptions, unless a turtle was captured in one of its first two growth seasons, the ring method of estimating age could not be applied unequivocally.

Judged from published reports, there is geographic variation in the age at which growth rings are lost. Early loss of the hatching annulus was common in turtles studied in Illinois (Tucker, 1978). Sexton (1959b: 717) stated in reference to turtles on the Edwin S. George Reserve in Michigan that "the ridges marking the limits of the annuli become obliterated with time. The older ridges begin to disappear when the animals are about 5 to 7 growing seasons old." Working with the same population, Wilbur (1975a: fig. 1) identified animals with complete sets of annuli only into the fourth growing season. This is somewhat less than Sexton's figure, but still greater than in my Long Island turtles. J. W. Gibbons (personal commun.) assures me that the hatching annulus is definitely visible in turtles at Sheriff's Marsh and the George Reserve (Michigan) after more than three years. In reference to turtles from southwestern

Minnesota, Ernst and Ernst (1972: 78) found that "Scute ecdysis and wear obliterated plastral growth annuli and made it difficult to determine age of individuals over five years old," a figure also in excess of mine. Working with *Chrysemys* in Saskatchewan, MacCullough and Secoy (1983b) were able to utilize annuli for ageing some turtles up to 12 years, the maximum retention of annuli of which I am aware. For several turtles, these authors confirmed that scute annuli agreed in number with those counted in osteochronological analysis.

A commonly used method of estimating the size of an individual turtle at the ends of earlier growth years involves ageing the turtle by ring counts and calculating the proportional relationship between present plastron and abdominal scute lengths. The earlier size of the abdominal scute is determined by measuring the length of its annulus, and the corresponding plastron length may then be calculated (Ernst, 1971c; Ernst and Ernst, "1972" [1973]). The method depends, of course, on the presence of the zero annulus so that ageing is accurate. Another possible source of inaccuracy would be if turtles growing at different rates tended to lose the annulus at different ages. If, for example, a slowly growing turtle retained the annulus longer than a rapidly growing one, the first could provide growth data whereas the second could not. The growth estimates would then be biased on the slow side. With this in mind, I compared slow and fast growing individuals but could find no evidence that rate of growth influenced loss of growth rings.

Sexton (1959b) devised a means by which the ages of turtles with early growth rings missing could be estimated by comparing the dimensions of their annuli with those of annuli of turtles of known age, fitting the data for a turtle of unknown age into an established range of variation. Gibbons (1968a), studying *Chrysemys* in southwestern Michigan, could not use Sexton's method because plastral annuli seldom were visible on older turtles. Instead, he used a combination of annulus counts on younger turtles and an estimated age-length relationship for older animals (but see comments below). Quinn and Christiansen (1972), for a study conducted in Iowa, presumably used Sexton's method, as

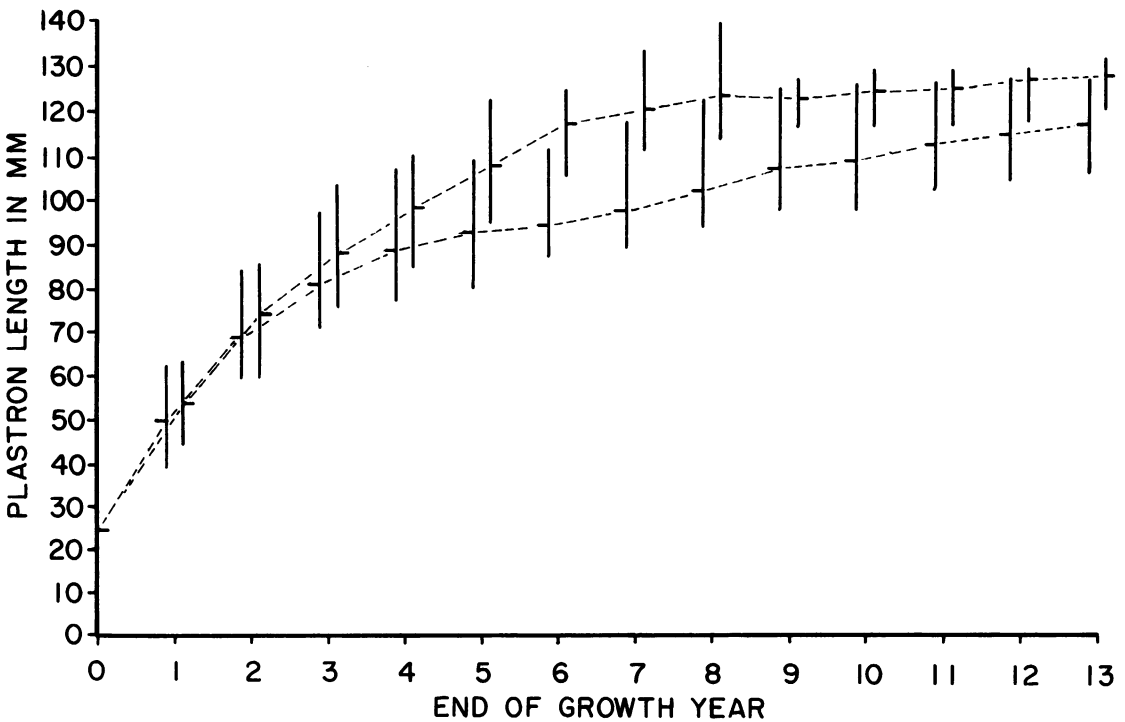


Fig. 5. Growth curves expressed as plastron length for *Chrysemys* males (lower) and females; vertical bars show ranges, horizontal ticks means. See table 1 for numerical data.

they cite "Sexton (1959)," though this reference is missing from their Literature Cited.

In my study I inferred ages of some individuals with one or two growth lines missing, but only where the sizes and growth patterns of animals of known age indicated a high probability of accurate placement of the unknowns.

SEX IDENTIFICATION: Adult *Chrysemys* differ in ways that permit determining the sex of a living individual. Males have conspicuously longer front toenails than females of similar size. The male tail is longer at a given body size and the cloaca is situated just anterior to the midpoint of the tail rather than less than one-quarter of the way along (Ernst, 1971a: table 1). Elongation of the toenails is perhaps the easiest character to use, though cloacal position is often helpful in questionable cases. The long toenails of males in my population were noticeable in some individuals as small as 76 mm PL and were evident in most if not all males by 90 mm PL. Female turtles were in a sense sexed by default: a

turtle 90 mm PL or greater that did not have elongate toenails was almost certainly a female. The sex of living juveniles could be determined only in retrospect if they were recaptured as adults.

LENGTH OF GROWING SEASON: I used measurements of turtles captured in the fall and again in the spring to estimate the times at which growth ceases and recommences. I have used data only from turtles up to the beginning of their fourth growth year on the assumption that these young turtles are growing rapidly enough so that changes in growth rate would readily be detected.

Growth may cease as early as mid-August, or in rare instances may continue into late September. The latest date for a turtle with no growth since the previous fall is June 7, and the earliest verified resumption of growth is May 14. Collecting in the spring and fall was infrequent compared to the summer and does not provide an adequate base for comparing lengths of growing seasons in different years. Given a late start in the second week

TABLE 1
Plastron Length^a at End of Growth Year

Year	Males				Females			
	Mean	σ_m	Range	N	Mean	σ_m	Range	N
1	49.6	0.80	(39–62)	44	53.2	1.74	(44–63)	12
2	68.5	0.92	(59–84)	43	74.0	1.58	(59–86)	20
3	81.3	0.99	(71–97)	45	87.5	1.81	(76–103)	20
4	88.7	1.00	(77–107)	43	97.5	1.72	(85–110)	17
5	92.7	1.16	(80–109)	36	106.9	2.38	(95–122)	15
6	94.7	1.47	(87–112)	19	116.7	2.03	(106–125)	11
7	97.9	2.52	(89–118)	12	120.7	1.73	(111–133)	15
8	102.6	3.22	(94–123)	8	123.1	2.20	(114–139)	10
9	107.6	4.88	(98–126)	5	122.6	1.69	(117–127)	7
10	108.8	5.03	(98–127)	4	124.2	1.51	(117–129)	8
11	113.3	7.31	(102–127)	3	124.8	1.96	(117–129)	6
12	115.0	6.81	(105–128)	3	126.5	1.77	(118–129)	6
13	114.7	6.69	(107–128)	3	128.2	2.08	(120–131)	5
14	129.0	—	(129)	1	128.4	2.13	(120–131)	5
15	129.0	—	(129)	1	131.5	—	(131–132)	2

^a Measurements in millimeters.

of June and early cessation in mid-August, the season could be as short as about 70 days. The other extreme—mid-May to the end of September—could double the period. The data indicate that there is little or no growth between mid-September and the end of May, suggesting an average period of a little over 100 days. Growth is rapid when it begins in the spring, so variation in the date of spring resumption is probably much more significant than in the fall, when growth has been gradually decreasing.

The length of the growing season appears to be remarkably similar throughout the northern part of the range of *C. picta*. Estimates for Pennsylvania (Ernst, 1971b), southeastern Michigan (Sexton, 1965) and Saskatchewan (MacCulloch and Secoy, 1983b) agree on a three-month period, June through August, much as I found in New York. Gibbons (1967: 299) found that “at least some growth occurs during May and September” in southwestern Michigan, also as in my study population. In contrast, Cagle (1954) estimated that in Illinois the growth season extends from the end of May until the end of October (5 months), and in Louisiana from the end of February through December (10 months). Field verification of these inferences is needed, especially with respect to

the time of termination of what appear to be unusually long growth seasons.

ASPECTS OF GROWTH

Before discussing variation, it is desirable to establish the general trends seen in the study. Data for male and female turtles with up to 15 years of growth are summarized in tables 1 and 2 and in figures 5 and 6. These data include all individuals of known age (see above) whose length and weight were measured or could reliably be estimated for the end of a growth year. Male turtles grow at a rapid rate for the first three years to an average plastron length of about 81 mm and weight of 104 g. In the fourth year, coincident with sexual maturity, growth slows but continues. In females the change in growth rate is less obvious, being most evident in the ninth year after the average female turtle has reached a plastron length of 123 mm and a weight of 320 g. As in males, growth does not terminate at the curve inflection.

DIFFERENCES BETWEEN THE SEXES: That *Chrysemys* females attain a larger size than males is well known. This evidently depends largely if not wholly on the earlier maturity of the males; growth slows greatly at sexual maturity, so male growth decreases while fe-

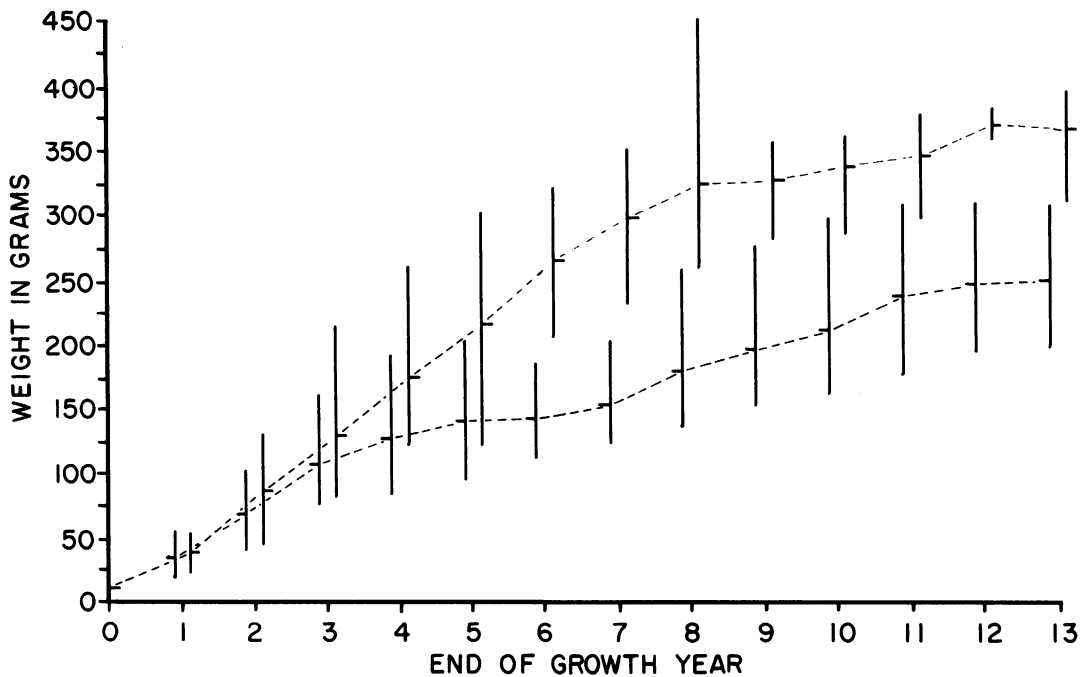


Fig. 6. Growth curves expressed as weight for *Chrysemys* males (lower) and females; vertical bars show ranges, horizontal tics means. See table 2 for numerical data.

males of the same age continue a high rate of growth for an additional two years or more, until mature. However, it is necessary to consider whether females may have an intrinsically greater rate of growth than males. This is best done by examining the data for growth in the early years of life, when presumably the hormonal influences associated with sexual maturity are minimal, though not necessarily negligible.

Ideally one would like to sample large numbers of young turtles of known sex growing in the same ponds at the same time, but annual cohorts in this study were mostly small to begin with, even zero in some years. And because baby turtles can be sexed only in retrospect—after they have grown for several years—the samples are further reduced by attrition. For only four samples were there enough individuals to permit comparing males and females within a cohort.

The 1965 cohort of three females and seven males (figs. 7, 8) shows a distinct difference between the sexes. Through the first four years females averaged markedly greater growth than males. In the fifth year, while the male growth rate continued the decrease expected

with the onset of maturity, the females moved further ahead.

The 1967 cohort (figs. 7, 8) consisted almost wholly of males. A single female followed for five years (not on the graph) was close to or even below the average male size for the first three years, moved to the top of the male range in the fourth year (i.e., with slowing of male growth), and exceeded the males in the fifth year. This sample with its meager female representation shows no difference between the sexes prior to male maturation. Two females and four to five males in the 1972 sample also showed no evidence of a difference between the sexes. Both males and females closely followed the curve for 1965 males (figs. 7, 8), with the females averaging smaller than the males.

The last cohort to provide data is the 1973 brood. Two to seven females and three to six males had similar average sizes for the first two years, some divergence (females larger but much overlap) in the third year, and no overlap in the fourth as the females moved ahead.

Thus among these four samples there are three different relationships between sex and

TABLE 2
Weight^a at End of Growth Year

Year	Males				Females			
	Mean	σ_m	Range	N	Mean	σ_m	Range	N
1	32.4	1.19	(16–55)	47	37.1	3.73	(25–55)	11
2	65.5	2.37	(40–100)	44	85.0	4.29	(44–130)	20
3	104.2	3.17	(73–160)	46	126.9	6.97	(82–213)	22
4	124.2	3.69	(82–190)	44	171.4	9.10	(120–260)	18
5	138.3	4.49	(91–200)	38	212.5	15.14	(120–300)	15
6	139.0	4.84	(110–185)	19	262.4	11.36	(205–320)	11
7	149.9	9.38	(120–200)	11	294.6	10.42	(230–349)	14
8	176.8	13.89	(135–260)	8	320.4	15.66	(260–450)	12
9	193.8	21.92	(150–274)	5	323.7	10.25	(280–355)	8
10	208.2	24.60	(160–296)	5	335.7	11.57	(285–360)	7
11	235.3	—	(175–306)	3	342.9	10.23	(295–375)	7
12	244.0	—	(190–307)	3	368.7	5.16	(360–380)	4
13	246.7	—	(194–305)	3	365.0	15.08	(310–395)	5
14	313.0	—	(313)	1	370.0	20.72	(310–400)	4
15	302.0	—	(302)	1	380.0	—	(370–390)	2

^a In grams.

relative growth rate. In one cohort (1965) females were significantly larger from the first year on. In two cohorts (1967, 1972) males and females grew at much the same rate for the first three years. In the fourth (1973), a suggestion of divergence in the third year is strongly reinforced in the fourth year. There may be special circumstances as yet not pinpointed (e.g., in the 1965 cohort) that favored female over male growth, but I prefer the hypothesis that prior to male sexual maturity (essentially, over the first three growth seasons), there is no inherent difference between the sexes in growth rate. I attribute the divergence between male and female growth lines seen in the third year (figs. 5, 6) to the statistically unbalancing effect of the large brood of 1967 which was overwhelmingly male and which grew at an unusually slow rate.

