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THE NATURAL HISTORY OF THE ALABAMA MAP TURTLE,
GRAPTEMYS PULCHRA BAUR, IN ALABAMA

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THE NATURAL HISTORY OF THE ALABAMA MAP TURTLE, *GRAPTEMYS PULCHRA* BAUR, IN ALABAMA

ROBERT M. SHEALY¹

SYNOPSIS: From June 1969 until October 1972 the natural history of the Alabama map turtle, *Graptemys pulchra*, was studied in southern Alabama. Over 500 specimens were collected, of which 286 were measured, marked, and released, and 91 were autopsied for reproduction and food studies.

Graptemys pulchra was the most abundant turtle in the study area and its primary food item, the imported oriental mussel *Corbicula maniliensis*, was the most abundant macro-invertebrate. Large, mature individuals of *G. pulchra* were more abundant than juveniles.

Home range was apparently more stable in males, but only females exhibited homing behavior. I found that females either returned to the home area or remained at the displacement site. Those returning to their original localities moved distances of 24 river channel km (15 mi) or more up- and downstream.

Growth is rapid in juveniles but declines sharply at maturity and approaches zero shortly after maturity. Males reach sexual maturity in their third or fourth year, but females apparently do not reach maturity until they are approximately 14 years old. Maximum size in females is reached in about 23 years, and natural longevity probably exceeds 50 years.

Sexual dimorphism with respect to size is pronounced, the largest male studied being about half the carapace length of the smallest female (120 mm vs 212 mm).

Although sperm were present in the male reproductive tract throughout the year, mating behavior was observed only in autumn months, suggesting that sperm is stored in females. The male courtship sequence is similar to that described for other aquatic emydines, except that the "titillation tool" of the male is the snout, rather than elongate fore-claws. Elongate fore-claws are not characteristic of adult males.

Predation probably resulted in the destruction of 95 percent of the natural nests during the study period, although some reproductive seasons were much more successful than others. The major diurnal predator on nests was the fish crow, and the major nocturnal predator was the raccoon. The only significant enemies of adults are man and possibly the alligator snapping turtle, *Macroclemys temmincki*.

Reproductive potential varied from 7 to 71, depending on the size of the female, and averaged 29 eggs per season per female. An average of 4 (1-6) clutches were laid per season per female. Extra-uterine migration of ova was usual.

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Nests were located 1-20 m from the water's edge, usually on large, exposed sandbars. Coarseness of the sand seemed to be the major criterion on which nest site selection was based.

Incubation required from 74 to 79 days at 29°C, the average nest chamber temperature in natural nests. Infertility of individual eggs and entire clutches was common.

Males and females under 100 mm carapace length were primarily insectivorous, whereas juvenile and adult females in the study area subsisted almost entirely on *Corbicula*. Feeding generally began in May and ended in October. Since growth ceased in early September, food assimilated during September and October was probably stored for winter.

The most significant determinant of seasonal activity was water temperature. Activity and feeding decreased sharply at water temperatures below 19°C (66°F). Complete inactivity (hibernation) of the entire population during the winter was not observed. No significant interspecific competition with other turtle species was found.

TABLE OF CONTENTS

INTRODUCTION	49
ACKNOWLEDGEMENTS	54
METHODS	54
DISTRIBUTION AND VARIATION	56
GROWTH	60
Ontogenetic Growth	60
Seasonal Growth	62
Age	64
Longevity and Senility	67
REPRODUCTION	69
Maturity and Sexual Dimorphism	69
Reproductive Cycles	71
Reproductive Potential and Eggs	73
Mating	74
Sperm Storage	75
Nesting	77
Incubation	80
Hatching	83
Hatchlings	86
POPULATION DYNAMICS	86
Population Density	86
Composition	87
Mortality	90
Post-natal Mortality	90
Home Range and Homing	91
FOOD AND FEEDING	94
ACTIVITY	99
Seasonal Activity	99
Diel Activity	101
PREDATORS AND PARASITES	104
Predation	104
Parasites	108
INTERSPECIFIC INTERACTIONS	108
LIMITING FACTORS	109
LITERATURE CITED	110

INTRODUCTION

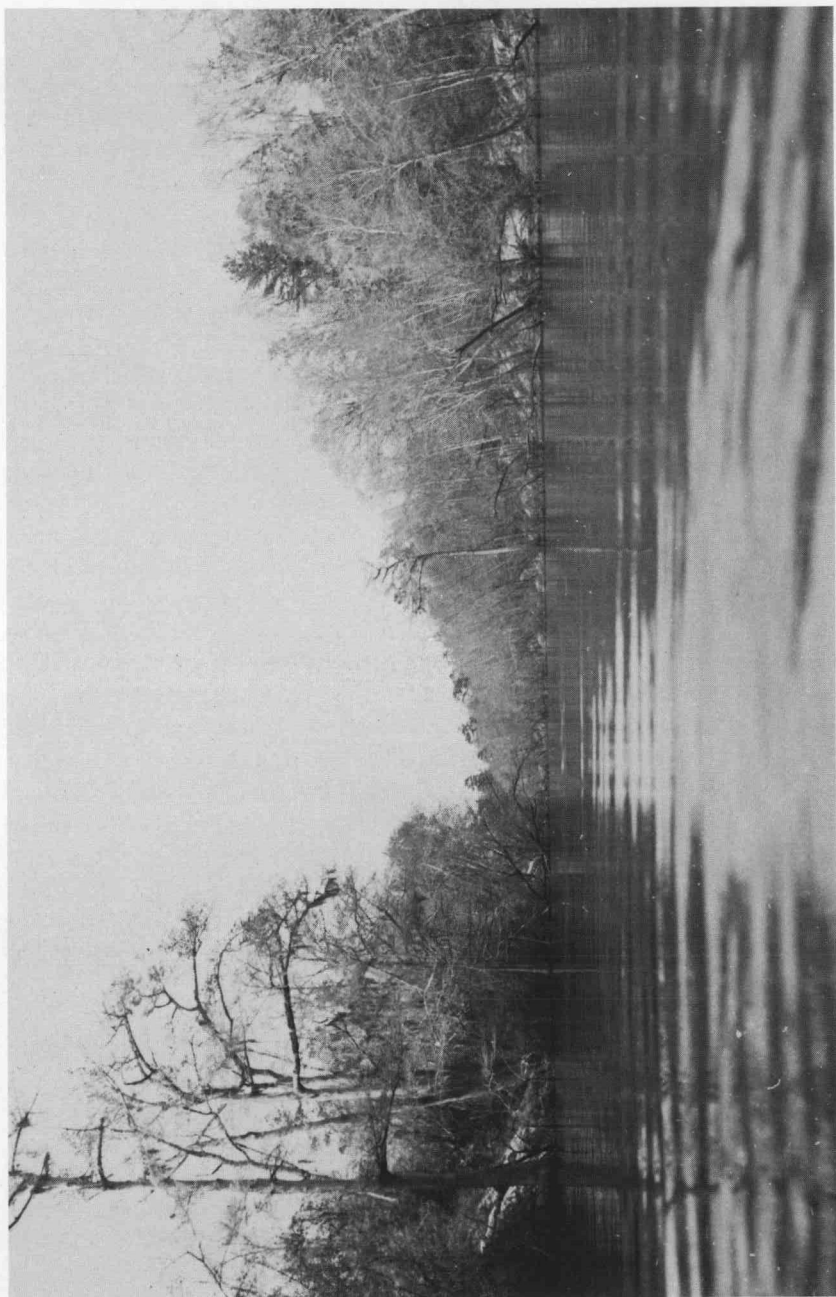
The genus *Graptemys* is confined to eastern North America and includes nine species of strongly aquatic turtles. It belongs to the family Emydidae, a nearly cosmopolitan and mostly aquatic group. *Graptemys pulchra* was described by Baur in 1893 from a lake near Montgomery, Alabama.

From June 1969 until October 1972 studies were conducted on the natural history of the Alabama map turtle, *Graptemys pulchra* in Alabama. Emphasis was placed on field observations of behavior, studies of movements, and growth (using mark and release techniques), and on laboratory studies of the reproductive cycle and food habits. Over 500 specimens were collected, of which 91 were autopsied and 286 were measured, marked, and released.

The population selected for most intensive study inhabits a 30-mile segment of the Conecuh River, Escambia County, extreme southern Alabama (87°00'W, 31°05'N; R11E, T1N). The upstream limit of the study area was the U. S. highway 29 bridge (McGowan's Bridge). Downstream, the limit was state highway 41 at East Brewton, Alabama. The segment is bisected by Escambia County road 4, approximately 13 km due east of East Brewton. Collections were confined to the 24 km of channel between U.S. 29 and county road 4 and to a kilometer stretch immediately downstream from state road 41. No collections or observations were made between Escambia 4 and Alabama 41.

The 8 km of river channel immediately downstream from U.S. 29 is comparatively straight, with very few large, exposed sandbars (Fig. 1). The banks consist mostly of exposed limestone and stabilized sand deposits, with overhanging hardwood canopy. The banks erode very slowly, probably because of the limestone bed. Thus, few trees are undercut to be added to the supply of natural basking sites and hiding places. The channel in this area consists of straight stretches up to 2 km long with water 2 to 3 m in depth, alternating with occasional holes up to 10 m deep (during low water). The bottom substrate is quite stable and consists of coarse sand, bare limestone, or occasionally silt and detritus.