GROWTH OF OLDER TURTLES: The data for known-age turtles suggest that average growth slows greatly for females at about 120 mm PL and for males at about 80–90 mm (fig. 5). Because these data are limited to individuals with 15 years or less of growth and because of the small numbers of older turtles in the sample, I cannot demonstrate growth trends in older turtles of known age. However, growth in older turtles can be investigated in large turtles that were captured repeatedly, even though their ages are not known.

The plastron lengths of 10 female turtles over a range of years are plotted in figure 9. I direct attention first to those individuals whose initial plotted length is greater than 125 mm. Four individuals appear to have established growth plateaus over a range from about 129 to 139 mm. Turtle no. 13 grew from about 126 to 129 mm in three years and then stayed the same length for the next 14 years, while no. 19 established a plateau at 133 mm that held for 11 years. Turtle no. 23 showed 1 or perhaps 2 mm of growth over 13 years, settling in at about 135–136 mm, whereas measurements of no. 16 vary between 138 and 139 mm over 15 growth seasons. Records for no. 8 vary somewhat, but differ from the others in indicating a gradual increase of as much as 5 mm over the course of nine seasons (127–132 mm), with no obvious leveling off.

Also plotted in figure 9 are curves for some turtles that may show the early stages of cessation of growth. Turtle no. 63 resembles no. 13 in slowing its growth at a relatively small size (no. 63 completed its 13th year of growth in 1979), whereas no. 9 appears to fall in with no. 23 at around 135 mm. No. 25 may be leveling out at 138 mm, nos. 27 and 59 cut through all other growth plateaus to 142–143 mm, and no. 59 continued slow growth (4 mm in seven years) after the inflection in its curve at 139 mm PL.

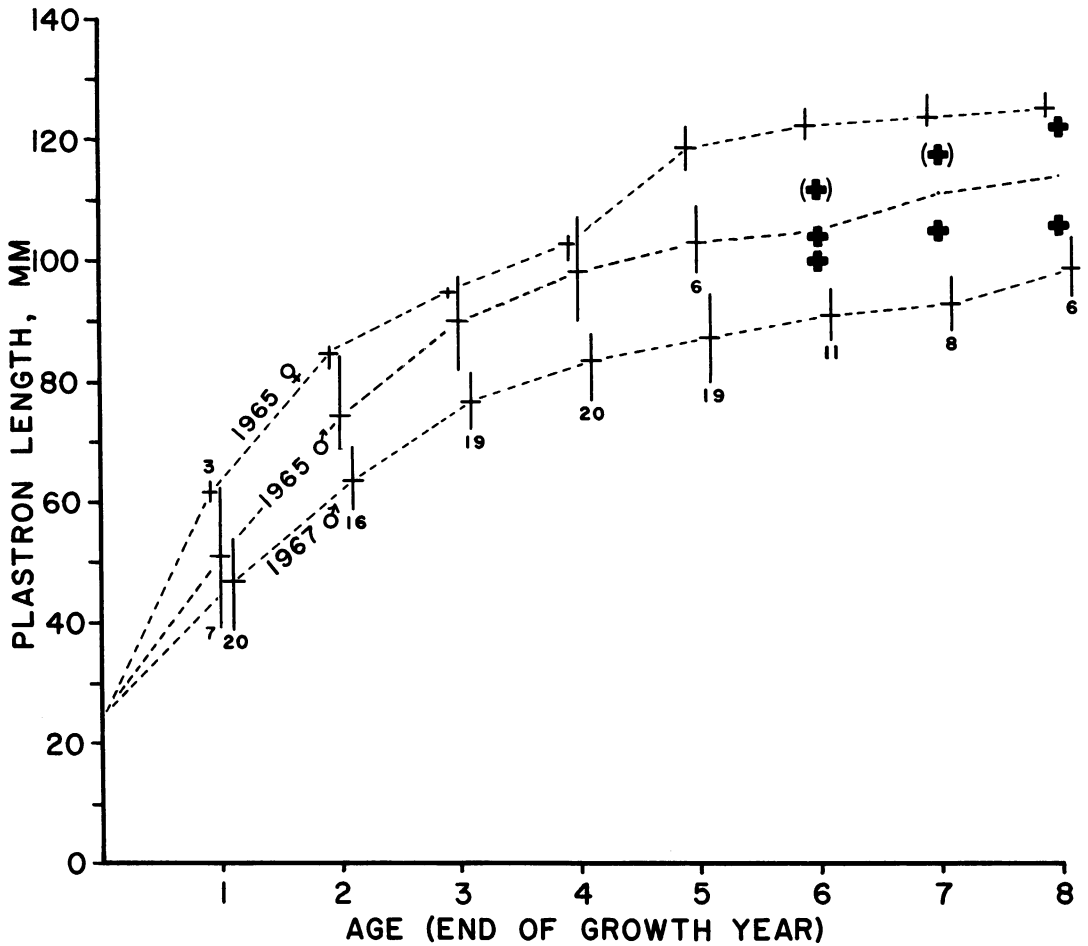


Fig. 7. Growth in plastron length of three *Chrysemys* samples over eight years, illustrating difference between the sexes in one year and variation between samples of males of two cohorts. Numbers are sample sizes, crosses represent individual turtles.

There are too few long-term records to establish if the sort of variation seen in females occurs also in males. An unusually rapidly growing male reached 123 mm in eight years and 126 mm in the ninth. Thereafter it slowed to 0.5 mm per year, reaching 129 mm by its last capture at the end of the 15th year of growth. Another grew no more than 1 mm (119 to 120) in 1964, 1965, and 1966, reached 123 mm in 1968 and stayed that size through 1971. A male that measured 110 mm at the end of 1966 added 11 mm by the end of 1971 but only 3 mm in the next nine years. The fourth and last individual with a long record of adult size grew less than 3 mm (ca. 116–119 mm) in 10 growing seasons. As in the females, there appears to be a tendency for

individuals to undergo a considerable decrease in growth or an actual cessation at different sizes. Unlike the females, however, three of the four males seem to have continued very slow but measurable growth.

It is clear from my data that at least some painted turtles, females especially, cease measurable growth. This contrasts with Wilbur's (1975: 341) finding of "no evidence that growth is asymptotic at large body size." Furthermore, growth stops in different individuals over a considerable range—at least 14 mm PL in my sample of females. Therefore, estimates of ages of older turtles based on assumed annual increments of an average amount (e.g., Gibbons, 1968a; Wilbur, 1975) must be considered highly questionable.

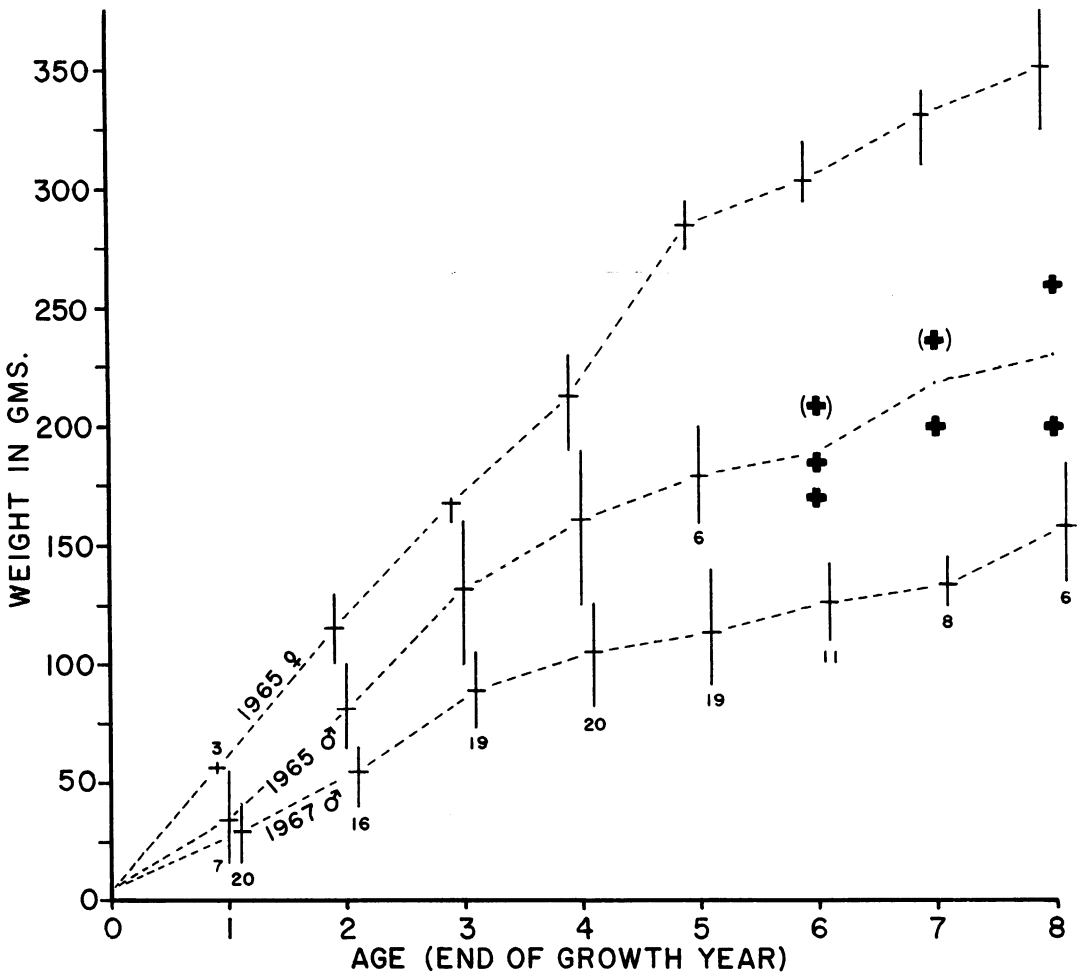


Fig. 8. Growth in weight of three *Chrysemys* samples over eight years; presentation as in fig. 7.

GROWTH SPURTS: Growth typically slows at maturity but there are perturbations that should lead to caution about generalizing. The history of five males of the 1967 cohort that survived through the 1975 growth season provides a good example of the risk in accepting short-term growth rates as characteristic over the long run. These turtles, members of a cohort that exhibited less than average growth in its juvenile years (figs. 7, 8), were on the borderline of maturity at the beginning of the fourth season of growth (1971); average plastron length was 79 mm (range 77–81) and by July of that year all were readily identified as males. They showed substantial growth in 1971 and moderate growth in the fifth year, 1972 (fig. 10). The next two years supported very little growth—a total of

2.8 mm increase in mean plastron length (3.1%) and 9.1 g (7.3%) in weight. Taken alone these data would fit well into the pattern of growth retardation with maturity. But in the eighth growth season, 1975, all five turtles had an astonishing surge in growth. The mean plastron length increased by 6.6 mm (7.1%) and the mean weight by 29.3 g (21.8%). They more than doubled the length increase of the previous two years and more than tripled the weight increase.

The causes for this increase in growth rate may be multiple, but there is a strong correlation with one possible factor, rainfall. Figure 11 displays the relationship between mean percent weight gain and total rainfall from the first of May through the end of August. This time span covers most of the growing

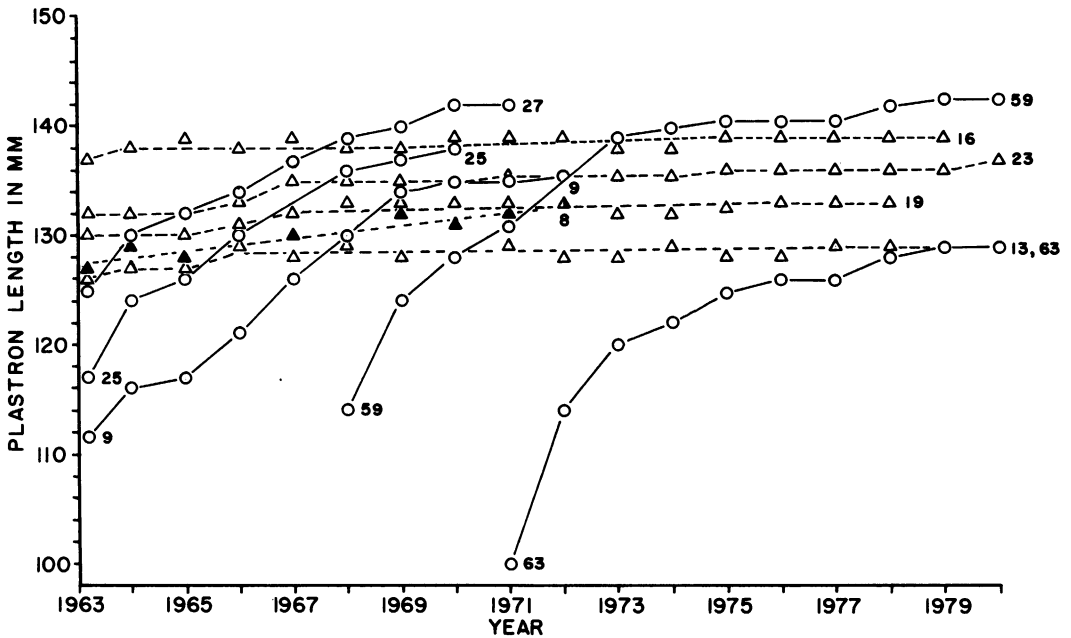


Fig. 9. Plastron lengths of several *Chrysemys* females in an 18-year period. Four individuals show no growth for most of the period, and others may show the initial stages of growth plateaus. Different symbols have no significance except to improve legibility; numbers are the turtles' field numbers.

season. I included the rainfall for May, mostly before the growing season, on the basis that this rainfall might contribute importantly to the conditions under which the turtles would shortly begin growing. I omitted September rainfall because even if substantial rain fell, it would be too late in the year for rain to contribute much if anything. The correlation between growth and rainfall is quite high: $r = +0.987$. Presumably greater rainfall results in more abundant food, better quality food (e.g., invertebrates vs. plants), or both.

LENGTH-WEIGHT RELATIONSHIPS: Curves describing the relative lengths and weights of male and female *Chrysemys* appear in figure 12. The numbers that these curves average are a subset of the voluminous data gathered during the 18 years of the study. They were selected in a random fashion with up to two weights for each millimeter interval over the range of plastron lengths represented in the data. The only conscious departure from randomness was that I included no weights for adult female turtles captured in the spring and early summer, in order to avoid fluctuations associated with egg-laying. The male sample comprised 177 weights over a PL

range of 24–129 mm, the female 166 over 38–142 mm.

Weights of male and female turtles of the same PL do not differ up to about the size where males mature (ca. 80 mm); thereafter there is a slow divergence. A large male at 120 mm PL would weigh on the average 275 g, compared to 292 g for a female of the same PL (female 6.2% heavier).

COMPARISONS WITH
PREVIOUS STUDIES

There are many published reports of growth in *Chrysemys picta*. Unfortunately, not all authors present the data in ways that permit meaningful comparisons. For example, some authors did not separate adult males and females in tabulating their data. One of the earliest field studies (Pearse, 1923b) falls in this category. A potential source of confusion exists if it is not clear whether growth is expressed in terms of growth years (seasons), as I have done, or in chronological age. Age determination, especially where adult turtles have been aged on the basis of estimated annual growth rates, may be questionable. In

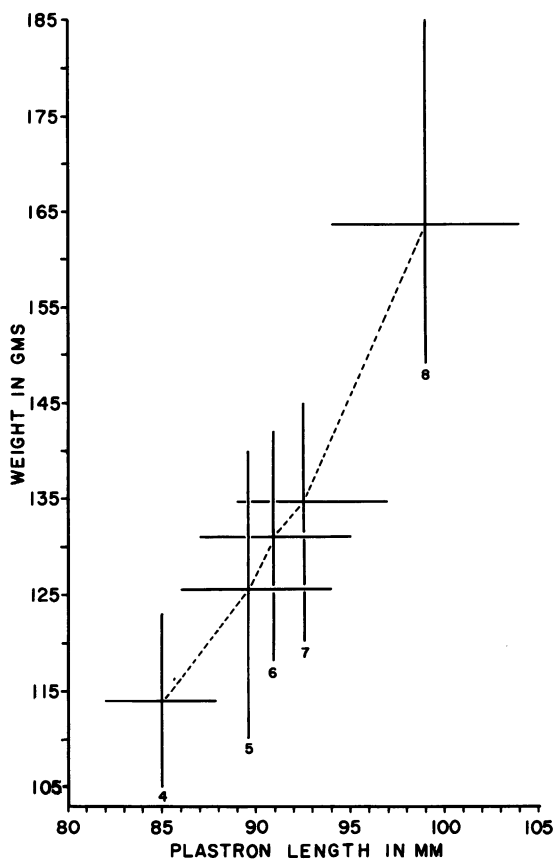


Fig. 10. Growth spurt in a cohort of five *Chrysemys* males the same age. The initial plot is for the end of the fourth growth year; horizontal and vertical range lines intersect at the common means for weight and plastron length.