Exposed limestone diminishes and large bare sandbars are increasingly frequent downstream from this area. Long straight stretches are infrequent, and sinuous undulations of the unstable channel result in a nearly continuous alternating series of sandbars (Fig. 2). The channel in these areas is characteristically shallow (1 m) between sandbars but deep (3 to 8 m) and narrow (5 to 10 m) opposite the sandbars. Banks across from the sandbars are rapidly undercut (up to 6 m per year), and the channel is often choked with fallen trees. Such places offer ideal sites for basking turtles and underwater hiding places for many aquatic vertebrates. The associated unstable and bare sandbars are preferred nesting sites for *Graptemys pulchra*, *Trionyx spinifer*, and *T. muticus*. During low water levels, the current velocity is approximately



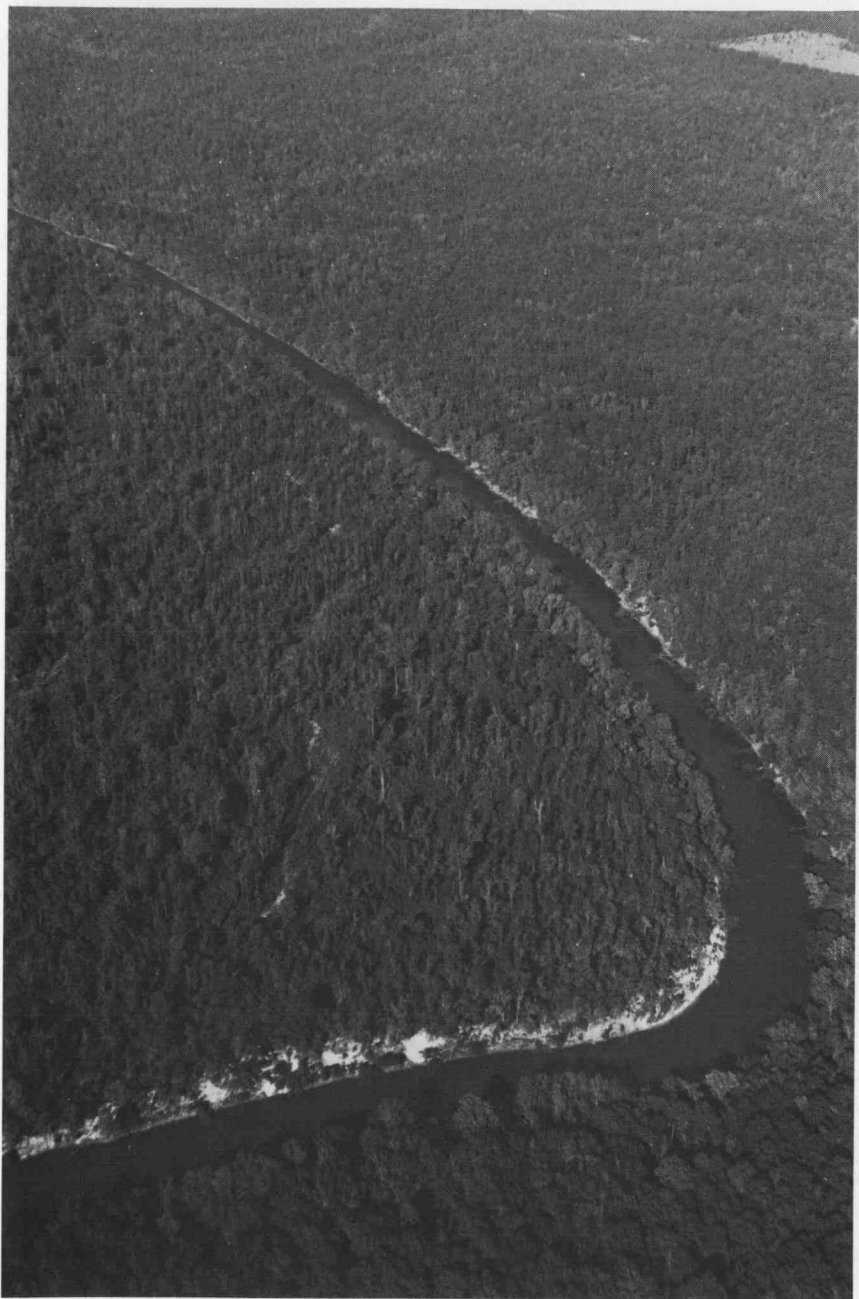
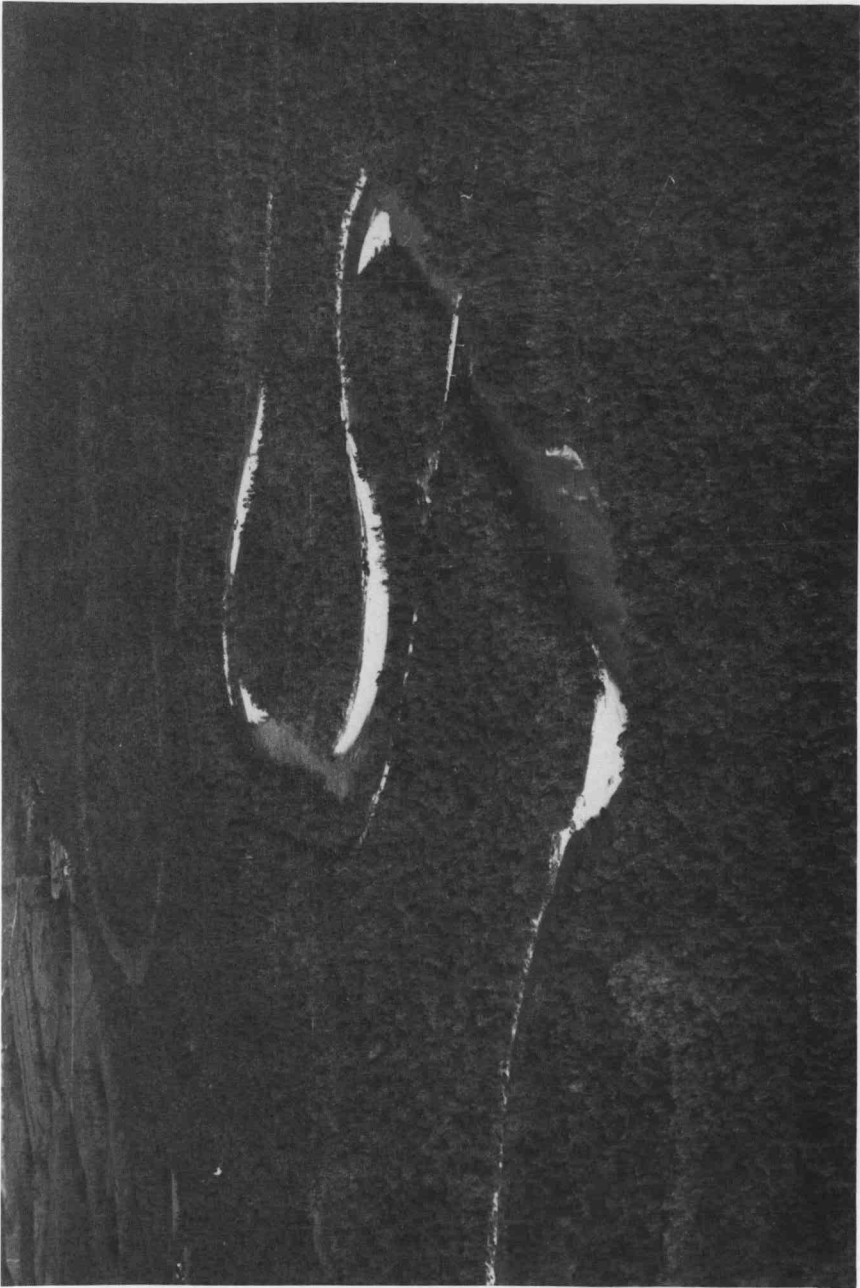


Figure 1. The Conecuh River near U. S. Highway 29, Escambia County, Alabama. Left, downstream view in April; Right, aerial view.



Figure 2. The Conecuh River near Escambia County Highway 4, Alabama. Upper, large sandbar used extensively by nesting *Graptemys pulchra* from May to July, 1971 (see Fig. 20). Fallen trees offer preferred basking sites over areas of deep water. The only alligator encountered during the study was observed on the bottom near the undercut bank. Lower, aerial view.



3 kmph in straight stretches and in shallow areas between sandbars and 1 kmph in deep areas across from sandbars. During periods of high water, current velocity is 1-6 kmph in all areas. The water level at East Brewton fluctuates about 5 m seasonally. At Century, Florida, a 30-year record of Escambia River discharges shows a variation from a low of 596 cfs (cubic feet/second) to a high of 77,200 cfs (mean = 5,460 cfs), according to U.S. Geological Survey records.

Several major studies of the natural history of emydine turtles have appeared during the past 22 years. *Pseudemys scripta*, a widely distributed and very generalized emydine, has been subjected to the most intensive studies, including both North Temperate and Tropical zone populations (Cagle 1950, Moll and Legler 1971). Legler (1960) studied the natural history of *Terrapene ornata*, a terrestrial emydine, in detail. Studies by Cagle (1954), Gibbons (1968), Sexton (1959, 1965), Ernst (1971), Christiansen and Moll (1973), and Moll (1973) provide a thorough natural history of *Chrysemys picta*.

Published information on species of the genus *Graptemys* consists mostly of general notes on behavior and ecology. The most detailed accounts are found in Webb's (1961) work on *G. pseudogeographica ouachitensis* and Cahn's (1937) observations on *G. geographica* and *G. pseudogeographica*. The apparent dissimilarities in ecology and life histories between these species and *G. pulchra* make these observations of little value in the interpretation of the natural history of *G. pulchra*.

Information on *G. pulchra* in the literature is likewise scant, consisting mostly of brief notes on basking behavior (Boyer 1965) and food preferences (Conant 1958). The most significant treatment of reproduction and growth is found in Cagle's (1952) work comparing *G. pulchra* with *G. barbouri*.