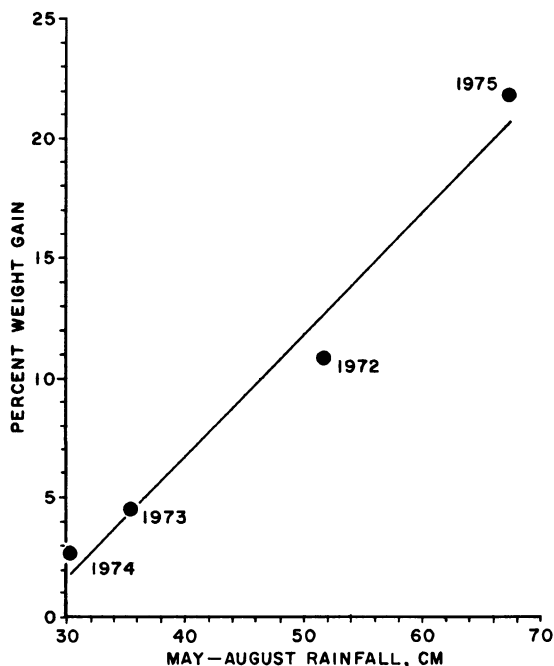


Fig. 11. Relationship of change in weight to rainfall among turtles undergoing a growth spurt (see fig. 10).

some populations, part of an annual cohort may emerge from the nest in the natal year rather than overwintering. These and other problems are taken up in the discussion where appropriate.

Figure 13 presents average growth curves reported for four populations of *Chrysemys picta*. The fastest growing turtles are the northern, river-dwelling population of *C. picta bellii* studied by MacCulloch and Secoy (1983b). The average size of males 12 years and older that they reported is 184.5 mm PL, so the curve as drawn presumably is nearing its inflection. Females, however, average 216.6 mm; the curve might not reach that level until about 15 years.

A lake-dwelling population of *C. p. bellii* from Nebraska (Iverson, 1982b) presents

quite a different picture, with the growth curves assuming shallower courses after the second year. These curves closely resemble those for *C. p. marginata* in Michigan (Wilbur, 1975a), whereas average growth in my Long Island population was less after the initial period than in any of the other three.

Ernst (1971c) presented data on a *C. p. picta* × *marginata* intergrade population in Pennsylvania that seem to indicate slower average growth in the early years even than my Long Island turtles exhibited. His graph of PL vs. age shows an average PL of about 65 mm at the end of the third year and 72 mm at the fourth. These figures not only are below the means for my sample, but are below the minima (table 1). Ernst noted that the amount of growth in the first season depended on whether the hatchling overwintered in the nest or emerged and grew in its first calendar year. His year-old category evidently includes both turtles that had only a short time to grow as well as those that overwintered and then had a full first growth season. If there were many turtles in the first category, this would significantly reduce the

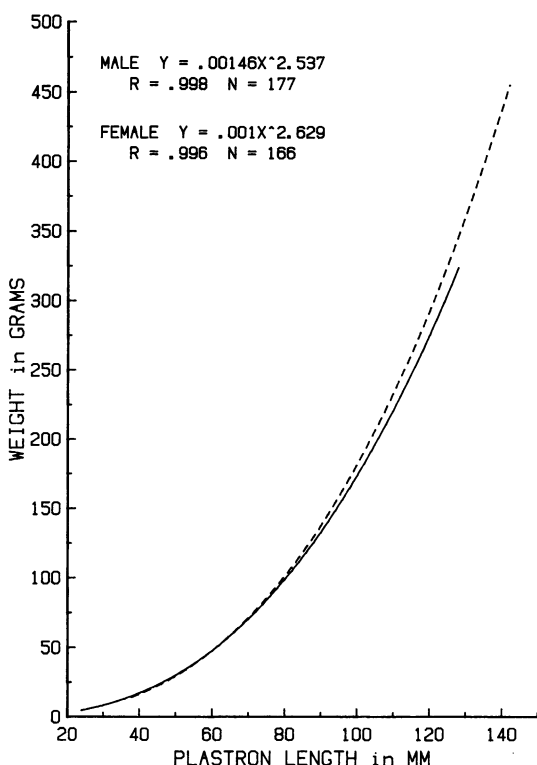


Fig. 12. Relationship of weight to plastron length in *Chrysemys* females (broken line) and males (solid line).

mean growth calculated for the first as well as subsequent years, as this unbalance (individuals from one year's brood being carried under two different ages) would be perpetuated through the years. The apparent differences between the population he studied and mine may to some extent reflect methodology and turtles' habits rather than a difference in growth rates. Ernst presented his growth data on older turtles as annual percentage increase in size without reference to age, which was unknown, so these data are not comparable with mine.

Gibbons' (1968a: fig. 2) estimates of growth in Michigan *C. p. marginata* also are well below the rates attained by Long Island turtles. The correctness and usefulness of his data for older turtles are questionable because ageing was based on assuming a growth rate of 1.1 mm per year that seriously underestimates the true growth potential, at least for the early years of maturity. For example, Gibbons' estimate of average female PL at

about 100 mm at nine years of age contrasts with Wilbur's (1975a: fig. 3) known age PL of about 130 mm, also based on Michigan turtles, and my figure (table 1) of about 123 mm.

The estimates for younger, known-age (ring-counted) turtles also require reinterpretation. Gibbons' (1968a: fig. 2) "age-plastron length" graph for turtles from Sherriff's Marsh, Michigan, would be taken to indicate the average size of turtles at the end of each growth year. In an earlier paper (Gibbons, 1967: fig. 1) the raw data for the same turtles (ages one to five) are graphed in a scatter diagram in which the individual plots are placed at various points through the growth years, illustrating an average increase in size over a growth season. It appears that the means in the 1968 publication represent the average sizes of turtles measured at various times in the growth season rather than the size attained at the end of the season.

Gibbons (1967: fig. 1) characterized and compared growth of immature *Chrysemys* in two populations by means of rectilinear growth curves calculated from data covering several seasons' growth. It is evident now (e.g., fig. 5; Wilbur, 1975a) that growth of younger turtles over two or more seasons clearly is curvilinear, though within any one season a straight line may describe growth adequately (see fig. 4). In an attempt to make Gibbons' data more comparable with mine and others discussed here, I estimated his (1967: fig. 1) data point values for the first three growth seasons and calculated a separate rectilinear growth curve for each. The intercepts of these curves give year-end PL estimates of 45, 58, and 66 mm for the first three seasons. These rough estimates are well above the means as shown in Gibbons (1968a: fig. 2), but still indicate that these were very slow-growing turtles, with rates comparable to those estimated by Ernst (1971c), which I regard as possibly underestimated (see above).

Variations in growth among and within populations of *Chrysemys* and their possible causes have received some attention in the literature. Gibbons (1967) compared river, lake, and marsh populations of *C. p. marginata* and demonstrated that young river and lake turtles grew more rapidly (my foregoing comments on methodology notwithstanding

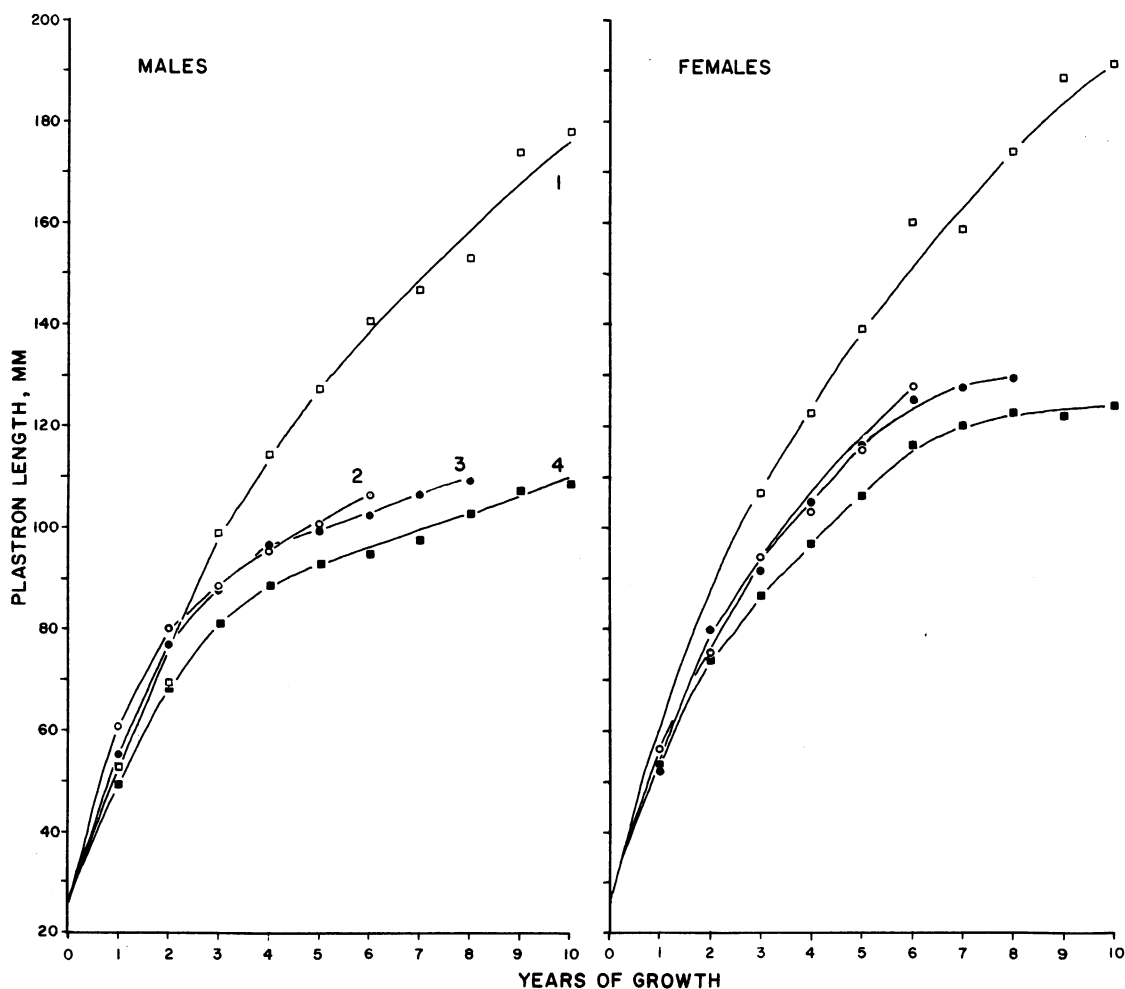


Fig. 13. Growth curves for males and females of four populations of *Chrysemys picta* compared: (1) river-dwelling *C. p. bellii* in Saskatchewan; (2) lake-dwelling *C. p. bellii* in Nebraska; (3) pond- and marsh-dwelling *C. p. marginata* in Michigan; (4) pond-dwelling *C. p. picta* (present study; see text for references to other studies).

ing), though age-size comparisons among older turtles are questionable because of the ageing technique.

Quinn and Christiansen (1972) compared populations of *C. p. bellii* from lotic waters with sandy vs. mud substrata and reported that turtles from sites with highly organic, mud substrata grew larger and apparently more rapidly. Again, the general conclusions probably are correct but distinctions are blurred because the sexes were not treated separately and the ages of older turtles were not known for certain but were estimated by Sexton's (1959b) method.

The data of Tucker (1978) for *C. p. bellii* × *marginata* in a lake in Illinois are of particular interest. Turtles in two presumably different local populations from almost 3 km apart (judged from the published map) in the same lake had grown at markedly different rates. The two samples differed little in the first season's growth and, in the case of females, in the second. Thereafter the growth rates diverge, with both sexes of one population approximating curves 2 and 3 in figure 13 and the others curve 1.

The foregoing studies are based on "horizontal" samples that average growth rates

over many years and are important in demonstrating differences associated with diverse habitats and localities. In addition to providing comparative average data, my study reveals something of the differences that can exist among yearly cohorts at a single site. For example, the fast growing 1965 males and females (fig. 7) conformed rather closely to the average growth shown in curves 2 and 3 (fig. 13), whereas the 1967 males grew almost as slowly as Gibbons' (1967) marsh turtles.

The reasons for variations in growth rate and size are material for speculation but have not yet received rigorous investigation. There must be genetic factors that set the bounds for variation, and these evidently show geographic variation. The southern painted turtle, *C. picta dorsalis*, is a much smaller animal than any of the more northern *Chrysemys*. Comparing *dorsalis* of Louisiana with *bellii* of Manitoba, Hart (1982) found that his largest Louisiana male (PL 86 mm) was smaller than his smallest mature Manitoba male (PL 100 mm), and a similar relation held for females as well. He suggested inherent differences between the populations in size at maturity and in potential for growth after maturity as an explanation.

Quality of food is implicated as an important contributing factor where turtles in different habitats show different growth rates and maximum sizes. A highly carnivorous diet has been associated with rapid growth and large size, whereas a largely vegetarian diet has the opposite relationship. Gibbons (1967) found that marsh-dwelling turtles feeding largely on plant matter were slower growing and smaller than river-dwelling turtles that fed mostly on invertebrates. Quinn and Christiansen (1972) studied *Chrysemys* from habitats with highly organic, mud bottoms and with relatively inorganic, sand substrata. They found faster growth among turtles living where the bottom held more organic matter and tentatively suggested that this was due to more animal matter in the diet. The largest, most rapidly growing *Chrysemys* yet studied are almost wholly carnivorous (MacCullough and Secoy, 1983b). Diet is certainly not the whole explanation, though. Hart (1982) noted that the vastly different Louisiana and Manitoba populations he sampled both were highly carnivorous.

Wilbur (1975a) factored environmental components into a model describing growth of *Chrysemys* in Michigan and found that these did not account for a significant amount of variation in growth. Ernst and Ernst ("1972" [1973]), commenting on Quinn and Christiansen (1972), found no differences in growth correlated with kind of substratum, but observed that turtles in their study area moved between areas with different substrata. Turtles in Wilbur's study area are highly migratory (Sexton, 1959a), which might similarly confound attempts at identifying environmental correlations.

Quantity as well as quality of food could influence growth, though I know of no direct evidence of quantity as a limiting factor. In the case of slow- and fast-growing cohorts that I compared (figs. 7, 8), the faster (1965) had two years of growth when there were only 29 or 30 turtles in the population, 12 of them juveniles. In contrast, the slow, 1967 cohort was part of a population of 56 or 57 individuals in its first two years, 38 or 39 of them juveniles (table 4). In the absence of more examples or of detailed information on food supply and other environmental conditions in the ponds, it cannot be concluded that population density and growth rate are meaningfully correlated, though the possibility should be kept in mind. The association of increased growth and higher rainfall (Growth Spurts, above) also points to an environmental influence on food supply and, by extension, growth.

Individual differences undoubtedly play a part in growth rates, though demonstrating this factor under natural conditions would be most difficult. Andrews (1982) presented an example of variability of growth rates in individual hatchling *Chrysemys* held under controlled conditions—in separate containers and fed ad libitum. Over five months, some individuals did not grow at all, whereas others ranged up to as much as three times their original mass of about 4 g. What is not immediately apparent is that even the largest of these hatchlings, after the equivalent of more than a normal length growth season, was woefully undersized compared to the average male (32 g) or female (37 g) weight of wild turtles in my sample (table 2). Conditions in captivity obviously were not optimal.

Differences in length of growing season

could contribute to both local and more widespread variation in growth. Unusually cool weather in the spring, for example, can delay the initiation of growth (Ernst, 1971c). In the broader context, length of season appears to be similar among more northern populations where there are reasonably good data (New York, Pennsylvania, Michigan, Saskatchewan) but where growth rates differ. North-south variation is more likely to prove significant when adequately investigated.