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METHODS

Two collecting techniques were used. When water clarity permitted, collecting was done with a mask and snorkel. During periods of high and turbid water this was accomplished by drifting downstream with only the collector's head exposed, netting turtles as they basked. Both techniques varied greatly in effectiveness, yielding from 0-30 specimens/hr. Generally, diving yielded mostly large mature individuals and few juveniles, whereas surface netting yielded a greater diversity of sizes. Night collecting, both by diving and by surface efforts, was attempted on several occasions but was unsuccessful. Submerged baited traps and basking traps used early in the study were also unsuccessful.

Behavior was studied during the nesting season from tree platforms or from banks across from nesting beaches. Field behavioral observations made at other times of the year were incidental to the regular collecting. However, turtles were also regularly observed in laboratory tanks and outdoor pools.

Measurements were taken on all specimens that were marked and released, autopsied, or preserved. Linear measurements to the nearest millimeter were made with a vernier or outside caliper. Measurements include carapace length (CL) (the distance from the anterior edge of the carapace to the posterior edge of the carapace), plastron length (PL) (the distance from the most proximal point of the anterior plastral notch to the most proximal point of the posterior notch), width (measured at the widest point of the carapace, usually at the level of the fifth or sixth marginal scutes), and height (the distance from the anterior edge of the second central scute to the nearest ventral point on the plastron). In males pre-anal tail length was measured from the posterior edge of the plastron to the anterior border of the vent. In females skull width was measured at the widest point. In some females the average length of the pectoral scutes at the medial seam was measured with calipers, and the total length of the medial seam was measured with a curvimeter. Weight was determined to the nearest gram for some individuals by means of a triple-beam balance.

Inter-annulus width, defined as the distance between annuli (growth rings) on the frontal plane of the femoral scutes, was measured to the nearest millimeter with vernier calipers (Fig. 3); this measurement was taken near the middle of the medial seam of the femoral scute. Normally, all visible inter-annulus widths were measured, as was the band in process of formation. Annulus lengths were not used because of the difficulty in discerning ends of the annuli. The abdominal scute was not used because it exhibited greater erosion and loss of annuli.

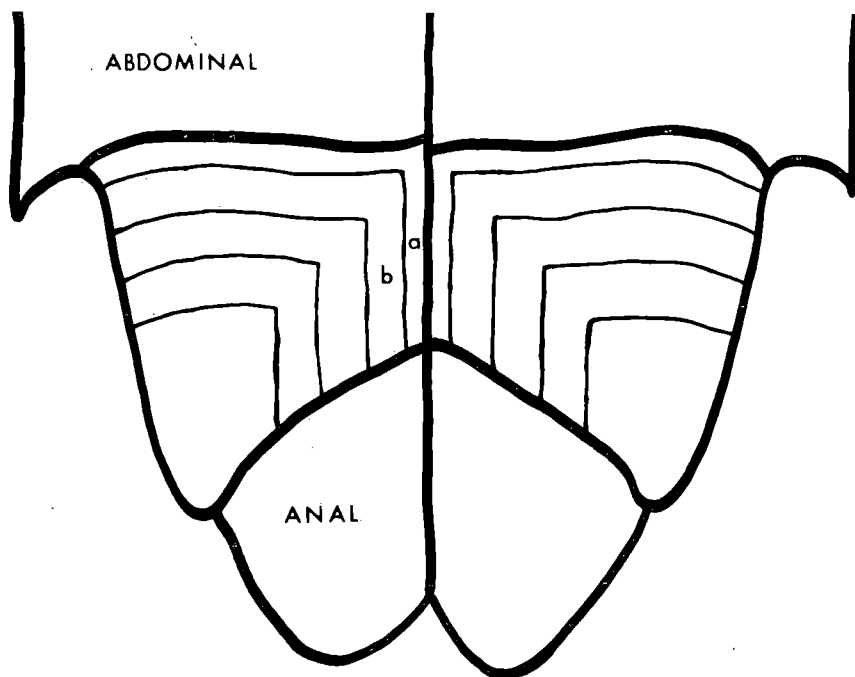


Figure 3. Ventral view of the posterior half of a plastron of *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama, showing annuli on femoral scutes. Inter-annulus width "a" shows growth since the previous winter. Width "b" shows growth during the previous year.

Routine field data included determinations of air and water temperatures with an alcohol thermometer, notes on water level and clarity, and weather conditions. Observations associated with nests encountered in the field included chamber temperature, distance from the water, elevation above the water, and substrate qualities.

Specimens that were captured and released were marked by notching the marginal scutes, using the following numbering system: units (1 to 9) were assigned to the right marginals 2 through 10, tens (10 to 90) to left marginals 2 through 10, number 100 to the first left marginal, and number 200 to the first right marginal. Thus, number 263, for example, would have notches on the first right marginal, seventh left marginal, and the fourth right marginal. Notches normally were clearly visible three years after release, even in rapidly growing individuals (Fig. 4).

In order to determine reproductive condition, food items, and parasites, autopsies were made at monthly intervals (weekly during critical months). Reproductive and digestive organs were removed from larger individuals through the inguinal pocket in order to avoid disrupting the shell.

Ova were measured at their greatest diameter and oviducal eggs at their greatest length and width. The number of corpora lutea was recorded when present. Testes were measured to the nearest millimeter at their greatest and smallest diameters and the values averaged. Notes were taken on the condition of the males' epididymides and on sperm presence and condition.

Intestinal food items and fecal samples were analyzed. The latter were collected by placing individuals in separate containers having sufficient water to cover the carapace, where they were retained from 2 to 4 days. The water was then decanted, and identifiable material picked out and preserved in 70% ethyl alcohol.

Eggs collected from oviducts or natural nests were incubated by one of two methods. One method involved placing the eggs in a plastic bag along with a paper towel saturated with water, sealing the bag, and storing it in a constant temperature chamber at temperatures close to those of natural nests (28°-30°C). No eggs hatched using this method, and all developed heavy fungal infestations. A second method utilized gallon containers or cinder blocks filled with clean, moist sand similar to that of natural nests. The eggs were buried in the sand at depths of from 10 to 15 mm. Some containers were kept indoors and others outdoors, under both shaded and sun-lighted conditions. Hatching success was high using this method.

DISTRIBUTION AND VARIATION

Gratemys pulchra is found in major drainage systems entering the Gulf of Mexico from the Pearl River in Louisiana and Mississippi to the Yellow River in Florida and Alabama (Conant 1958) (Fig. 5). It occurs in the Pascagoula, Mobile, and Escambia systems but is absent from the smaller Perdido, Blackwater, and Escatawpa drainages (the last river actually flows into the lowermost part of the Pascagoula system).

Ecologically, the species shows fairly broad requirements, occurring in all sizeable streams within its range that support reasonably large populations of aquatic molluscs. The heaviest populations in Alabama, and presumably elsewhere, are found in large Coastal Plain streams. The species is strongly aquatic, and specimens have never been seen on land except while basking under stress or nesting.

Although primarily a stream form, the species has evidently held its own in artificial impoundments, such as the Gantt Reservoir at Andalusia, Alabama. The species was originally described from two specimens captured in a "lake" near Montgomery, Alabama (Baur 1893). This lake was probably either an artificial impoundment or an oxbow of the Alabama River, since

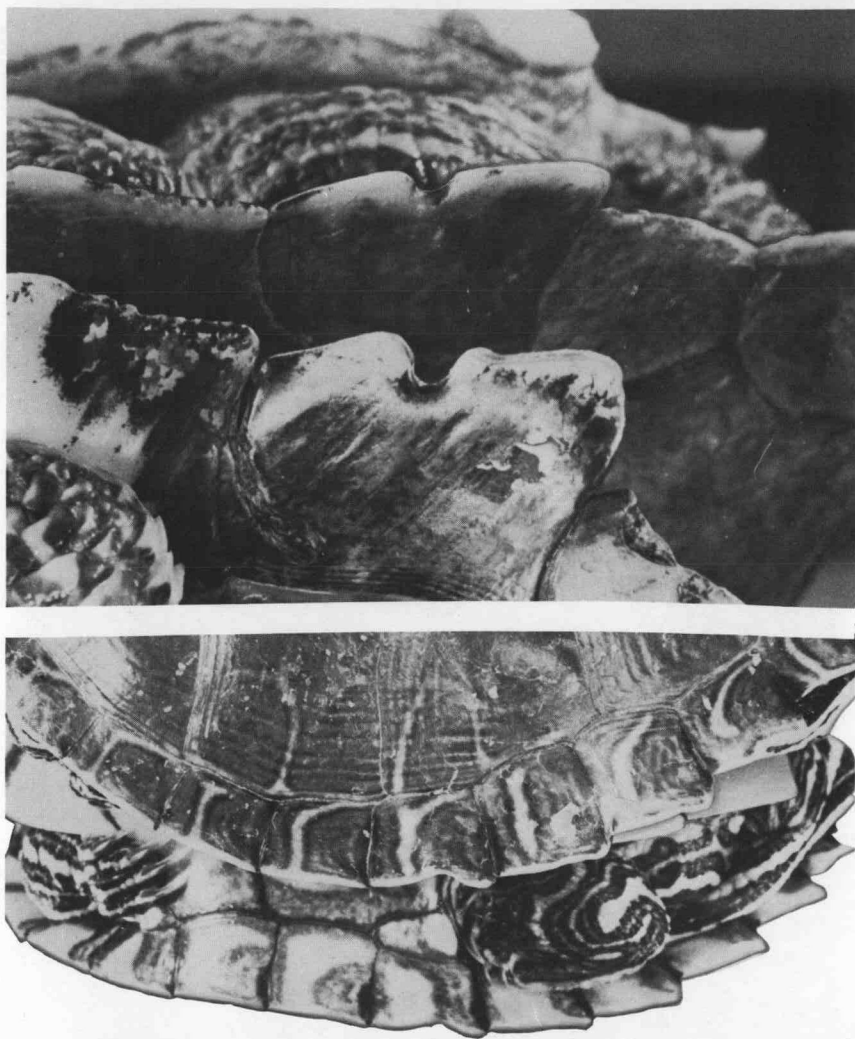


Figure 4. Marked specimens of *Graptemys pulchra* from the Conecuh River near East Brewton, Alabama, four years after release. Above, old female, tenth marginal notched. Below, young male, seventh marginal notched. On rapidly growing individuals, notches tend to be obscured within a few years after release. (Specimens photographed on mirror surface).