Published data on weights of *Chrysemys* at a variety of body lengths are few, and I am aware of only two papers in which both sex and length are considered as variables—Wilbur (1975a) and Iverson (1982b).

Wilbur (1975a: table 3) presented regression data derived from a large sample of Michigan *C. picta marginata*, subdivided into juveniles (<80 mm PL), adult males (>80 mm), subadult females (80–120 mm), and adult females (>120 mm). Estimates of weights of turtles of four sizes, based on Wilbur's data, are in table 3.

Iverson presented regression equations for his entire sample of *C. picta bellii* from Nebraska as well as for subsets composed of males, females, mature males, and mature females. I have entered estimates based on Iverson's equations in table 3 for all sexed turtles rather than using his equations for mature males and females, which give what appear to me to be unreasonably low figures. (Iverson's formulas use carapace rather than plastron length; I converted PL to CL according to the equations given at the beginning of this section.)

Weights of males and females of the same plastron length in my sample differ scarcely or not at all up to about the size at which males mature (fig. 12). The figures for Wilbur's mixed sample of juveniles differ little from those for juvenile males and females from New York. In contrast, Iverson (1982b: 413) found that "females are significantly heavier than males at any given carapace length" (see table 3). His data set lacked small individuals (smallest male 75 mm CL, 69 mm PL; smallest female 69 mm CL, 62 mm PL), and it would be worthwhile reexamining the question with a fuller representation at the low end of the curve.

Among turtles of adult size from three widely separated populations representing

TABLE 3
Estimated Weight of *Chrysemys* of Both Sexes and Four Sizes from New York, Michigan, and Nebraska^a

PL, mm	Male weight, g			Female weight, g		
	NY	MICH	NEB	NY	MICH	NEB
50	29.9	29.4	31.9	29.2	29.4	35.5
75	83.6	88.3	85.8	84.9	88.3	94.3
110	220.8	215.7	222.6	232.5	234.3	243.9
130	336.8	309.6	338.7	361.0	382.3	370.9

^a Michigan and Nebraska figures calculated from equations in Wilbur (1975a) and Iverson (1982b); Michigan figures for 50 and 75 mm from unsexed samples, so are carried in both male and female columns.

three subspecies, there are no differences that I consider significant in average weight at a given size (table 3). Estimated weights of males at 110 mm PL range over only 7 g, and of females over 11 g, or about 3–5 percent of the smallest weight. The situation is similar in the 130 mm group: 29 g in males, 21 g in females (6–9%). Turtles of these sizes in the population I studied would exhibit weight variation greatly exceeding the differences seen here.

NUMBERS AND RELATED TOPICS

In the present study individual turtles were recaptured sufficiently frequently and population size was small enough that it was unnecessary to resort to a proportional (Lincoln Index) method of estimating population size. Rather, for any point or period of time the composition of the population could be inferred with a high degree of accuracy merely through knowing which individual turtles were present before, during, and after the period in question.

I assume that hatchling turtles emerge from the nest in the spring (see Seasonal Activity), so an individual captured initially in its first growth year or not until a later growth year is counted as a member of the population from the spring of its hatchling year unless there is reason to believe it was an immigrant. Hatchlings that entered the population but were lost before ever being captured constitute a real but unmeasurable source of error.

A number of reports discuss the age and size at which *Chrysemys picta* attains sexual maturity but all treat populations somewhat

TABLE 4
Population Numbers and Biomass^a

Year	Males		Females		Juveniles		Total	
	N	Biomass	N	Biomass	N	Biomass	N	Biomass
1963	4	830 (15)	11	3930 (72)	6	687 (13)	21	5447
1964	7	1063 (20)	12	4220 (80)	3	12 (<1)	22	5295
1965	8	1265 (24)	11	3825 (74)	3	110 (2)	22	5200
1966	8	1350 (29)	9	3150 (68)	12	160 (3)	29	4660
1967	9	1515 (29)	9	3370 (64)	12	386 (7)	30	5271
1968	9	1515 (26)	9	3365 (59)	38	872 (15)	56	5752
1969	9	1590 (24)	9	3525 (53)	39	1570 (23)	57	6685
1970	6	1232 (15)	11	4215 (53)	38	2533 (32)	55	7980
1971	10	1708 (20)	12	4340 (50)	31	2550 (30)	53	8598
1972	24	2945 (33)	13	4695 (53)	16	1247 (14)	53	8887
1973	21	2590 (34)	11	3975 (53)	14	968 (13)	46	7533
1974	13	1804 (29)	10	3555 (57)	18	829 (13)	41	6188
1975	13	1868 (29)	11	3725 (57)	17	934 (14)	41	6527
1976	10	1675 (24)	11	3916 (56)	14	1384 (20)	35	6975
1977	15	2278 (30)	11	4065 (54)	12	1191 (16)	38	7534
1978	13	2102 (28)	13	4530 (60)	10	872 (12)	36	7504
1979	8	1520 (21)	14	4875 (69)	9	689 (10)	31	7084
1980	9	1645 (25)	13	4660 (70)	8	338 (5)	30	6643
Mean	10.9	1698 (25)	11.1	3996 (61)	16.7	963 (13)	38.7	6654

^a Numbers and biomass are for populations in spring; biomass in grams; figures in parentheses are percent of total biomass.

remote from my study area and many reports deal with turtles that reach a different size (both larger and smaller). Studies pertinent for comparison with mine include those of Ernst (1971a) in southeastern Pennsylvania and to a lesser extent (for geographical reasons) Mitchell (1985a, 1985b) in central Virginia. Ernst found that male *Chrysemys* mature at 80–90 mm PL usually in their fourth year and females at 110 mm “after their fifth year.” Mitchell (1985a) reported males mature at three to four years at a minimum of 72–77 mm PL, while females (1985b) mature at six years and a minimum of 105 mm. Average males in my population reached a mean PL of about 81 mm at the end of the third growth year and females about 107 mm at the end of the fifth (table 1). Males of this size show external morphological signs of sexual maturity but no such changes occur in females.

Male turtles measuring 80 mm or greater and females of 110 mm or greater at the beginning of the spring growth period are treated as adults in the tabulations. Thus, a turtle reaching the threshold in the fall would be

listed in the immature group at that time but the following spring would graduate to statistical adulthood. These arbitrary (but realistic) criteria for assigning sexual maturity could exclude some precocious individuals from the mature rolls, but this source of error may be balanced by turtles slower to mature.

NUMBERS

Table 4 and figure 14 summarize my estimates of population size over the 18 years of the study. These estimates are for the spring, when the population was usually at its maximum annual size. Attrition during the active period and emigration not balanced by immigration generally resulted in slightly smaller fall populations, about three fewer individuals. In only two years was the fall population size larger (by one individual) than that of the spring. The population was smallest in the year the study commenced, 1963, when there were only 4 adult males, 11 adult females, and 6 juveniles. Evidently there had been little successful recruitment for some time, as no turtles of the 1961 or

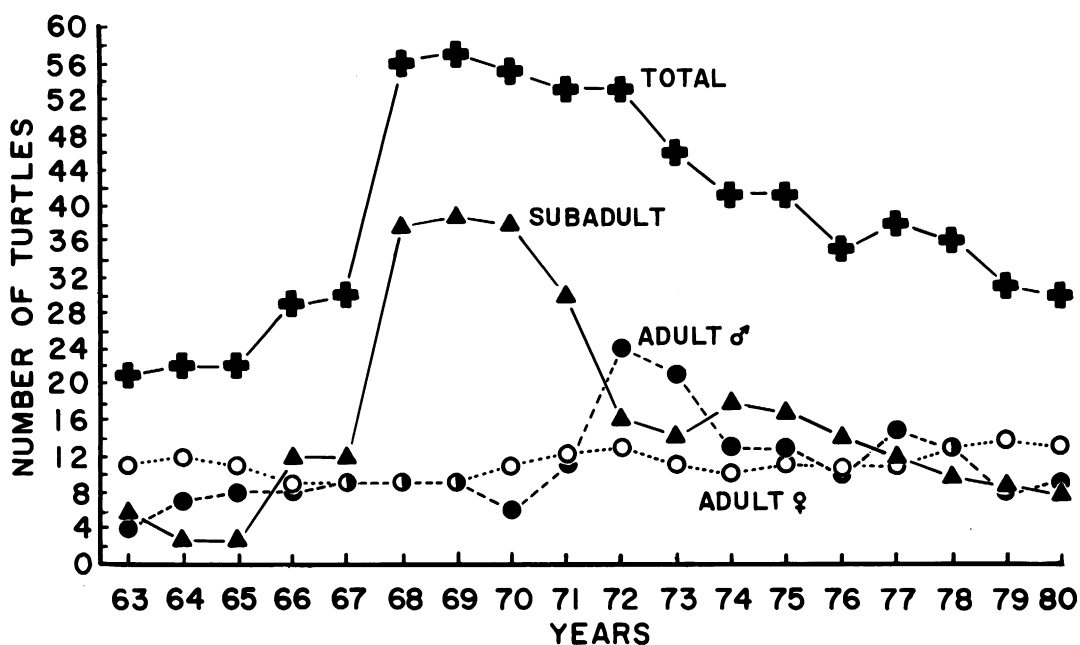


Fig. 14. Annual size (spring estimates) of study population: total and subadult (including juvenile) and adult components. Note relative stability of adult female numbers compared to males and subadults.

1962 broods were present. The numbers increased only slowly until the large, virtually all male brood of 1967 entered the ponds in 1968. This event almost doubled the number of turtles, but the numbers of adult males and females were little changed until the survivors of the 1967 year class matured in 1972. There were no more such conspicuously successful year classes. The number of adult females remained relatively constant while the total population size progressively decreased until at the end of the study in 1980 the numbers and relative proportions of males, females, and juveniles approached those seen in the early years.

DENSITY: The four ponds constituting the principal habitat of the population had a surface area when at their fullest in the spring of just under 0.3 ha. This was a temporary condition that gave way to sometimes drastically reduced water levels as the year wore on, but the figures of 0.296 ha for 1963–1972 and 0.266 ha for 1973–1980 (after Pond 4 became inaccessible) are useful for expressing minimum density. There was no such thing as a “typical” year, but I estimate that reduction to a total area of 0.1 ha of water surface over the summer was not uncommon.

The maximum reduction in the years of study occurred in 1965 when two of the ponds went dry late in summer and the other two were greatly lowered, leaving an estimated 0.06 ha of water surface.

The average density for the total pond area in spring was 137 turtles/ha, range 71–193 (table 5). Because the turtles tended to concentrate in Pond 1 during the spring (especially when conditions improved there after the drought years), these figures are much lower than the densities actually attained locally and temporarily. In most years trapping in the spring was not intensive enough to detail the distribution of individuals among the ponds with much precision, but for five years the data are deemed adequate (table 5). In these years the mean density was 348 turtles/ha (150–525) in Pond 1 for a time. Based on a total pond area of 0.1 ha for a “typical” late summer period, densities of about 210 to 560/ha may have occurred fairly often. It is of interest that the estimated density for the peak of the drought, 383/ha, is well below maxima regularly attained. The drought may have been less stressful than might be supposed, if the subnormal population size mitigated its influence.

TABLE 5
Numbers and Biomass of *Chrysemys*
per Hectare of Pond^a

Year	All ponds			Pond 1 only		
	N	N/ha	kg/ha	N	N/ha	kg/ha
1963	21	71	18.4	—	—	—
1964	22	74	17.9	12	150	37.6
1965	22	74	17.6	15	188	42.7
1966	29	98	15.7	—	—	—
1967	30	101	17.8	—	—	—
1968	56	189	19.4	—	—	—
1969	57	193	22.6	31	388	42.6
1970	55	186	27.0	—	—	—
1971	53	179	29.0	42	525	91.3
1972	53	179	30.0	9	488	88.1
1973	46	173	25.4	—	—	—
1974	41	154	23.3	—	—	—
1975	41	154	24.5	—	—	—
1976	35	132	26.2	—	—	—
1977	38	143	28.3	—	—	—
1978	36	135	28.2	—	—	—
1979	31	116	26.6	—	—	—
1980	30	113	25.0	—	—	—
Mean	38.6	136.8	23.5	28	348	60.5

^a Spring estimates of population size (N).

BIOMASS

Data collected for the study of growth make possible an estimate of the biomass of the population as a whole and of three components—adults of each sex and immature individuals. I use the term “biomass” in the loose sense as the gross weight of the living turtles. Population biomass estimates derive from summed weights of individual turtles. These data came from direct measurements where there were appropriate data, from interpolation between dates of measurement, or from extrapolation back prior to first capture. In the last two cases, knowledge of a turtle’s age and expected amount of growth in the time span coupled with data on size–weight relationships (fig. 12) permitted a sufficiently accurate estimate for turtles young enough to be growing at a significant rate. For older turtles with greatly reduced growth rates the problem was minimal. Because juvenile turtles almost never were captured before some growth had taken place, each was assigned 4 g as its initial hatchling weight. This is close to the average weight of hatchlings,

and any variation in the true weight of individual hatchlings would be insignificant in the total picture.

The total biomass of the population in spring ranged from a low of about 4.7 kg in 1966 to a maximum of about 8.9 kg in 1972 (fig. 15, table 4), mean 6.7 kg. Though the population size decreased slightly by the fall of most years, individual growth increased the total biomass slightly, about 5.4 percent. Biomass was below average when the study commenced in 1963 and remained so until the fall of 1969, well after the drought years of 1964 and 1965. Growth of the exceptionally large brood of 1967 (entering the ponds in 1968) was an important factor contributing to the increase. Adult female turtles contributed about 61 percent (50–80%) of the spring biomass, males 25 percent (15–34%), and immatures 13 percent (<1–32%).

DENSITY: The spring biomass for all ponds over 18 years ranged from 15.7 to 30.0 kg/ha, mean 23.5 (table 5). For the five years during which I have a good estimate of which turtles were present in Pond 1 in the spring, the biomass ranged from 37.6 to 91.3 kg/ha, mean 60.5 (table 5). Based on the estimate of 0.1 ha total pond area for an average late summer, density figures of from about 47 to 90 kg/ha may have been usual. At the time of greatest reduction of pond levels in late summer of 1965, the biomass was about 93 kg/ha. The relatively small population size at this time—23 turtles—explains why the density was not dramatically higher than the levels attained under more normal conditions.

PRODUCTIVITY: With estimates of the population biomass available for both the beginning and end of most growth seasons, it is possible to make an educated guess as to the amount of biomass produced each year. (I have not included the first and last years, 1963 and 1980, considering these data inadequate.) The spring biomass sums given in table 4 and corresponding figures for fall cannot be used directly, but must be adjusted to account for individuals that died or otherwise disappeared during the year, and for immigrants appearing late in the growth season. The resultant data presented in table 6 and graphed in figure 15 derive from the individuals assumed to have been present through-

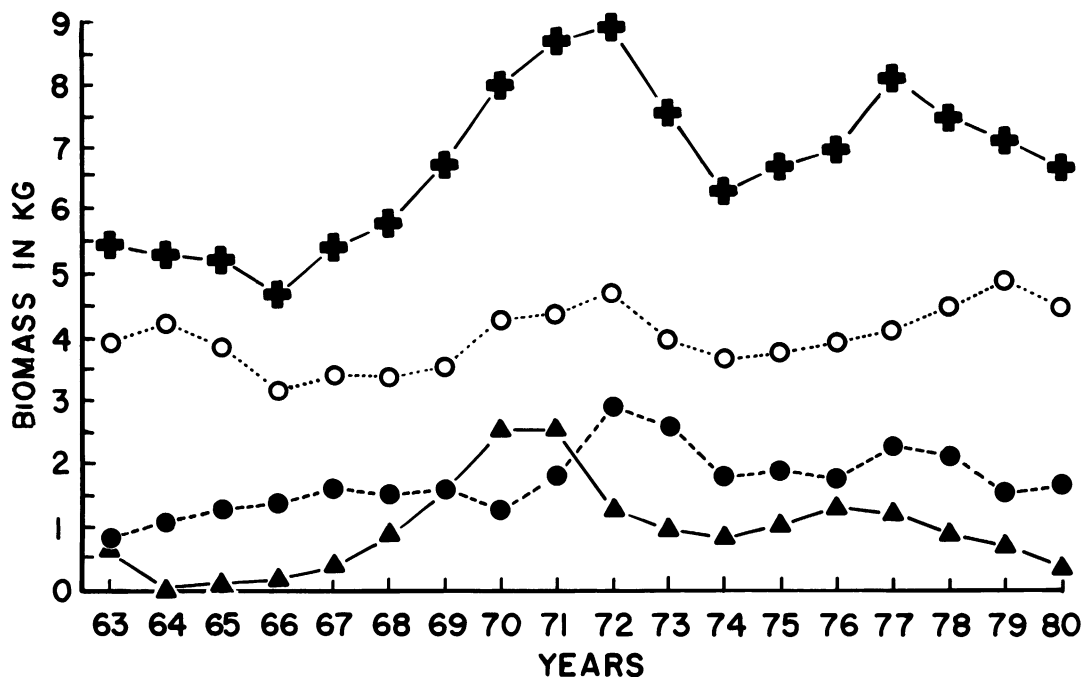


Fig. 15. Annual biomass (spring estimates) of study population: total and subadult (including juvenile) and adult components. Note that adult females, though numerically inferior to males and subadult turtles, comprise more than half the biomass.

out the growth year, which constitute the vast majority of turtles in the population.