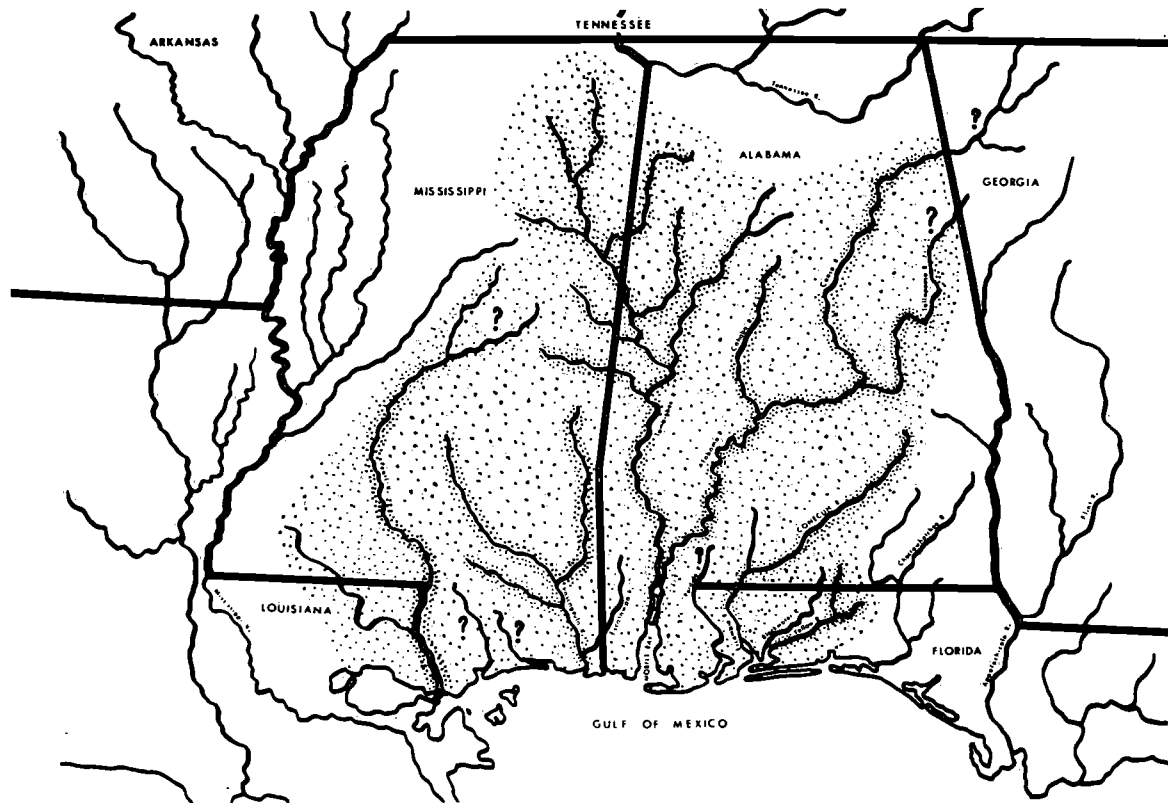


Figure 5. Geographical distribution of *Graptemys pulchra*. Known area of occurrence is indicated by stippling. Unknown areas are indicated by question marks. Major drainages, from west to east, include: Pearl River, Pascagoula River, Mobile Bay, and Escambia-Yellow Rivers.

G. pulchra has not been observed in any other type of lake. The comparative degree of success of the species in lentic versus lotic situations has not been determined.

The species comprises at least four geographical variants: one in the Pearl River drainage, a second in the Pascagoula drainage, a third in the Mobile Bay drainage, and a fourth in the Escambia and Yellow River drainages. Shell proportions separate members of the Mobile Bay drainage from all others, the adults having proportionately much flatter shells than adults from other drainages (Fig. 6). The adaptive significance of this shape is unknown, but may possibly be linked with adaptations to greater turbulence of streams above the Fall Line. The Mobile Bay drainage has the most extensive drainage area above the Fall Line of all the systems in which *G. pulchra* occurs. Gene flow from such a large area of selective pressure could account for the flattened body form in Coastal Plain individuals within the drainage.

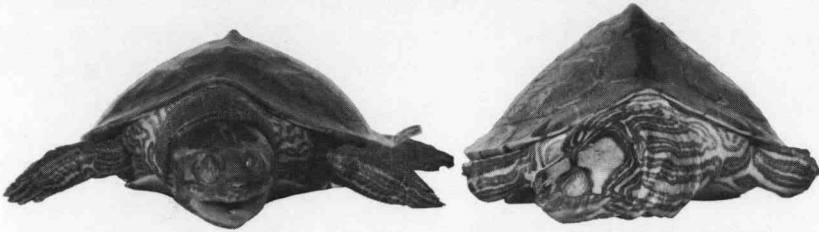


Figure 6. Geographical variation in *Graptemys pulchra* in Alabama. The individual at left shows flattening of the shell characteristic of Mobile Bay drainage specimens. The individual at right shows higher shell characteristic of the Escambia-Yellow River drainage form. Carapace lengths are similar.

The Pascagoula form has more light pigmentation on the head and carapace marginals than does the Escambia River form. Also, a grayish hue tints the basic green ground color in the Pascagoula form.

Specimens from the Pearl River appear to be intermediate in coloration between the Pascagoula and Escambia River forms, although resembling the Escambia River form more closely. Cagle (1952) remarked that females from the Pearl River differ from those of the Escambia River in that "the markings of the lower jaw tend to be broken into erratic lines that constitute a longitudinal pattern in some and a transverse one in others." Tinkle (1961) showed that, with respect to laminal seam arrangements, specimens from the Pearl River more closely resemble those from the Escambia River than from the Pascagoula River. Variation among the forms also occurs with respect to other head patterns, plastral and carapacial markings, and shell width to length ratios. The extent and consistency of such differences, however, are yet to be evaluated. An intensive study of variation between populations in the four drainages will probably reveal distinctiveness requiring several sub-specific designations.

GROWTH

ONTOGENETIC GROWTH

Data on growth were derived in part from 257 individuals that were captured, marked, and released in the Conecuh River between U.S. 29 and East Brewton from August 1969 to September 1971. Between May 1970 and October 1972, 59 were recaptured. To distinguish slight growth increments and to minimize the effects of measurement error, the product of length, width, and height measurements was used as a size index. Cessation of growth during winter months was discounted by using only the number of months of growth (from inter-annulus data) between release and recapture. Growth rate was variable among females (Fig. 7). If rates among size classes are averaged, however, a significant trend may be seen. The first level includes females of less than 160 mm carapace length. Although molluscivorous (see pp. 94-95), this group fed only on smaller bivalves, which were observed to be much scarcer and much more seasonal in abundance than larger ones. Thus, limited food resources may have resulted in less than maximal growth.

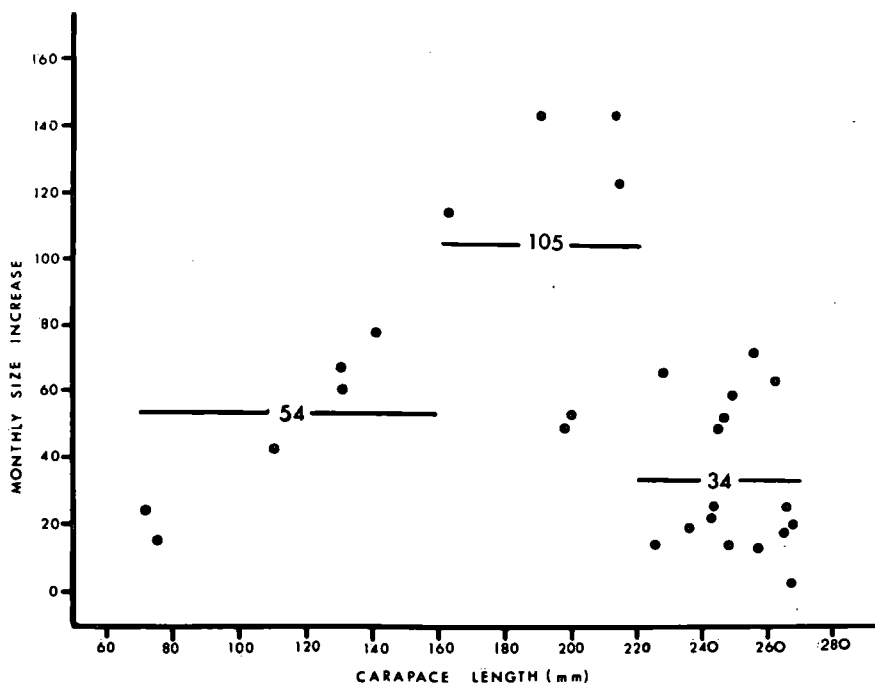


Figure 7. Growth in juvenile and female *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama, based on release and recapture data. Numbers are averages over the ranges indicated. Size=carapace length X width X height X 10^{-3} (mm). Only months in which growth occurred were counted.

The second level includes individuals from 160 to 220 mm in length. Members of this size class comprise sub-adults and young adults which were able to utilize a nearly "unlimited" bivalve resource and thus to show maximum growth. Growth surges at puberty have been observed in *Pseudemys rubriventris*, and hypothetically correlated with dietary shift (Graham 1971). Patterson and Brattstrom (1972) found growth surges in the desert tortoise, *Gopherus agassizi*.

The third and lowest level includes large females which are also able to utilize the bivalve resource, but presumably because of redirection of energy to reproductive output show a minimal growth rate. Moll and Legler (1971) attributed cessation of growth in adult *P. scripta* to redirection of energy toward gametogenesis.

Growth in mature males (Fig. 8) showed a marked decline after maturity. This is consistent with data illustrated in Figure 25, showing that there was less variation in size among mature males than among mature females. The existence of selective forces in this direction is probable, but the cause and mechanism of such selection is not apparent.

Using space between annual growth rings (annuli) as indicators of growth rate essentially confirms the above interpretations of growth in both males and females. The last complete inter-annulus width as a function of carapace

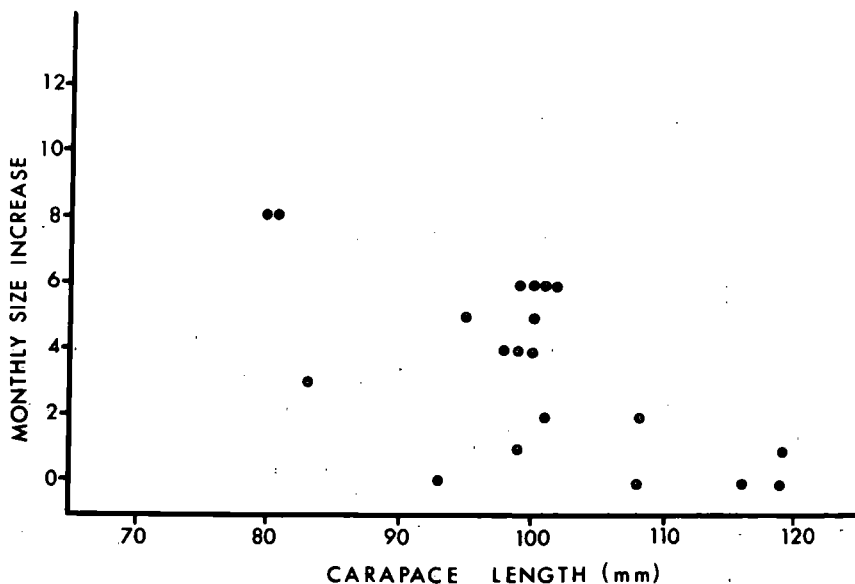


Figure 8. Growth in adult male *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama, based on release and recapture data. Size = carapace length X width X height X 10^{-3} (mm). Only months during which growth occurred were counted.

length in the lower Conecuh River population is described in Figures 9 and 10. Among females, a fairly stable growth rate is evident between 45 mm and 160 mm CL, followed by a peak just prior to maturation (160 to 220 mm) and a sharp decline approaching zero among large individuals (Fig. 9). There is a stable growth rate in juvenile males, which is followed by a sharp decline after maturation and slowing markedly in large individuals (Fig. 10).

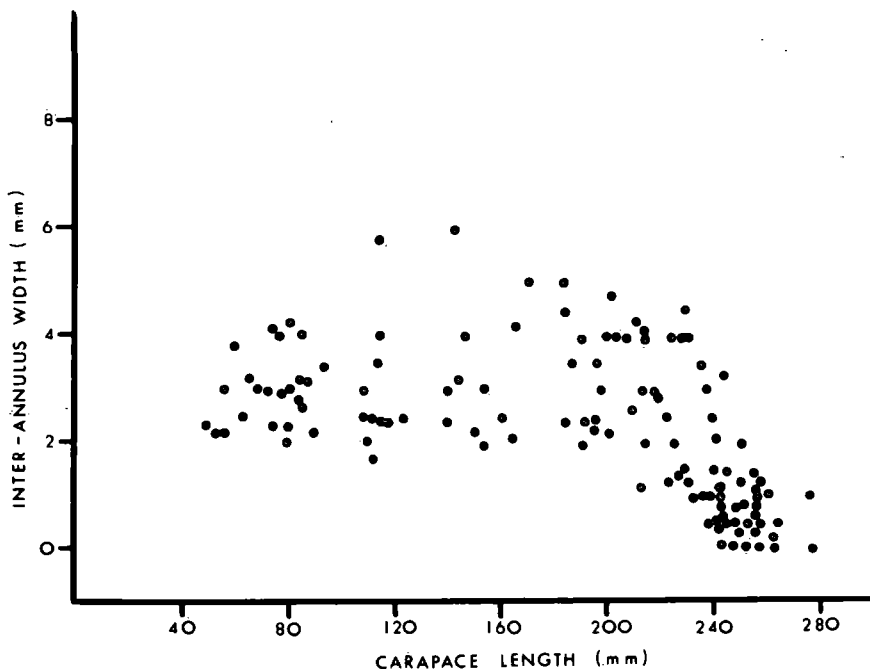


Figure 9. Growth in juvenile and female *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama, based on measurements of last inter-annulus widths.

SEASONAL GROWTH

Determination of seasonal growth was made by correlating date of capture with the ratio of new growth (last inter-annulus width) to the preceding year's growth (next to last inter-annulus width). An evident trend can be seen in Figure 11, although the results were highly variable, presumably because of "false annuli." The earliest distinguishable growth appeared in May and was probably roughly linear until August, when it averaged 67% of that of the preceding year. After August growth declined sharply, reaching an average of 76% by October.

Studies of fecal samples showed feeding began in April and ended in October. Theoretically, then, growth would be 100% at least by October. Much of the discrepancy between this and the observed rate of 76% was al-

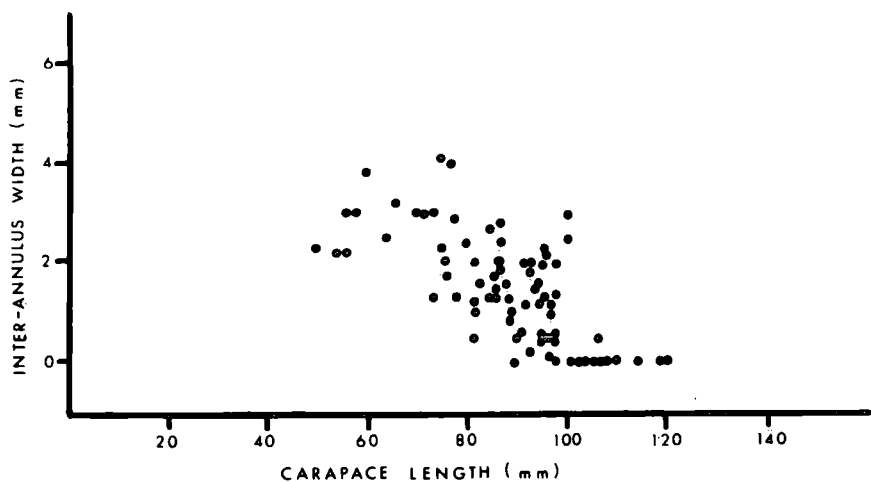


Figure 10. Growth in male *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama, based on measurements of last inter-annulus widths.

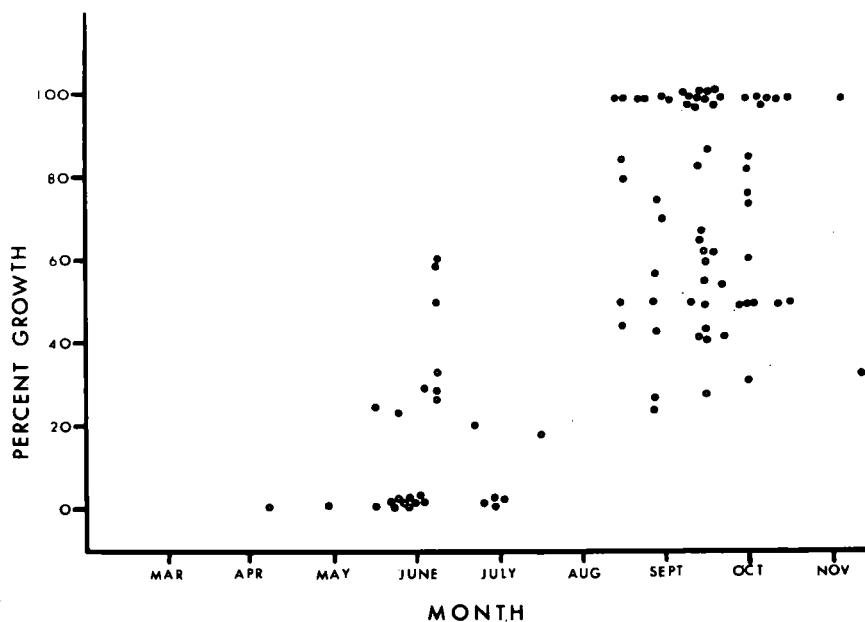


Figure 11. Seasonal growth in *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama, based on last inter-annulus width expressed as a percentage of the next-to-last inter-annulus width (last complete width).

most certainly due to "false annuli," which resulted from temporary cessation of growth not associated with winter inactivity. Environmental upsets, such as periods of extremely high water, have been shown to result in the formation of such "false annuli." Moll and Legler (1971) found that minor growth rings may form in two days and major ones in five days, presumably because of cessation of feeding. Specimens of *G. pulchra* collected during periods of high water levels, however, showed no reduction in fecal volume. Since two or more such annuli may be formed in a single growing season, their inclusion in the data may have significantly depressed estimates of growth, especially in the later months. It is probable that growth essentially ceased in September.