In addition to producing turtle biomass, the population (or more specifically, a subset of the adult females) produces biomass in the form of eggs. Though the number of adult females present is known with high accuracy, I have no direct knowledge of how many of the turtles may have laid eggs each year or of the turtles' fecundity. In a following section I estimate the annual egg production (see table 10), and here use those figures multiplied by a factor of 4.1 g/egg (Congdon and Tinkle, 1982) to approximate the egg component of productivity.

Total turtle biomass production varied annually from a low of 140 g to a maximum of 1649 g. The estimated egg biomass varied much less (168–250 g) because of the relative stability of the number of adult female turtles. The actual variation possibly was much greater if conditions in different years promoted or inhibited reproduction. The maximum estimated total productivity was five times that of the leanest year (table 6, fig. 16).

No doubt, environmental quality signifi-

cantly influences productivity, judged from variations in individual growth rates documented here (see Growth). But the population age and sex structure determines to a large extent the amount of productivity. Older turtles—males over four or five years of age, females seven years or older—add to their mass less rapidly than do younger ones, and long-lived females may maintain essentially the same weight for years.

SEX RATIO

There are four aspects to be discussed: sex determination; ratios found among hatchling turtles; the ratio of the whole population; and the ratio of sexually mature individuals. Ratios are stated as male : female.

SEX DETERMINATION: Until recently it was reasonable to explain deviations from the theoretical 1:1 ratio in terms of sampling error introduced by "improper methodology and selective sampling" (Gibbons, 1970; see also Bury, 1979). Then a report by Pieau (1971) on a relationship between incubation temperature and sex of the hatchlings in the tor-

TABLE 6
Annual Biomass Production

Year	Turtle biomass,		Egg biomass,		Total biomass,
	g	g/ha ^a	g	g/ha ^a	
1964	140	473	221		1220
1965	195	659	221		1405
1966	765	2584	168		3152
1967	694	2345	168		2912
1968	1240	4189	168		4757
1969	1132	3824	168		4392
1970	1649	5571	197		6736
1971	1054	3561	221		4307
1972	1032	3486	250		4331
1973	797	2996	197		3737
1974	862	3241	197		3981
1975	1245	4680	197		5421
1976	404	1519	197		2259
1977	496	1865	197		2605
1978	429	1613	250		2553
1979	667	2508	250		3447
Mean	800	2820	216		3545

^a Based on maximum pond area of 0.296 ha.

toise *Testudo graeca* and the pond turtle *Emys orbicularis* initiated a wave of research on temperature-mediated sex determination in turtles and other reptiles. Pieau (1975) reviewed his early work, Bull (1980) gave a later general review, and Vogt and Bull (1984) provided more recent references. In turtles of several genera and families, the sex of an embryo depends on the temperature within the nest during a critical period of embryonic development. The effect is strong, and under both experimental and field conditions can produce clutches entirely of one sex or the other (Vogt and Bull, 1984).

Chrysemys picta is a species with temperature-dependent sex determination. Bull and Vogt (1979) reported that males hatched from 81 of 102 *picta* eggs incubated at 25°C and females from 81 of 101 at 30.5°C (in each case the remaining eggs were infertile or dead at early stages). Results of experiments by Schwarzkopf and Brooks (1985) agree with and extend the findings of Bull and Vogt (1979). Other studies define the sensitive period in embryogeny (Bull and Vogt, 1981), reveal geographic variation in critical temperatures (Bull et al., 1982), establish a lower temperature threshold for sexual differentiation (Gutzke and Paukstis, 1984), and dem-

onstrate skewed brood ratios under natural conditions (Schwarzkopf and Brooks, 1987; Vogt and Bull, 1984). In a related area, Gutzke and Paukstis (1983) and Paukstis et al. (1984) showed that the moisture content of the nest also can influence the sex of the developing embryos. Clearly, any demographic study of *Chrysemys picta* must take into account the possibility that each annual cohort's initial sex ratio may be strongly biased, which may have significant consequences for population growth and survival.

SEX RATIOS AMONG HATCHLING TURTLES: As there was no opportunity in this study to sex discrete broods of hatchlings, the only practical approach was to determine sex ratios in yearly cohorts. The low level of recruitment mitigates against satisfactory amounts of data as does the inability to sex living juvenile turtles—many are lost from the population before they are old enough to be scored. Nevertheless, some data are available.

Table 7 gives the total number of nonimmigrant turtles known to have entered the population in the years 1964 through 1980 (brood years 1963–1979), categorized by sex. Of the total of 86 turtles, 26 disappeared before being sexed, 44 were males and 16 females. In most instances the number of young in a given year is too small to provide the sex ratio of a statistically reliable sample. One year is a conspicuous exception, however. The brood of 1967 was the largest recorded in 17 years and was almost wholly male—21 of 22 turtles that were sexed. Even in the unlikely event that the six turtles not sexed were all female, the ratio would still be 3:1.

Use of the totals in table 7 to approximate hatchling sex ratio would be misleading, as females entering the population later than 1975 probably would not have grown enough to be scored before the fieldwork terminated. The subtotals through 1974 (there having been no 1975 recruits identified) are 41 males, 16 females, and 19 not sexed. The preponderance of males holds even if the unusual brood of 1967 is subtracted, leaving 20 males to 15 females (1.3:1). Differential mortality is not an adequate explanation, as mortality of both sexes appears to be about the same in the early years and females have a much higher rate of survival later on. It appears

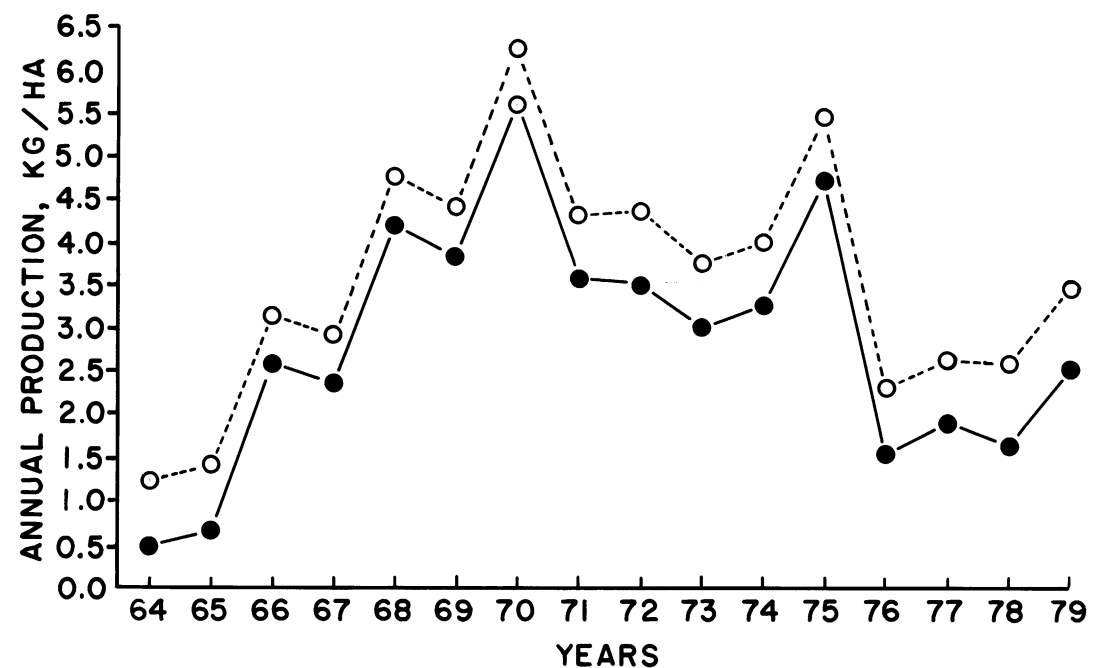


Fig. 16. Estimates of annual biomass production. Solid symbols indicate increment to body mass, open symbols add the estimate of egg biomass giving total productivity.

that conditions during most years of this study favored induction of male phenotypes at a greater rate than female.

POPULATION SEX RATIO: Except for the initial year, for which I have only a single estimate, figures given here derive from population estimates for the period prior to July 1 of each year; ratios for the latter half of the year are little different. Calculation of the sex ratio for the population as a whole has an inherent uncertainty due to the immature individuals that were lost before being sexed. But in most years the sex of more than 90 percent of the population is known, so the uncertainty is relatively insignificant.

The population sex ratio ranged over the years between 0.62:1 and 1.80:1, mean 1.08:1 (fig. 17, table 8). The highest ratio occurred in 1968 with the emergence of the nearly all-male brood of 1967, and males dominated in 11 of 18 years.

ADULT SEX RATIO: As for population sex ratio, the figures for adults are the estimate for the first half of the year except for 1963. The principal potential source of error in these statistics was in judging which females were mature, which had to be done on the basis of size. I have no reason to suspect a bias that

would consistently either inflate or underestimate the numbers of adults of either sex.

Over the course of 18 years the adult sex ratio fluctuated widely, from 0.36 to 1.91,

TABLE 7
Sex Ratios in Cohorts of *Chrysemys*

Brood year ^a	Males	Females	Not sexed	Total
1963	2	0	1	3
1964	0	0	0	0
1965	5	3	2	10
1966	0	4	0	4
1967	21	1	6	28
1968	1	2	3	6
1969	0	0	1	1
1970	1	2	1	4
1971	1	0	4	5
1972	2	2	1	5
1973	6	2	0	8
1974	2	0	0	2
1975	0	0	0	0
1976	2	0	1	3
1977	1	0	1	2
1978	0	0	2	2
1979	0	0	3	3
Totals	44	16	26	86

^a Recruits enter the pond the following year.

TABLE 8
Population Sex Ratio: Males per Female

Year	Adults only	All turtles ^a
1963	0.36	0.62
1964	0.58	0.69
1965	0.73	0.77
1966	0.89	1.23
1967	1.00	0.88
1968	1.00	1.80
1969	1.00	1.48
1970	0.55	1.20
1971	0.83	1.41
1972	1.85	1.41
1973	1.91	1.19
1974	1.30	1.16
1975	1.18	1.28
1976	0.91	1.06
1977	1.36	1.11
1978	1.00	0.89
1979	0.57	0.63
1980	0.69	0.67
Mean	0.98	1.08
Range	0.36–1.91	0.62–1.80

^a Includes all turtles that were sexed, adults as well as juveniles.

with a mean of 0.98 (fig. 17, table 8). In nine years females were more abundant, the sexes were equal in four years, and males were more numerous in five. The high-ratio years (1972 and 1973) are associated with the maturation of males of the brood of 1967, when in the space of three years the ratio changed from approximately one male for two females to two males per female. Variation in sex ratio is largely a function of relative abundance of males. The adult female population varied only between 9 and 14 individuals, whereas males ranged from 4 to 24.

SEX RATIO IN BROODS OF ONE FEMALE: From 1963 to the end of the study of the turtles on the Havemeyer Estate there was a small population of *Chrysemys* in the pond on the Research Station that originated through introductions. For several years only one adult female was present, so young of those brood years must have been her offspring. The numbers and sexes of five year classes were as follows: 1972, 4 males; 1973, 5 females, 1 not sexed; 1974, 4 males, 2 females; 1975, 1 female; 1976, 1 male, 1 female, 1 not sexed. Summed, these figures give a perfect 1:1 ratio (9 of each sex and 2 not

sexed), whereas from year to year the ratios vary greatly. These and figures given above emphasize that sex ratio averaged over several years does not necessarily imply that the 1:1 condition is the usual state in most years.

AGE STRUCTURE

At the start of the study in 1963 all turtles present were too old to be aged by counting scute annuli. For statistical purposes I assigned ages to these individuals according to the youngest age at which a turtle might have reached its size, based on growth data for the population (see Growth). Immigrants whose actual ages were unknown also received assigned ages. The proportion of turtles whose age had to be estimated ranged from 100 percent in 1963 to 13.9 percent in 1974, mean 34.7 percent, but for 13 of 18 years 75 percent or more of the turtles present were of known age. The assigned ages were conservative, and especially the large females present in 1963 (three of which survived to 1980) may have been much older than my estimates.

Figure 18 and table 9 summarize the age structure inferred for my study population. At the start the population comprised mostly older turtles, probably rather older than the conservative age estimates indicate (see above). Recruitment of a few young over the next four years evened out the age distribution somewhat, but the large and almost all-male brood of 1967 (which entered the population in 1968) introduced an asymmetry that persisted for years—unbalanced by any similar enrichment of females. The age-sex polygons (fig. 18) are notable not only for the sexual imbalance they reveal in most years but also for the gaps that result from years of little or no recruitment. The oldest individuals present in the last year, three females at least 25 years of age, were present in the first year. If, as I suspect, these animals are older than is indicated, the true age structure is even more attenuated and uneven than it appears in the figure.

The average age of adult females climbed steadily over the years, relieved only by drops in 1970 and 1971 as members of the 1965 and 1966 broods matured. Males followed a less even trend, with an initial rise and subsequent fluctuations averaging to a gradual

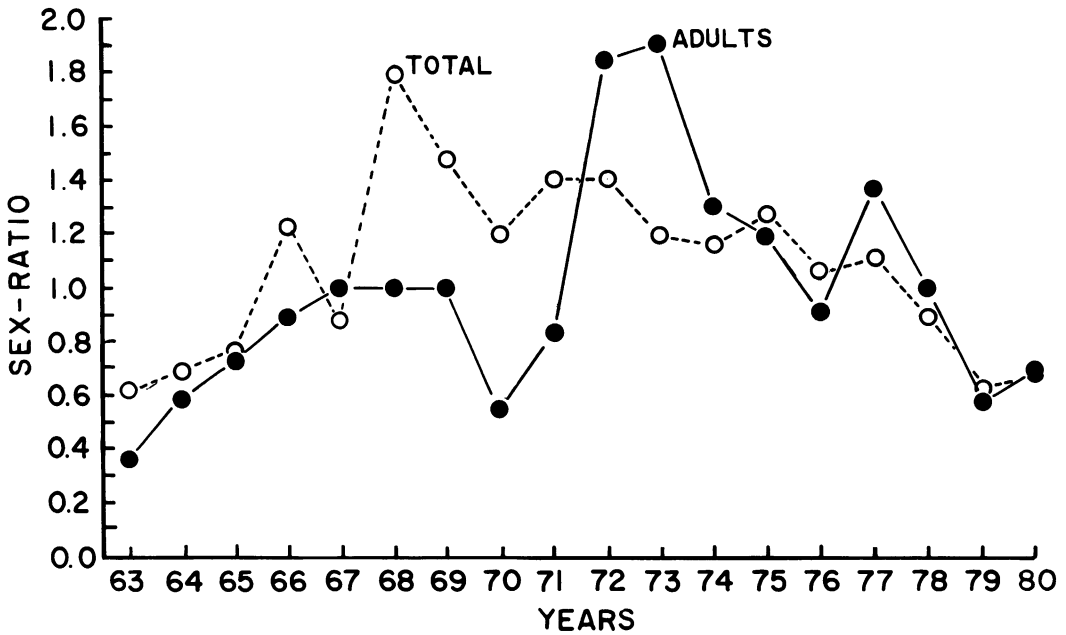


Fig. 17. Annual sex ratio expressed as males per female. Recruitment of a large, almost all-male cohort in 1968 expressed in the total population sex ratio is tracked four years later by a similar upswing in adult males.

increase in mean age. Parallel reductions in mean ages of adult males and females in 1971 are a coincidental result of different ages at maturity, with males of the 1967 and females of the 1965 broods maturing in the same year. Because female maturity is delayed for two years compared to that of the male, it is not astonishing that adult females average somewhat older than adult males (table 9). The difference, however, exceeds the disparity in age at maturity. The younger average age of adult males is due also to greater longevity of females and to the imbalance in sex ratio among younger animals.