The cause of the decline in growth between August and October is not apparent. Redirection of energy from growth to fat storage, preparatory to overwintering, was postulated by Sexton (1965). It has been demonstrated, however, that preparation for winter in *G. pseudogeographica* consists of storage of liver glycogen rather than fat (Emerson 1967). In female *G. pulchra*, accelerated follicular development occurs from September to November and undoubtedly requires considerable food reserves, as Moll and Legler (1971) found for *P. scripta*.

AGE

Estimates of age were based on measurements of annual growth (inter-annulus width) on the femoral scutes, which were correlated with width of the scutes. Essentially the same technique has been used for determining age, at least in the first few seasons of growth, in *C. picta* (Sexton 1959a), *P. scripta* (Moll and Legler 1971), *P. rubriventris* (Graham 1971), *Terrapene ornata* (Legler 1960), *G. pseudogeographica* (Webb 1961), and *Gopherus agassizi* (Patterson and Brattstrom 1972). Measurements of annual increases in femoral width of recaptured specimens served to validate inter-annulus measurements. The high variability of growth after maturation confined reliable estimates of age to immature individuals. In females at maturation (220 mm) the average femoral width was 103 mm, whereas in hatchlings the average width was 20 mm. The difference between the two figures indicates a growth increase of 83 mm since hatching. This figure, when divided by the average annual increase in femoral width among immature females (6 mm), results in an average of 14 growth seasons between hatching and maturity. In nine recaptured, immature females the average increase in femoral width per year was 6 mm, confirming the inter-annulus average used. These findings contrast with those of Moll and Legler (1971) for *P. scripta* in Panama, in which females matured in 5 to 7 years. The tropical climate probably allowed a longer growth season and shorter juvenile life in this form. Legler (1960) calculated a juvenile period of 10 to 11 years for female *T. ornata*, and Graham (1971) demonstrated an 11-year juvenile period for female *P. rubriventris*.

In males at maturation the average femoral width (80 mm carapace length) was 38 mm, an increase of 18 mm from hatching. Inter-annulus measurements showed an average annual increase of 6 mm in femoral width in both immature males and females (Table 1). Therefore, an average of three years elapses between hatching and maturity in males. This figure agrees with Moll and Legler's (1971) findings for male *P. scripta* (2 to 4 years), and with Webb's (1961) observation of *G. pseudogeographica* (2+ years). Cagle (1952) described a small mature male *G. pulchra* from the Pearl River in its fourth season of growth. Many mature, or nearly mature males, with three or four annuli were observed in the Conecuh River population.

TABLE 1.—GROWTH AND ESTIMATED AGE, BASED ON RELEASE AND RECAPTURE DATA, OF *G. pulchra* FROM THE CONECUH RIVER, ESCAMBIA COUNTY, ALABAMA*.

C.L.	F.W.	Inc. F.W.	A Inc. F.W.	Years	N
FEMALES					
40-220	20-103	83	6.0	14.0	14
220-240	103-111	8	4.6	1.7	6
240-270	111-124	13	1.8	7.2	23
				Total	22.9
MALES					
40-80	20-38	18	6.0	3.0	2
80-90	38-42	4	3.3	1.2	4
90-110	42-50	8	1.9	4.2	21
				Total	8.4

*Abbreviations: C. L. = carapace length in millimeters; F. W. = combined width of femoral scutes at the carapace length interval; Inc. F. W. = increase in femoral width over the interval; A Inc. F. W. = average annual increase in femoral width; Years = number of years required to traverse the interval; N = number of individuals in each group.

As previously indicated, post-maturation growth is highly variable in both sexes but rapidly approaches zero in large individuals (Fig. 7). Estimates of average numbers of years required to traverse three size intervals, based on interannulus measurements, are given in Table 1. From these estimates, it can be seen that maximum size is attained in an average of 23 years in females and 8.4 years in males. Above these levels, there is no discernible correlation between age and size.

On the basis of skull width, ages of old adult females may also be estimated. If the maximum skull width observed (65 mm) is used as an intercept with the CL-skull width regression line for females under 240 mm long (Fig. 12), proportional growth would result in a CL of 330 mm at 65 mm skull width. An individual of this CL would have a femoral width of approximately 151 mm, or 40 mm over that of the width after 15.7 years. Assuming a stable femoral width increase of 4.6 mm per year (Table 1), 8.7 years would

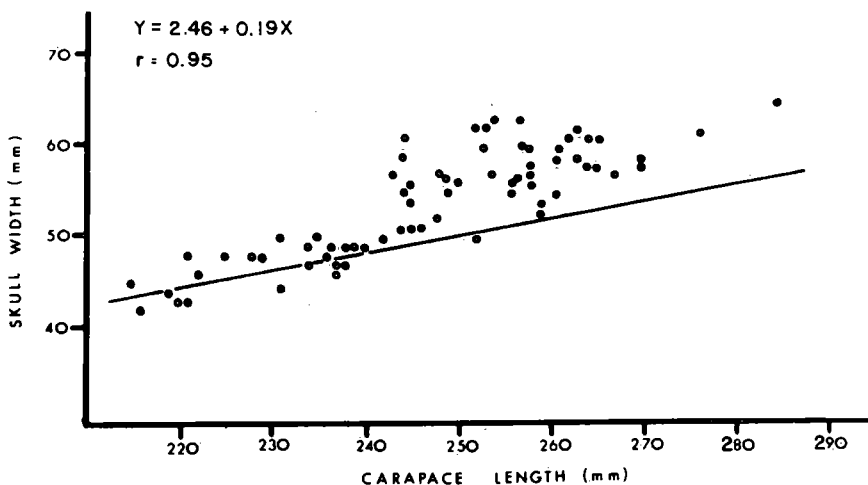


Figure 12. Skull width as a function of carapace length in female *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama. Regression line, equation, and correlation coefficient (r) derived from individuals less than 240 mm in carapace length.

be required to reach this size, for a total of 24.4 years. This figure agrees rather closely with the estimate of 23 years based on shell growth.

That considerable variability exists is well illustrated by an exceptional female that showed all signs of advanced age, *i.e.* shortened pectoral scutes, extensively wandering plastral sutures, and loss of head pigmentation. The size (220 mm CL), however, corresponded to that of a female in her first reproductive season.

The extent of allometric growth in skull width in females is shown in Figure 12. There is a relatively close correlation between CL and skull width at carapace lengths under 240 mm, but this declines sharply at lengths over 240 mm. Above this size, all points are found on the positive side of a regression line derived from skull measurements of immature females. This indicates not only a high degree of variation in the size at which growth stops but also a persistence of growth in skull width independent of body growth.

In very old females, extensive wandering of plastral seams occurs, often resulting in the formation of small additional scutes near the midline. Also, differential growth among plastral scutes results in reduction of some scutes and expansion of others. The length of the pectoral scute relative to the PL decreases with increased medial seam length (Fig. 13). The close correlation between pectoral scute reduction and medial seam length in older females may indicate that both measures are equally affected by age. An increase in length of the humeral scute is apparently associated with the decrease in pectoral scute length.

Such a relationship is not shown between medial seam length and skull

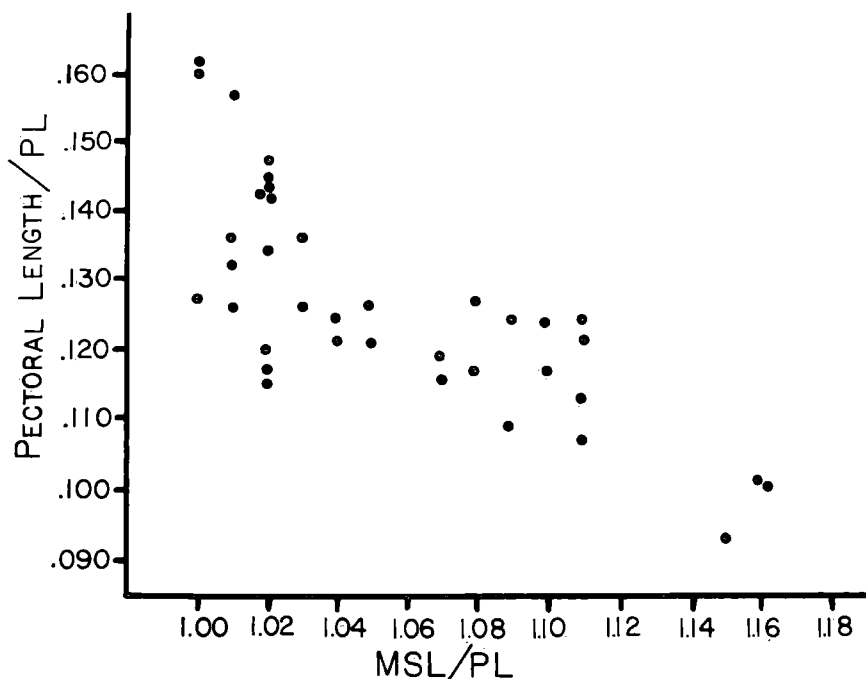


Figure 13. Pectoral scute length relative to plastron length (PL) as a function of medial seam length (MSL) relative to plastron length in adult female *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama.

width (Fig. 14), except in young females (skull width less than 52 mm). This close correlation decreases with age, indicating a sharp decline in skull growth, if not complete cessation. It is probable that those individuals having enlarged skulls and slight wandering of seams were still growing.

In Figure 15 a similar, though less pronounced, condition in males with respect to pre-anal length can be seen. Again, there is a pronounced decrease in correlation after maturity, and the pre-anal length of nearly all large males lies above the regression line derived from measurements of immature individuals.