COMPARISONS WITH PREVIOUS STUDIES

Reasonably good estimates of the numbers of individuals in natural populations of turtles are extremely difficult to obtain. Bias introduced by different methods of capture and other variables may render capture-recapture calculations of numbers highly questionable. Estimates of population density based on such numbers may be further flawed by the difficulty of deciding how much of the area is

used by the turtles and is thus appropriate in the denominator of the density equation. Biomass studies rarely deal with the actual weights of turtles comprising the population, but are based on estimated weights of turtles of estimated average size. Generally only the ages of individuals comprising the younger segment of the population can be known with accuracy, so population age structure determinations may be at best rough approximations. The value of the product of this compounding of uncertainties is further lessened because most population studies are short-term compared to the life span of the subjects: natural intrapopulation variation goes largely unobserved. With this background, I shall briefly review several papers offering estimates of these numbers-related topics for populations of *Chrysemys picta*. The order is largely chronological, papers dealing mainly with numbers being taken up first.

NUMBERS AND DENSITY: Possibly the earliest published estimate of *Chrysemys* population size was that of Pearse (1923a) for part of University Bay on Lake Mendota, Wisconsin. Unfortunately, the paper had

TABLE 9
Annual Age Structure of a Population of *Chrysemys picta*^a

Year	Adult males			Adult females			Total sample			Ad/Juv
	Mean	Range	N	Mean	Range	N	Mean	Range	N	
1963	5.0	(4-7)	4	6.8	(5-8)	11	5.5	(3-8)	21	2.50
1964	4.9	(4-8)	7	7.4	(5-9)	12	5.8	(1-9)	22	6.33
1965	5.8	(5-9)	8	7.4	(6-10)	11	6.1	(2-10)	22	6.33
1966	6.9	(6-10)	8	9.4	(7-11)	9	5.4	(1-11)	29	1.42
1967	7.1	(4-11)	9	10.4	(8-12)	9	5.9	(1-12)	30	1.50
1968	5.9	(3-12)	9	11.4	(9-13)	9	3.7	(1-13)	56	0.47
1969	6.9	(4-13)	9	12.4	(10-14)	9	4.5	(1-14)	57	0.46
1970	7.7	(5-14)	6	11.9	(5-15)	11	5.3	(1-15)	55	0.45
1971	7.1	(4-15)	10	11.3	(5-16)	12	6.1	(1-16)	53	0.71
1972	5.8	(4-14)	24	11.6	(6-17)	13	6.4	(1-17)	53	2.31
1973	6.3	(5-11)	21	11.9	(7-18)	11	6.6	(1-18)	46	2.29
1974	7.5	(6-12)	13	12.4	(8-19)	10	6.4	(1-19)	41	1.28
1975	8.2	(4-13)	13	12.5	(7-20)	11	7.1	(1-20)	41	1.41
1976	8.3	(3-14)	10	13.5	(8-21)	11	7.6	(2-21)	35	1.50
1977	7.2	(4-15)	15	14.5	(9-22)	11	8.2	(1-22)	38	2.17
1978	8.4	(4-20)	13	14.4	(8-23)	13	9.2	(1-23)	36	2.60
1979	10.6	(5-21)	8	14.8	(7-24)	14	10.3	(1-24)	31	2.44
1980	10.6	(4-22)	9	14.9	(7-25)	13	10.2	(1-25)	30	2.75
Mean	7.2		10.9	11.6		11.1	6.7		38.7	2.16

^a Based on censuses made in spring. Data are expressed as growth years the turtles were in, not years of life completed; e.g., "1" is the "age" of a hatchling that just entered a pond.

mathematical errors. Petokas (1981) noted that Pearse's density estimate was unusually low (5.02/acre, or 13.55/ha) and found that Pearse had misplaced a decimal point, so his study area was 20.25 ha, only one-tenth of the size he had calculated. Petokas used Pearse's proportional index estimate of 2774 turtles to recalculate the density at 135.5/ha, but even that figure requires adjustment, as Pearse erred also in his calculation of numbers. With a base of 402 marked turtles, he captured 314 unmarked and 46 marked and estimated the population as $402(314)/46 = 2774$ rather than $402(360)/46 = 3146$, or about 155/ha. Pearse noted that "the distribution of the turtles was very unequal" in his study area, with "probably three quarters of it 'barren' of turtles." Hence, the "economic density" (density in the area actually used by the turtles) presumably was even higher.

Ream and Ream (1966) conducted their important study of sampling methods at the same site as Pearse (1923a). Their two estimates of population size for periods a month apart were 891 and 878. They offered no density figures, but Bayless (1975) estimated the study area at 66 acres (26.7 ha), which yields

an average density of 33.1/ha for the two size estimates.

Sexton (1959a) estimated that about 1000 *Chrysemys* inhabited his study area on the E. S. George Reserve in Michigan in 1954, where the suitable habitat varied from 2.4 to 10.1 ha between extreme drought and high water. Corresponding densities are 417 and 99 turtles per ha. Wilbur (1975b) studied the same population and found a population size of only 186 turtles 17 years later (77.5 and 18.4/ha using Sexton's area extremes). Congdon et al. (1986) provided a third estimate (1975-1983) of 39.9/ha (292 turtles) based on an average of 7.3 ha of usable aquatic habitat.

For a marsh in Michigan with about 4 ha of *Chrysemys* habitat, Gibbons (1968a) estimated a population of 2328, density 576/ha.

Comparing differing collecting methods in a 1 acre (0.405 ha) pond in Quebec, Bider and Hoek (1971) derived a best estimate of 112 individuals, equivalent to a density of 276/ha.

Ernst's (1971b) estimate of 1913 turtles in 8 acres (3.24 ha) of pond and marsh in Pennsylvania converts to 590/ha. Ernst and Ernst

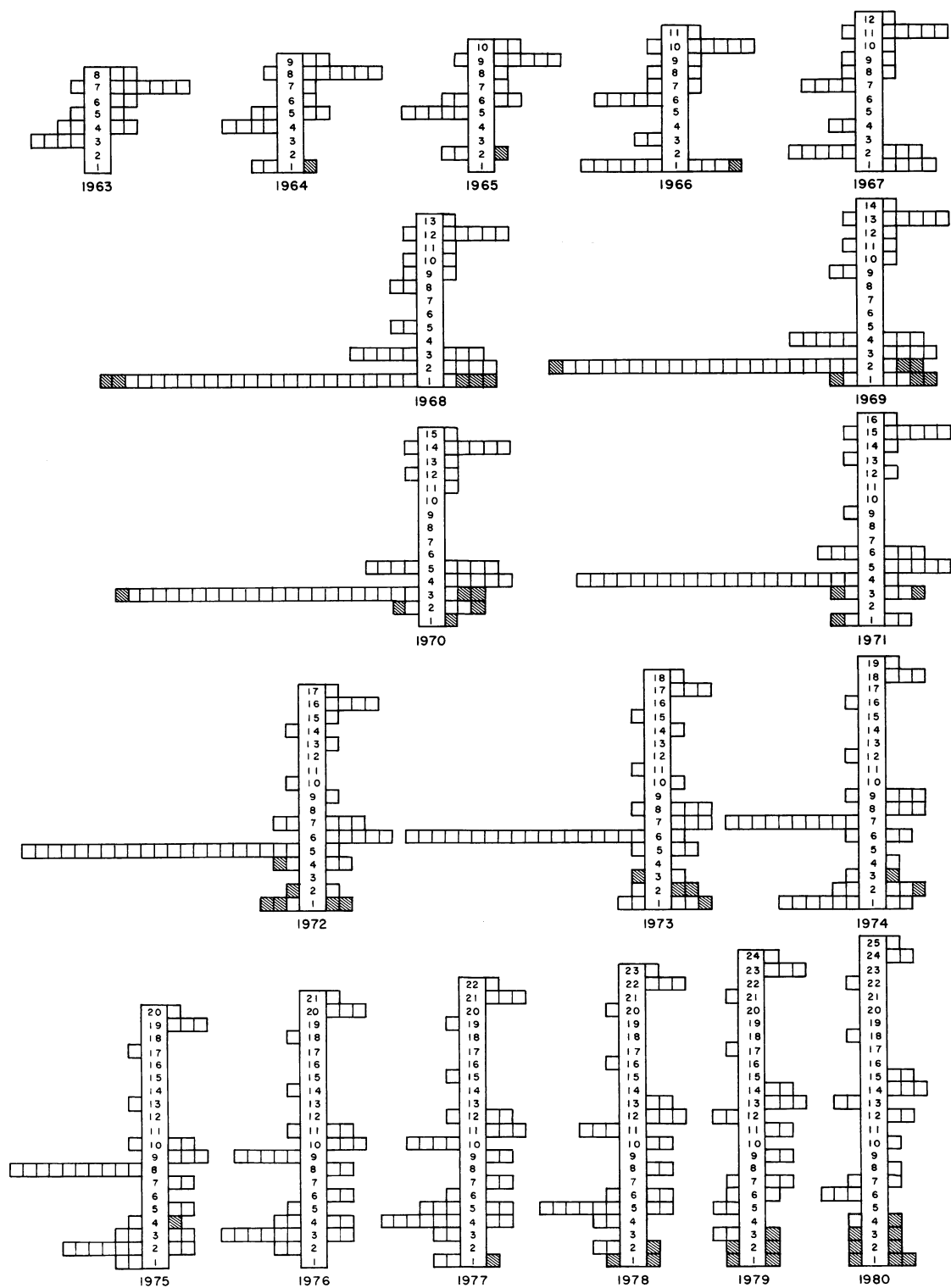


Fig. 18. Estimates of annual age structure. Each box represents one turtle—males left, females right. Numbers in central columns are growth years—i.e., 1 = hatchlings. Shaded boxes represent unsexed individuals distributed equally among males and females except uneven numbers graphed as females.

("1972" [1973]) estimated four turtles per acre (9.9/ha) for 81 ha of shoreline of a lake in Minnesota, but recognized that this figure probably erred on the low side. These two Lincoln Index estimates do not engender confidence. The first is based on a two-day sampling period with nine marked turtles (302 at risk) in a sample of 57; Ernst calculated 95 percent confidence limits of 777 to 3049 turtles. The second was based on only one marked turtle in a sample of 14 (57 at risk).

Bayless (1975) studied *Chrysemys* in a pond (4 ha) in New York and for three consecutive years obtained Lincoln Index estimates of 65, 77, and 78 turtles, yielding density figures of 22.2, 24.7, and 27.2/ha. In contrast, a smaller (2.75 ha), shallow, and eutrophic reservoir in Virginia had an estimated density of 188/ha (Mitchell, 1988).

Study of an oxbow lake complex in Nebraska (McAuliffe, 1978) gave estimates of changes in density that took place as parts of the complex dried from 8.5 ha of open water in spring to about 1 ha in a dry summer and turtles migrated to the slough with water remaining. The population estimate of 360 turtles for late summer suggests minimum and maximum densities of about 42 and 360/ha.

The only data for numbers in a river population are those of MacCulloch and Secoy (1983b). Their Lincoln Index estimates (and 95% confidence intervals) for three years were 149 (127–175), 186 (161–215), and 167 (144–194) turtles along 15 km of river. Using an average river width of 10 m and accepting the last estimate as the best, these authors calculated a density of 11.1/ha. However, they also noted that prey items (*Chrysemys* here is wholly carnivorous) "were concentrated within 1 m of the banks" of the turbid river. If only this area that provides food is considered, the economic density would be 55.7/ha.

The estimates of population size quoted above are of variable quality. Ream and Ream (1966) and Bider and Hoek (1971) concentrated on obtaining representative samples and presumably derived reasonable figures. Collecting at the E. S. George Reserve (Sexton, 1959a; Wilbur, 1975b; Congdon et al., 1986) took advantage of seasonal movements to intercept a large proportion of the population at drift fences. Gibbons (1968a)

and MacCulloch and Secoy (1983b) worked intensively for the activity seasons of three years to obtain their estimates. McAuliffe (1978) and Bayless (1975) had relatively high percentages of recaptured turtles in their samples, which implies greater accuracy of the estimates. Bayless, however, excluded "newly recruited juveniles" from his calculations. As it is likely that his "juveniles" were actually in their second growth year (see Seasonal Activity) and were in the population during the marking period, they should have been considered and would increase his population estimates. The estimates for Pearse's (1923a) and Ernst's (1971b) populations are based on relatively small percentages of recaptured turtles and may be less accurate. That of Ernst and Ernst ("1972" [1973]) may be ignored.

Even allowing for the imprecision of the data, the range of numbers and densities in *Chrysemys* populations evidently is wide, with densities varying at least by a factor of 10, perhaps as high as 20. Considering the variety of habitats under which different populations live, this is not astonishing. It is perhaps unexpected, though, to find more than a sevenfold range in a small population of limited, probably suboptimal habitat (table 5).

The range of numbers in my population over 18 years was from 21 to 57, the maximum being 2.7 times the minimum. The meager comparative data suggest that large populations may undergo proportionally even greater changes. Petokas (1981) compared the population estimates of Ream and Ream (1966) with that of Pearse (1923a, as revised by Petokas) for the University Bay site in Lake Mendota and noted the apparent decline in numbers in the 40 years between sampling. Using my additional refinement of Pearse's estimate, the population in the early years may have been 3.6 times as large as when Ream and Ream worked. Even though the early estimate may not be of a high level of accuracy, turtles clearly were quite abundant in Pearse's time—witness his capture of 360 *Chrysemys* in three days of dip-netting.

The long-term studies carried on in Michigan's E. S. George Reserve allowed Congdon et al. (1986) to document changes in density from about 134/ha in 1953–1955 to 25/ha in

1968–1973, and rising to 40/ha in 1975–1983. The greatest density here is 5.4 times the smallest.

The reasons for various and varying densities are no doubt manifold and have not clearly been elucidated. In the case of my population the peak in density resulted from the recruitment of one unusually large year class, but what the conditions were that combined to favor successful nesting and hatchling survival that one time is unknown. Wilbur (1975b) speculated on the reasons for the decline in the E. S. George Reserve population and concluded that a rapid reduction in the carrying capacity of the habitat possibly related to deepening the pond by drag-line was responsible.

Quality of the habitat must bear heavily on the number of turtles it can support. Bayless (1975) noted that high densities reported in the literature were for sites where there was a high ratio of marsh to open water, even though the turtles might not make much direct use of the marsh. The population that Bayless studied had little marsh relative to the pond size and had a low density of turtles (ca. 24/ha). The low density of turtles in a river reported by MacCulloch and Secoy (1983b, 11/ha) correlates with the small proportion of the habitat that provides food (see above).

BIOMASS: There are few published data on painted turtle biomass. Iverson's (1982a) paper summarizing biomass in many turtle species included estimates for three populations of *C. picta*. These estimates covered a wide range: 11.2 (lake in Indiana), 28.2 (pond in Michigan), and 106.4 (pond in Pennsylvania) kg/ha. For the most part, the figures derive from published estimates of population density and estimates of mean body size and weight. At least some of these data are open to reinterpretation. Congdon et al. (1986) regarded Iverson's estimate of 28.2 kg/ha for the Sheriff's Marsh, Michigan, population (Gibbons, 1968a) to be based on too small a mean turtle size. The recalculated biomass, based on a larger mean size, is considerably greater: 73.6 kg/ha.

The biomass of 106.4 kg/ha is the largest estimated for *C. picta* and is based on Ernst's (1971b) density figure of 590 turtles per ha. I have (above) expressed some reservations

about the adequacy of the sampling for this density figure and cannot accept it as reliable.

In addition to their recalculation of the Sheriff's Marsh population, Congdon et al. (1986) provided biomass figures for three *Chrysemys* habitats on the well-studied Edward S. George Reserve in Michigan. Single estimates for East Marsh and George and Burt Ponds are, respectively, 16.6 and 7.4 kg/ha. Estimates for the Southwest Reserve cover a period of years with varying population size: 1953–1955, 24.2 kg/ha; 1968–1973, 4.6 kg/ha; 1975–1983, 7.2 kg/ha.