LONGEVITY AND SENILITY

Estimates of longevity cannot be based on body size, since growth essentially stops at a relatively early age. Since skull width also fails to increase in very old individuals, its use is also limited. *G. pulchra* probably attains ages far beyond the above estimates, but estimates of advanced ages are restricted to much more comparative and qualitative approaches. Legler (1960) and Cagle (1950) estimated natural longevity in *Terrapene ornata* and *P. scripta*,

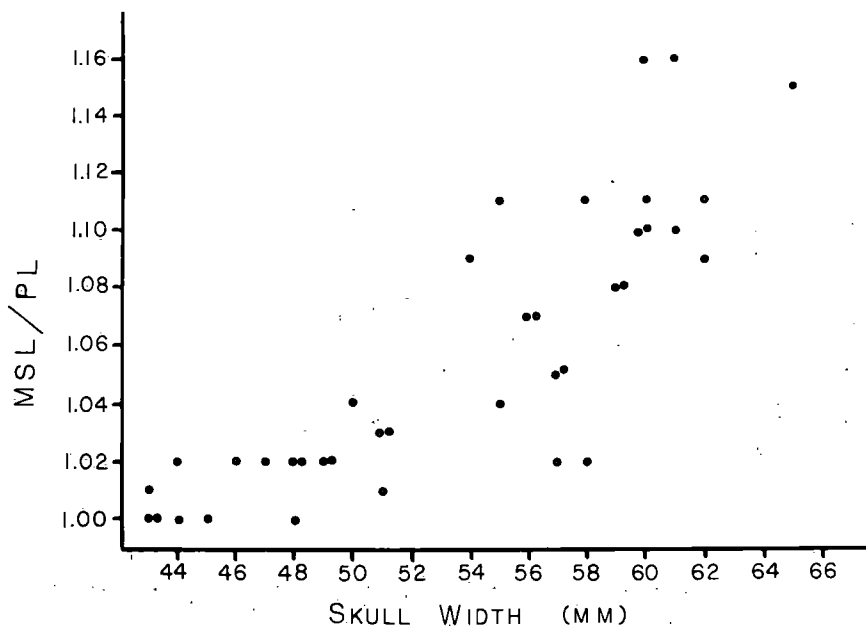


Figure 14. Medial seam length (MSL) relative to plastron length (PL) as a function of skull width in adult female *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama.

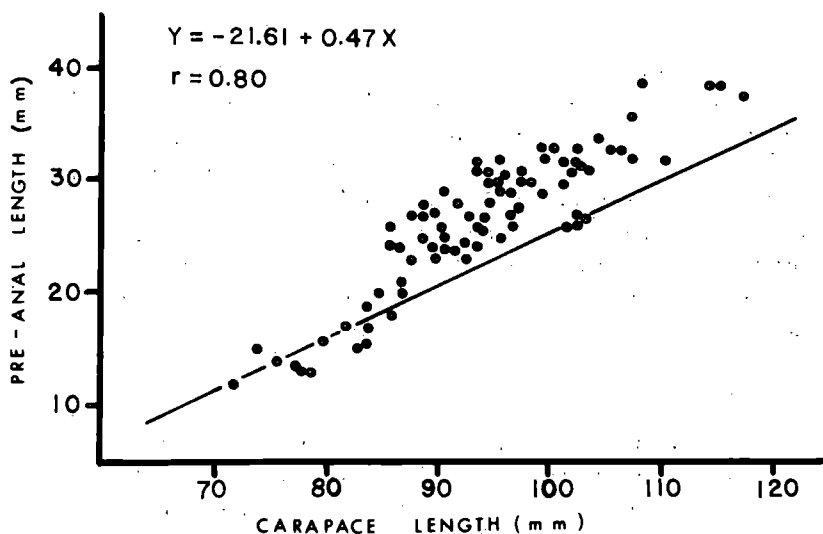


Figure 15. Pre-anal tail length as a function of carapace length in male *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama. Regression line, equation, and correlation coefficient (r) derived from individuals less than 85 mm carapace length.

respectively, to be in excess of 50 years. Longevity in *G. pulchra* is probably comparable.

Indicators of old age in emydines have been described by Moll and Legler (1971) and Cagle (1950, 1952). In *P. scripta*, "continued molting without growth produces the progressively shallower interlaminal seams and the fusions of scutes . . ." (Moll and Legler 1971). Cagle (1952) observed that very old *G. barbouri* showed an increase in black pigmentation, irregular plastral sutures, and a thickening and erosion of the shell. Indicators of advanced age in *G. pulchra* include: wandering plastral seams, decrease in pectoral scute length with associated increase in humeral scute length, loss of contrast in head pigmentation, and a disproportionate increase in skull width of females and pre-anal length of males.

No specimens with "senile" gonads (degenerate ovaries or testes) were found during this study. However, a few individuals of both sexes, showing signs of advanced age, were apparently waning in vigor. Areas of erosion were evident in the shell and alveolar surfaces of the jaws. Efforts to escape seemed to be less vigorous and a generally emaciated appearance was shown. These individuals, although evidently senile somatically, apparently had normal reproductive organs. Probably such individuals died before reproduction was impaired, or their lack of vigor was due to some factor other than age.

REPRODUCTION

MATURITY AND SEXUAL DIMORPHISM

Sexual maturity in male *Graptemys pulchra* was determined by the presence of sperm in the epididymides. The smallest mature male autopsied was 80 mm CL and 16 mm pre-anal tail length. Studies of growth reveal that this size may have been attained within 3 or 4 years after hatching (Table 1). Cagle (1952) reported male *G. pulchra* from the Pearl River having plastron lengths of from 89 to 117 mm, which would correspond to carapace lengths of 110 to 145 mm. In all probability the measurements he recorded as plastron lengths were actually carapace lengths.

Sexual maturity in females, as determined by the presence of corpora lutea or ovarian follicles over 15 mm in diameter, is achieved at a size of about 220 mm CL and 43 mm skull width. Based on growth studies, it is estimated that this size may be attained in an average of 14 years (Table 1). Although all follicles over 10 mm in diameter in mature females are ovulated, adolescent females may develop follicles in the 10-15 mm size range one year prior to their first ovulation.

Size at maturity among females is somewhat variable. The largest immature female was 220 mm CL, whereas the smallest mature female was 212 mm long. Cagle (1952) reported that the smallest mature female he studied

had a plastron length of 170 mm, which would correspond to a carapace length of 210 mm, using proportions from the Conecuh River population. Variation in size at maturity was also noted in *Chelonia mydas* by Carr and Goodman (1970), who stated that "some mature at small and others at large sizes; and that once they are mature, i.e., once they have made their first trip to the nesting beach, their growth becomes negligible . . ."

The sexes differ greatly in overall size, pre-anal length, skull width, food habits, and to a lesser degree in body pigmentation and behavior.

Size is by far the most distinguishing character in adults. The largest male recorded had a CL slightly more than half that of the smallest mature female (120 mm and 212 mm, respectively). Mature males ranged from 80 mm to 120 mm CL, whereas mature females ranged from 212 mm to 285 mm in length.

Pre-anal tail length is noticeably greater in males as early as the third season of growth, at which time the vent extends beyond the rear edge of the carapace. Increase in pre-anal length continues after growth of other body proportions effectively ceases (Fig. 15), and thus serves as an indicator of advanced age in older specimens.

Relative skull width is noticeably greater in females than in males after the first few years of growth and, as in male pre-anal length, continues to increase after body growth ceases (Fig. 12). This character is closely linked to differences in food habits. Females in the first few years and males of all ages are primarily insectivorous, and older juvenile and adult females are almost entirely molluscivorous (Fig. 27). The enlarged jaws and correspondingly widened head is clearly an adaptation for crushing molluscs, as observed by Carr (1952) and Conant (1958).

Other observed differences between the sexes are more subtle. Differences in behavior include a somewhat greater reluctance of males to abandon basking sites. This may be linked to the fact that males, which are much smaller than females, are much less conspicuous to enemies. Since the only significant enemy of adults probably is man, the reduced conspicuousness serves to offer a smaller and less noticeable target to "plinkers" (shooters of nearly any wild-life or inanimate target that presents itself). The conspicuousness of adult females, on the other hand, has probably resulted in selective pressure favoring greater wariness.

Red pigment occurs occasionally on the heads of adult males, but not in adult females. The red blends with the usual yellow, resulting in an orange coloration. Individuals with orange head patterns were found among hatchlings, very young females, and approximately 10 percent of the adult males. Shells of adult males are also noticeably thinner and more fragile than those of females of similar size.

Very slight differences between the sexes were observed in their micro-habitat preferences. Males, although commonly found among concentrations of females, were also found in all-male aggregations, usually in areas of rela-

tively shallow water. Such areas were avoided by adult females during the day. All-female aggregations were also commonly found. On several occasions over 30 mature females were taken from an area without encountering a single male. During daily periods of submersion and apparent inactivity, males were more commonly found among roots and limbs of fallen trees, and females were usually seen resting against the bottom beneath these objects.

REPRODUCTIVE CYCLES

MALE.—Active sperm were present in the epididymides of mature males throughout the year, indicating that mating may occur at any time. Times of mating and seasonal variation in male fertility were not determined.

The few instances of courtship activity that were observed occurred from September to November. Testis size was greatest in September (Fig. 16) and was coincidental with greatest follicular development in females. The male reproductive cycle, therefore, may be centered around an autumn mating season, during which sperm are stored by the female until the following nesting season. This pattern may be followed in neotropical *Pseudemys scripta* (Moll and Legler 1971), but is not followed by some other emydines. *Graptemys pseudogeographica* mates in April and possibly also in the fall (Carr 1952). *Terrapene ornata* also exhibits a spring and autumn mating period (Legler 1960), as does *P. scripta* in the Temperate Zone (Cagle 1950).