The minimum biomass figures (all ponds at highest water level, table 5) for my population of *Chrysemys* averaged 23.5 kg/ha (range 15.7–30.0). But at the time of greatest concentration of individuals in a single pond, a peak of 91.3 kg/ha was attained. I think it is clear that knowledge of *Chrysemys* biomass (and that of other turtles too) is in a most primitive state. Biomass per unit area may differ by a factor of 20 (4.6 vs. 91.3) among different populations at different times, and by nearly as much in a single population. Any attempt to relate biomass to habitat will have to be based on far better data than are currently available.

PRODUCTIVITY: If there is little reliable information on biomass, there is even less on productivity. Iverson (1982a) used data from Wilbur (1975a, 1975b) and Sexton (1959a) in deriving an estimated annual production of 6 kg/ha/year for the Southwest Reserve population on the George Reserve. The calculations involved several assumptions that have turned out to be not necessarily valid: 1—the population was stable (Congdon et al., 1986, indicate that this was not the case); 2—the life table data are accurate (Tinkle et al., 1981, present data that substantially alter the life table); 3—the population density was approximately 520 turtles/ha (Congdon et al. believe that this density figure is inflated).

The annual production calculated for my population averaged about 2.8 kg/ha, range 0.5–5.6, considering only turtle growth. Adding to this the estimated production of egg biomass (an admittedly tenuous figure) gives a total mean annual production of 3.5 kg/ha, range 1.2–6.2 (table 6). Productivity figures from future studies, if they are to be useful in a comparative fashion, must take into ac-

count not only differences among habitats, but also the age structure of the population at the time of sampling.

SEX RATIO: The literature on sex ratios of *Chrysemys picta* populations is scanty, confined to adult turtles, and in part of questionable value.

Ream and Ream (1966) demonstrated clearly the problems associated with deducing sex ratio from capture data. They compared several methods of collecting *Chrysemys* and found that none sampled adult males and females in their true proportions. A combination of hand capture and various trapping methods, intensively applied, provided what they considered a reasonable estimate of 1.3:1 for a lake-dwelling population in Wisconsin.

Several studies have provided estimates at or quite close to 1:1, notably Ernst (1971b), Gibbons (1968a), MacCulloch and Secoy (1983b), Mitchell (1988), and Wilbur (1975b). Bider and Hoek (1971) developed a movable blind that facilitated hand capture and produced, they felt, a reliable adult sex ratio estimate of 0.82:1. Studies by Balcomb and Licht (1987) and Bayless (1975) produced disparate ratios (0.54:1 and 1.4:1, respectively), but in both cases the authors had doubts about the reliability of the estimates.

The estimates in the literature generally represent ratios calculated from relatively short-term sampling or data averaged over a few years. In neither case does this reveal anything about annual variation and may be misleading if it assumed that the data represent a usual condition in a population with stable age structure. As an example, I call attention to Wilbur's (1975b: table 3) summary of seven years of age structure in the George Reserve population. Wilbur states (p. 72) that the "adult sex ratio . . . is not significantly different from unity." If the ratio for each of the seven years is calculated from the data in the table, and these yearly ratios are averaged, the mean of the years truly is close to unity (1.03:1). But the ratios for the individual years range from 0.63 to 1.27:1.

It is curious that the seemingly wide range of adult sex ratios reported in the studies cited (0.54–1.4:1) is exceeded by that found in my study (0.36–2:1), especially since I consider my figures to be more accurate. A contrib-

uting factor in my population was its small size—fewer than 40 adult turtles at most. In this circumstance, the occurrence of a large, virtually all-male year class strongly perturbed the sex ratio for years. Swinging sex ratios such as those I observed may be less common in larger, better buffered populations, but this cannot be known from data available at present. Not only is the methodology for assessing the ratios inadequate to most field situations, but the durations of the studies have been too short, generally only two or three years. I endorse Mitchell's (1988: 52) statement: "Comparisons of this population characteristic among populations should be based only on multiple mark-recapture methods in multi-year studies."

AGE STRUCTURE: The literature holds no good data on *Chrysemys* population age structure. There are no studies in which the proportion of the very youngest turtles is known with a high degree of accuracy (owing to sampling bias), none in which the sexes of immature turtles other than females too large to be adjudged adult males are known, and none in which the ages of most individuals too old to be aged by counting annuli are known. Furthermore, most studies report the situation at only a brief slice of time; annual variation usually goes unreported. Nevertheless, some interpopulational comparisons can be made.

All data suggest that *Chrysemys* populations have a great age span, possibly well over 30 years. (Gibbons and Semlitsch, 1982, extrapolated to a maximum age of 30 years for a population of the related *Pseudemys scripta*.) Gibbons (1987) described *Chrysemys* on the George Reserve marked in 1953–1957 and recaptured in 1975–1986. The average "age pyramid" probably would be more of a narrow tower than a pyramid, heavier on the female side in the upper reaches. This shows in the figures of Wilbur (1975b: fig. 2) and Mitchell (1988: fig. 3), with their preponderance of individuals in the 11+ age group, and in figure 18, where the ages of the topmost individuals most likely are underestimated.

The ratio of adult to immature turtles is reported in many studies. Estimates of this ratio may be biased in favor of the smallest turtles if hand capture predominates or biased against them if one or another trapping meth-

od is emphasized (Ream and Ream, 1966). The ratios in several papers by Cagle (included in Ernst's [1971b] table 5) evidently are biased toward juveniles (Ream and Ream, 1966), so are not considered further here. The lowest ratio of adults to juveniles among several of the probably more reliable studies is 0.67 taken from estimated population data in Gibbons (1968a: table 3); his count of actual captures gives a ratio of 0.92. (Ernst, 1971b: table 5, used the higher figure.) Much higher ratios may be calculated from data in several other studies: 3.0 (Bider and Hoek, 1971); 4.2 (Ernst, 1971b); 4.6 (MacCulloch and Secoy, 1983b); and 5.0 (Bayless, 1975). Two papers have data for several years: Wilbur (1975b: table 3) combined his data with earlier studies on the same population, yielding ratios of 0.75 to 2.11 (mean 1.46) over seven years. Mitchell's (1988) data cover three consecutive years with similar ratios: 1.2, 1.0, 1.3. The range in ratios for my 18 year sample exceeds that found before: 0.45 to 6.3, mean 2.16 (table 9). It may be noted that there is no obvious correlation between habitat type and adult/immature ratio. The highest and lowest ratios come from the same (small pond) population in different years, and other samples appear to vary without regard to habitat.

These figures, crude as they may be, make it evident that population age structure, or at least the relative proportion of juveniles, is not stable. Varying annual recruitment probably is the principal factor in the variation in numbers of younger turtles, while high survival of older turtles, females especially, gives some stability in the higher levels of the age pyramid. Demographers without pertinent data should not assume that an age structure is stable.

NATALITY, RECRUITMENT, AND SURVIVAL

NATALITY AND RECRUITMENT

NATALITY: The basic data pertinent to estimating annual population natality include the number of reproductively active females, the number of eggs per clutch, the fertility rate, and the number of clutches per female. In the present study, such data are lacking. Only the number of adult females, which is not necessarily the same as the number ac-

tually nesting, is known. Any estimate of natality for my population must necessarily involve a large amount of guesswork and should be taken as only a rough approximation.

Recent reports cast considerable doubt on the adequacy of estimates of natality parameters in earlier works. The occurrence of multiple nesting within one season has been a point of contention. Numerous reports of multiple nesting based on examination of reproductive tracts (e.g., Sexton, 1959a) provided inferential rather than direct evidence, and Ernst (1971a: 199) noted that multiple nestings "have never been proven." He went on to speculate that if such nestings do occur, the short northern egg-laying season would restrict them to southern populations. Yet subsequent unquestionable reports of multiple nesting dealt with northern populations: one in the Upper Peninsula of Michigan (Snow, 1980), another Michigan population (Tinkle et al., 1981), and two in Ontario (Balcombe and Licht, 1987; Schwarzkopf and Brooks, 1986). Tinkle et al. (1981) estimated that about 6 percent of the females produced two clutches, and 50–70 percent of the females nested. Schwarzkopf and Brooks (1986) estimated that 43–73 percent of the adult females in their study population nested in a given year, and 12–13 percent of these nested twice in a year. For the purpose of estimating annual natality in my population I have roughly averaged the estimates of the foregoing two studies, assuming that 60 percent of the females of breeding age nested and 10 percent of these nested twice each year. I use the number of adult females known to be present as the basis for estimating breeding cohort.

Data on clutch sizes for turtles in my study area are available from several publications: Finneran, 1948 (Connecticut); Nichols, 1933 (Long Island); Schlauch, 1971 (Long Island); Wilcox, 1933 (Long Island). In addition, Mr. Michael Klemens has given me data for several turtles from Connecticut and New Jersey. For 28 egg complements the range is 4–11, mean 6.8 ± 0.3 . I have used this average in computing estimated natality values presented in table 10. For the breeding group of 6 to 9 females (out of a population of 9 to 14 adult females) the estimated annual natality ranged from about 41 to 61 eggs, mean 49.7.

TABLE 10
**Estimated Reproductive Potential
 and Observed Recruitment**

Year	Number of females	Estimated clutches ^a	Potential eggs ^b	Number of recruits ^c
1963	11	7	48	3
1964	12	8	54	0
1965	11	7	54	10
1966	9	6	41	4
1967	9	6	41	28
1968	9	6	41	6
1969	9	6	41	1
1970	11	7	48	4
1971	12	8	54	5
1972	13	9	61	5
1973	11	7	48	8
1974	10	7	48	2
1975	11	7	48	0
1976	11	7	48	3
1977	11	7	48	2
1978	13	9	61	2
1979	14	9	61	3
Mean	11.0	7.2	49.7	5.1

^a Based on 60% of females nesting and 10% laying two clutches, rounded to nearest whole number of clutches.

^b Based on 6.8 eggs per clutch, rounded to the closest whole number.

^c Tabulated in the year in which eggs were laid, but hatchling turtles enter the population in the following year—e.g., 3 recruits of the 1963 brood emerged from the nest in 1964.

RECRUITMENT: The number of young known to have entered the population in any one year ranges from zero to 28, mean 5.1. This represents an annual mean of 10.3 percent of the estimated natality actually recruited, or a mean of about 0.7 recruits per breeding female.

The number of recruits tabulated certainly underestimates the total hatched and those that actually reached the ponds. Intensive fieldwork did not commence until June, and very young turtles were captured only by chance until later in their first year in the ponds when they more frequently entered traps. Of seven hatchlings captured initially in May and June, five were never seen again whereas two survived for 5 and 14 years. In contrast, among 41 turtles captured first in July of their first year or later, 25 lived for at least six years and 8 for five years. I infer that a hatchling that lives to midsummer of its

first year in the pond has survived a most perilous period. It would be extrapolating from too few data to assume that my midsummer and later captures represent only 2/3 of the actual number to reach the ponds, but it would be equally naive to think there was no successful nesting just because no young were captured.

SURVIVORSHIP

Ideally, one would wish to gather survivorship data from large samples of cohorts of known age, commencing with conception and terminating with the death of the last individual. Such conditions are probably never attainable in the field and the present study is no exception. In the absence of any hard information on the natality in my population (though some speculation has been offered), it is still possible to examine the survival of turtles known to have been present in the first year of study as well as those entering the population later.

SOURCES OF MORTALITY: Over the 18 years of field study we identified 118 turtles as members of the population. At least 30 of these still were alive in the last year, and the deaths of only 11 were verified. The balance of 77 must include some that died in the study area but whose remains were not found as well as others that emigrated (see Movements) and also probably a small number actually alive and present in the last year but that evaded capture. Considering the remoteness of the study area from other suitable habitats, emigration must have carried with it a high probability of death within a relatively short time. Whatever the cause, any instance of permanent disappearance from the population must for demographic purposes be treated as mortality.

Some of the mortality resulted directly from human intervention. An ill-advised treatment of a pond with rotenone (to remove an equally ill-advised introduction of exotic fish) resulted in the known deaths of three turtles. Two others not seen after the poisoning may have died then, but are not included in the total of 11 known deaths. Two turtles died, evidently drowned, when entangled below water level in traps. Four others possibly died when ponds were dredged in a time of drought

as they were not captured subsequent to the dredging.

Potential predators that might take turtles of any size included raccoons, red foxes, and dogs. Small turtles would be vulnerable also to large bullfrogs (which are known to eat turtles, including *Chrysemys picta*—Lewis, 1962) and herons. Four turtles found dead apparently had been killed and at least partly devoured by predators. Unidentified diseases evidently were a source of mortality. One turtle found on shore in the fall in a highly infected condition (throat badly swollen, unable to withdraw its head) was a well-decomposed corpse when seen next the following spring. Another turtle in even worse condition when last seen presumably also succumbed to disease but is not included among the 11 known deaths. One turtle found floating in a pond showed no apparent cause of death.

TURTLES OF KNOWN AGE: The first data presented pertain to animals of known age, those captured initially when still young enough that their age could be determined by growth ring counts. The basic data are in table 11, which gives the number of turtles of each age class present at the beginning of the year and the number known to have survived into the next year. Year "0-1" (growth year 1) is the initial year in the pond, the young turtles presumably having hatched in the late summer or fall of the previous year and remained in the nest over the winter (see Seasonal Activity). Samples of both sexes are pooled for the first two years. The sex of many of the juveniles was known, but the advantage of larger sample size outweighs, in my estimation, segregation of these small juveniles. Sample sizes decrease markedly in the older age classes, not only because of attrition but because with a finite study period many animals entered the population too late to contribute much information on the extent of their longevity. Samples of younger turtles contain many more males than females. This is due largely to a single large year class that was almost wholly male (see Sex Ratio).

The data of table 11 are normalized in table 12 as a partial life table, and survivorship is graphed in figure 19, where curves for cohorts of 100 male and 100 female turtles are superimposed. These represent turtles *estab-*

TABLE 11
Survival of *Chrysemys picta* of Known Age

Year ^a	Males and (years 0-2) all juveniles			Females		
	N1 ^b	N2	N2/N1	N1	N2	N2/N1
0-1	81	73	0.901			
1-2	70	67	0.957			
2-3	42	40	0.952	16	16	1.000
3-4	40	39	0.975	16	15	0.937
4-5	39	26	0.667	15	14	0.933
5-6	24	13	0.542	14	12	0.857
6-7	12	11	0.917	11	10	0.909
7-8	11	6	0.545	9	9	1.000
8-9	6	5	0.833	9	8	0.889
9-10	5	4	0.800	7	7	1.000
10-11	4	3	0.750	7	7	1.000
11-12	3	2	0.667	5	5	1.000
12-13	—	—	—	5	5	1.000
13-14	—	—	—	2	2	1.000

^a Year 0-1 is the turtles' first year in the pond.

^b N1 = number alive at beginning of year, N2 = number surviving to next year.

lished in the ponds and do not take into account earlier mortality. If my estimated natality and recruitment figures have any reality, a cohort of 100 established represents the survivors of about 1000 eggs.

Once established in the pond and through their first four years, male and female turtles alike experience a high rate of survival. An average of almost 95 percent of marked turtles alive in one year survived to the next year. But by the end of year 5, a remarkable dichotomy develops: female survival continues at much the same rate as before, but loss of males assumes a new and vastly steeper rate. The adequacy of my data for the far-right segments of the curves may be questioned because of the small sample sizes, but the schism develops much earlier. In year 4-5, one-third of 39 male turtles disappeared, whereas only one of 14 females was lost (table 11). Similarly, in the next year nearly half of 24 males but only two of 14 females were lost. Male survival thereafter fluctuated from year to year, possibly a random effect of the small sample size. Females, however, were not similarly influenced, and had a continued high rate of survival.

The sudden increase in apparent male mortality at about five years correlates both

TABLE 12
Partial Life Table for *Chrysemys picta*^a

x	dx		lx		qx	
	M	F	M	F	M	F
0-1 ^b	9.9		100		0.901	
1-2	3.9		90.1		0.957	
2-3	4.1	0.0	86.2	86.2	0.952	1.000
3-4	2.0	5.4	82.1	86.2	0.974	0.937
4-5	26.6	5.4	80.0	80.8	0.668	0.933
5-6	24.5	10.8	53.4	75.4	0.541	0.857
6-7	2.4	5.9	28.9	64.6	0.917	0.909
7-8	12.1	0.0	26.5	58.7	0.543	1.000
8-9	2.4	6.5	14.4	58.7	0.833	0.889
9-10	2.4	0.0	12.0	52.2	0.800	1.000
10-11	2.4	0.0	9.6	52.2	0.750	1.000
11-12	2.4	0.0	7.2	52.2	0.667	1.000
12-13	—	0.0	4.8	52.2	—	1.000
13-14	—	0.0	—	52.2	—	—

^a Column definitions: *x*, age groups; *dx*, number dying in interval of 100 recruited; *lx*, number surviving at beginning of interval of 100 recruited; *qx*, mortality rate per 100 alive at beginning of age interval.
^b Sexes not segregated in 0-1 and 1-2 age groups.

with sexual maturity and with a considerable increase in the amount of interpond and probably emigratory movement (see Movements). Increased movement on land could contribute to actual mortality in rendering the turtles more exposed to predation while emigration would contribute to apparent mortality.

SURVIVAL OF THE 1963 POPULATION: Another way of looking at survivorship is to chart the survival of all animals in the population at a given time regardless of their age. I have assembled (table 13) such data for the population in the initial year of study, 1963. There were at the time 13 females and 8 males, the smallest population size in 18 years of study. No exact ages were known, though males clearly averaged younger than females (see Age Structure). The pattern of survival is similar to that seen in the sample of animals of known age: males declined abruptly after the first few years while females survived at a much higher rate. The last male turtle to die was the oldest and was killed by accident. It might otherwise have extended the male curve for several years, as it obviously was an old and well-established individual.

The view of survivorship given in figure

19 is unrealistic, however, as it does not consider the environmentally induced sex ratio of *Chrysemys*. Among 60 nonimmigrant individuals that entered the population over 17 years, about 73 percent were male (table 7). With this in mind, I present a pair of survivorship curves (fig. 20) based on the same rates of survival as the preceding but assuming that in a cohort of 1000 eggs, those that produce recruits do so in a male-female ratio of 73:27, resulting, after losses of nests and hatchlings, in 73 males and 27 females that become established in the ponds. With annual survival equal in the two sexes for the first few years, males remain numerically dominant. By the time females begin maturing in their sixth year in the pond (seventh since conception), male numbers have begun to drop, resulting in rather similar numbers of males and females for a time in the region where the lines cross.

It is tempting to infer a relationship between the differences in rate of survival between the sexes and the initial sex ratio, whereby similar numbers of the two sexes exist when the females first mature. However, there is no assurance that the sex ratio of recruits I observed is valid over long periods of time—it could result from chance fluctuations in a small sample.

COMPARISONS WITH
PREVIOUS STUDIES

There have been few attempts to set numbers to the course of natality and survival in *Chrysemys*. One of the first was that of Gibbons (1968a), treating a population in Michigan. He suggested that only about 2 percent of eggs produced hatchlings that were recruited into the population, that juvenile mortality was close to zero, and that the higher adult mortality was at a constant rate independent of age. Subsequent research suggests that some of the assumptions leading to Gibbons' conclusions were incorrect. His estimate of natality assumed that every adult female laid two clutches a year totaling 13 or 14 eggs. Applying the averages I used in estimating natality (60% of females nesting, 10% double clutching) would reduce Gibbons' natality estimate by about two-thirds, increasing the recruitment to about 6 percent. Also, it seems likely that the age structure Gibbons

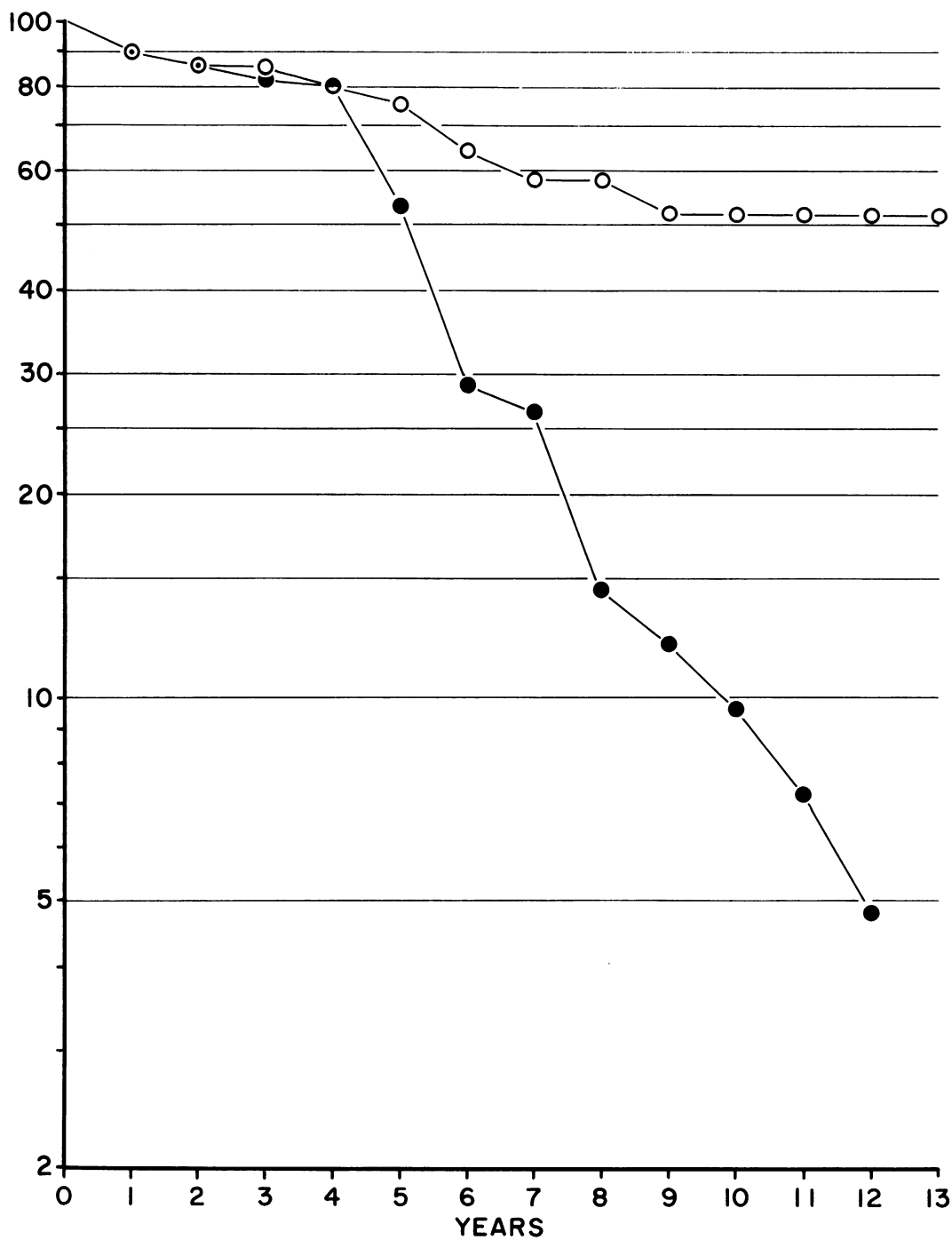


Fig. 19. Survivorship of *Chrysemys* males (solid symbols) and females, based on cohorts of 100 turtles recruited. Year zero is the time the hatchling enters the pond, almost one year after oviposition.

used in estimating adult survivorship is inaccurate (see Growth).
Ernst (1971b) assumed that his study population was static in size, so that recruitment

equaled mortality. Estimating population size and natality, he derived an annual population turnover of 51 percent. Because of his low numbers of captures and recaptures of young

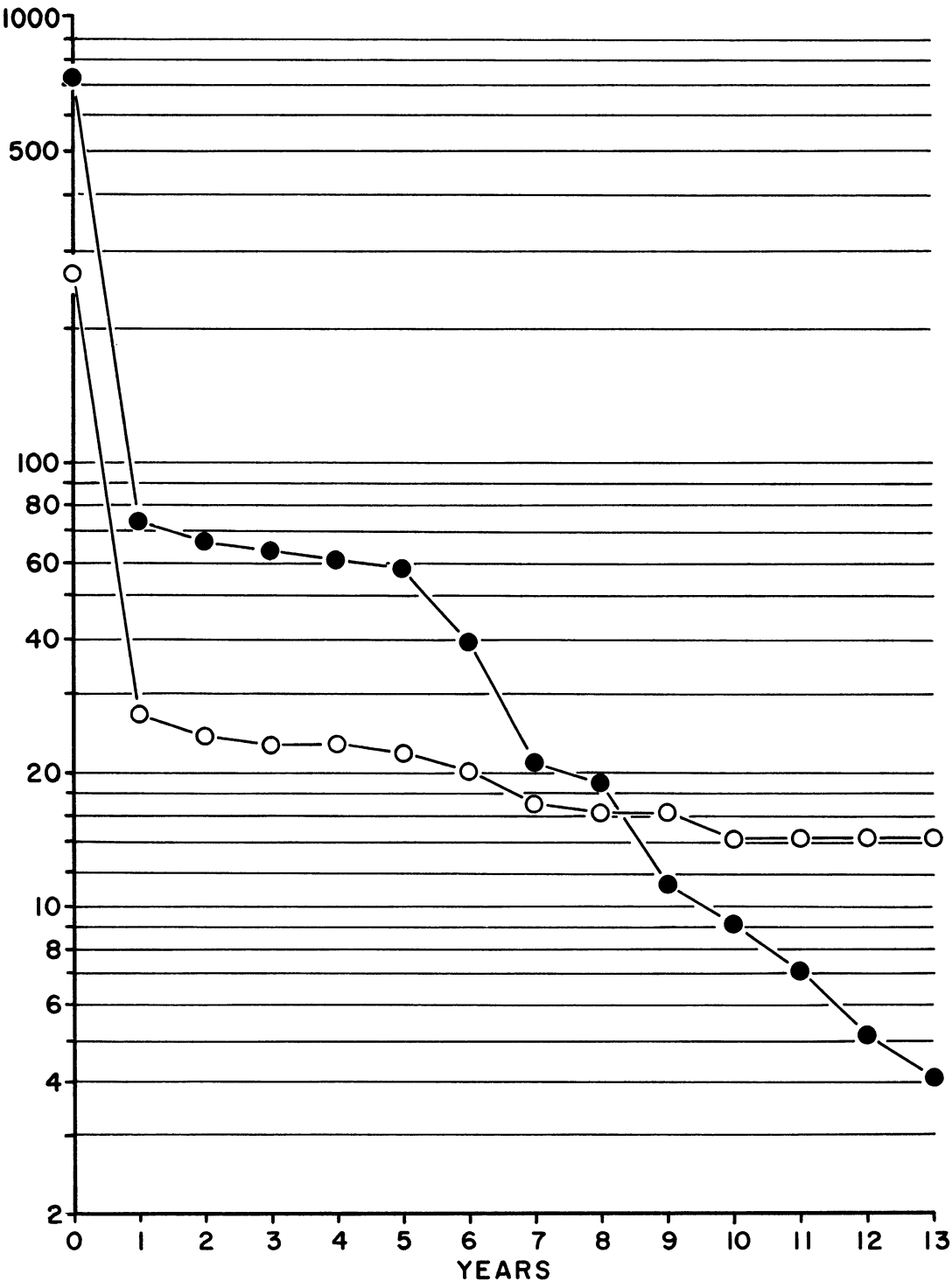


Fig. 20. Hypothesized survivorship of a cohort of 1000 turtles, with initial numbers of males and females adjusted to the sex ratio of recruits observed in the study population. The initial point in this graph is oviposition, not recruitment to the pond as in fig. 19.

turtles, he assumed that most of the mortality took place in these younger stages.

There are questionable areas in Ernst's treatment. The initial assumption that the population size was static is not supported, as it was only estimated once (by Lincoln Index) early in the first of three years of study. The average clutch size (4.7) and percent hatching (55%) estimates seem low, but the assumption that all females nested annually would tend to offset any underestimates. He was aware of the possibility of more than one clutch per female but had no basis for adjusting his estimate for this.

Wilbur (1975b) was the first to venture life tables and a survivorship curve for a population of *Chrysemys*. His data came not only from his own studies on the E. S. George Reserve but also from Sexton's earlier studies of the same population. He calculated first year survival (oviposition to recruitment) of 0.08 for the 1954 cohort and 0.18 for 1972. With recaptures of Sexton's turtles providing a long-term basis, Wilbur estimated adult female survival of 0.83 annually based on the 1954 data and 0.76 based on his later sample. He considered these to be constant annual rates, and noted a somewhat higher mortality rate for male turtles.

Tinkle et al. (1981) continued the study of the George Reserve population and gathered data that required revision of assumptions made in calculating Wilbur's life table. Whereas Wilbur assumed that all adult females nested twice annually, Tinkle et al. presented evidence for considerably fewer females nesting and few of these nesting twice. Furthermore, these authors presented data from direct observation showing much greater survival to hatching—almost four times the higher rate postulated by Wilbur (see below). Tinkle et al. also assumed a steady mortality rate from hatching on.

The most recent estimates of survivorship in *Chrysemys* are those of Mitchell (1988) for a Virginia population. For two years, Mitchell calculated that 16.2 and 22.4 percent of eggs produced recruits. Like Wilbur, Mitchell assumed that all females nested each year and all nested twice. Here too the possibility exists that the annual production of eggs was much lower than estimated so that the survival to recruitment was larger than the per-

TABLE 13
Survival of 1963 Population of *Chrysemys picta*

Year	Males			Females		
	N1 ^a	N2	N2/N1	N1	N2	N2/N1
1963	8	7	0.875	13	12	0.923
1964	7	7	1.000	12	11	0.917
1965	7	6	0.857	11	9	0.818
1966	6	6	1.000	9	9	1.000
1967	6	4	0.667	9	9	1.000
1968	4	3	0.750	9	9	1.000
1969	3	1	0.333	9	9	1.000
1970	1	1	1.000	9	8	0.889
1971	1	0	0.000	8	7	0.875
1972	—	—	—	7	5	0.714
1973	—	—	—	5	4	0.800
1974	—	—	—	4	4	1.000
1975	—	—	—	4	4	1.000
1976	—	—	—	4	4	1.000
1977	—	—	—	4	4	1.000
1978	—	—	—	4	4	1.000
1979	—	—	—	4	3	0.750
1980	—	—	—	3	?	—

^a N1 = number alive at beginning of year, N2 = number surviving to next year.

centages given, which compared known recruits to estimated eggs.

Mitchell's capture-recapture data indicated 94–96 percent annual survival for adults and immature females, and 46 percent survival for juveniles.

The area of natality and recruitment has, as the above discussion indicates, been one of the softest spots in calculations of survivorship. Important recent contributions provide significant, hard data that conflict with the common assumptions of high nesting rates and high nest mortality. Tinkle et al. (1981) inferred that 50–70 percent of females reproduced each year and about 4 percent nested twice in a given year. Direct observation of nests revealed survivorship to age one (age zero being oviposition) of 67 percent over three years of study. Christens and Bider similarly monitored nests (in Quebec) and in one year recorded hatchlings emerging from 25 percent of the eggs laid. Schwarzkopf and Brooks (1986) estimated that 43–73 percent of females nested, and 12–13 percent of these twice.

Yet we should not regard these data as necessarily "typical"; there may be no such thing, at least where a range of habitats is consid-

ered. Gibbons (1987) illustrated different survivorship curves for three populations of *Pseudemys scripta* (*Trachemys scripta*) in different habitats in the same general area, and showed how these curves are virtually duplicated in three species of turtles living in the same pond.

Fluctuations in numbers of females nesting, in numbers of double nestings, in nest predation, and in the abiotic environment may act in various combinations to promote or reduce recruitment. The population I studied exhibited a remarkable ability to maintain itself despite a low level of recruitment and one biased against females. The principal contributing factors here seem to have been the low mortality rate of females and the occasional "good" year that made up for the loss in females. It remains to be discovered whether small populations such as mine are a special case with respect to variance in reproductive parameters. Large populations may be better buffered, but the detailed data needed to show this are not yet in the literature.

Information on small populations is of special interest because of the question of minimum size for population viability (Soule, 1987). In the present instance, a population with only 9 to 14 adult females survived on an apparent average annual recruitment of slightly less than the equivalent of one clutch of eggs, and with many fewer immigrants than there were recruits. Of course, any extrapolation from this experience to other species of turtles should be undertaken with much caution, given that *Chrysemys picta* is a notably adaptable species.

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