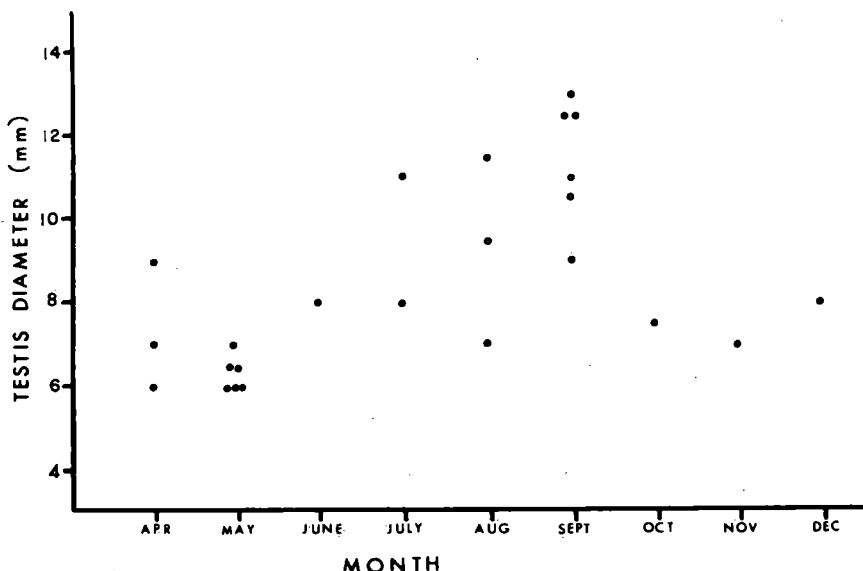


Figure 16. Monthly variation in testis diameter in male *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama.

FEMALE—As shown in Figure 17, from May to September there was a reduction in the enlarged follicles (over 10 mm diameter), expressed as a percentage of reproductive potential or maximum number of eggs produced in a season, found in Conecuh River specimens of *Graptemys pulchra*. The number of eggs is complementary; i.e. if 30 percent of the reproductive potential in a given month were in the form of enlarged follicles, then 70 percent would be expressed as egg production up to that time.

The female reproductive cycle consists of oviposition and follicular growth from May to August and rapid follicular growth from September to November, during which time feeding and activity ceases. A very similar pattern was reported for *P. scripta* (Moll and Legler 1971), *Terrapene ornata* (Legler 1960), and *Chrysemys picta* (Moll 1973, Christiansen and Moll 1973).

The failure of the described line to reach zero during August, after which no nests or oviducal eggs were found, implies that some follicles were not ovulated. Atretic follicles were not common and accounted for no more than 5 percent of the reproductive potential. Atresia is also unimportant in *T. ornata* (Legler 1960), as is probably true for most emydines (Moll and Legler 1971). The fate of remaining follicles is unknown but they probably are ovulated very late in the season or represent follicles developing early in preparation for the following nesting season.

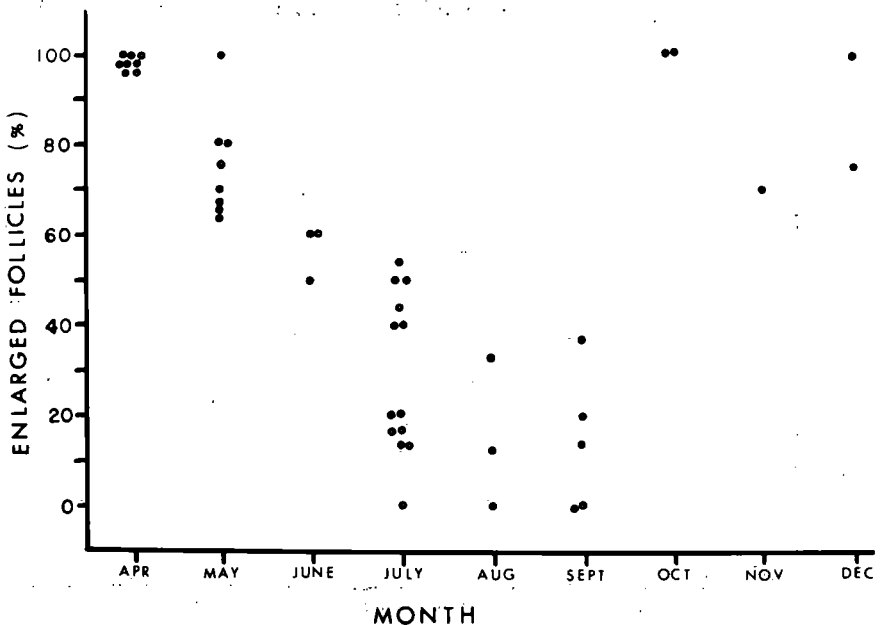


Figure 17. Monthly variation in numbers of enlarged follicles (over 10 mm diameter) expressed as percentages of observed or calculated reproductive potentials (from Fig. 18) in adult female *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama.

REPRODUCTIVE POTENTIAL AND EGGS

Reproductive potential as used here is defined as the maximum number of eggs that may be produced in a season by a single female. Since very few follicles over 10 mm in diameter were present at the end of the reproductive season (August), I assume that most follicles over 10 mm in diameter at the beginning of the season developed and were ovulated during the season. Determination of reproductive potential for each female was made by counting all follicles over 10 mm in diameter and adding the number of corpora lutea, if present. This method was applicable only until July, at which time the possibility of corpora lutea regression could lead to erroneous estimates. Figure 18 shows that although reproductive potential is variable, it is obviously correlated with CL ($r=0.79$). Associated with increased reproductive potential in larger females is an increase in clutch size (Fig. 19) and possibly also the number of clutches. The most important effect, however, is the extension of the nesting season. Large females are thus the first and last to nest during a particular season. The average reproductive potential among 31 autopsied females was 29. The smallest potential observed (7) was in a small female probably in one of her first reproductive seasons. The largest potential (71) was in the largest specimen captured during the study (285 mm CL, AUM # 21970). Whether 71 eggs would have been produced is questionable, but 33 corpora lutea were present at the time of autopsy (July 4). Since ovi-

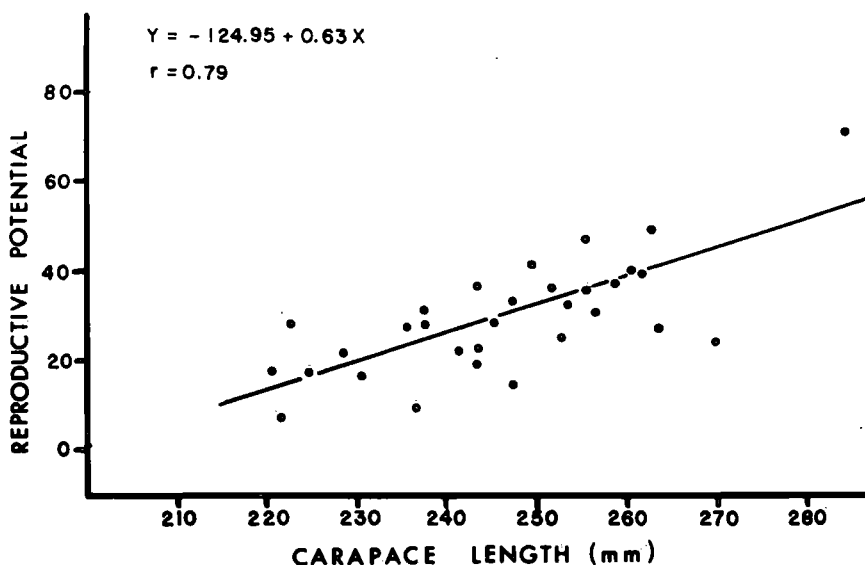


Figure 18. Reproductive potential (number of corpora lutea plus enlarged follicles) as a function of carapace length in adult female *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama. All determinations were made from March through June.

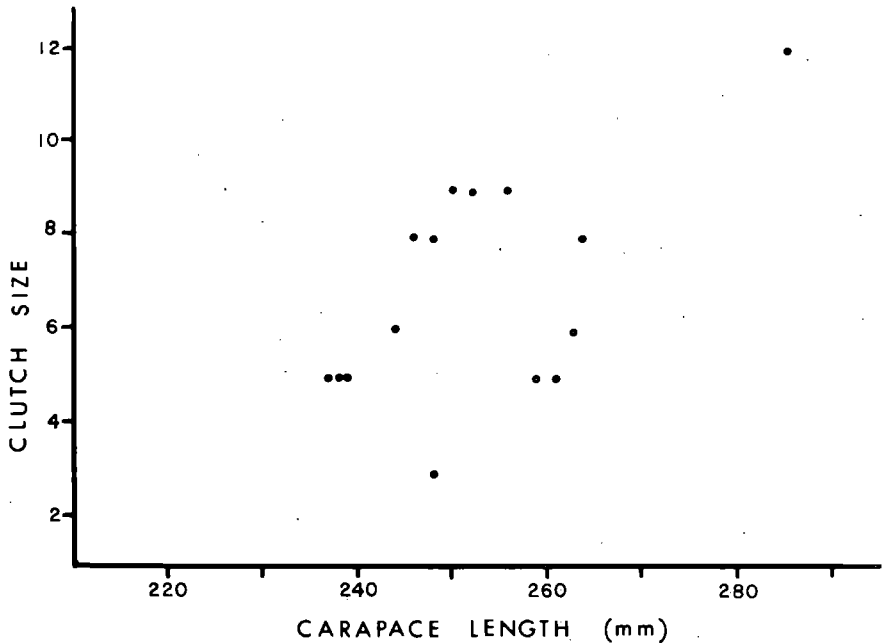


Figure 19. Clutch size as a function of carapace length in adult female *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama.

position was observed throughout July and the period of oviposition was extended in larger females, it is probable that most of the remaining follicles (38) would have been ovulated. In *G. barbouri*, Cagle (1952) found reproductive potentials of from 11 to 51 (average 17). He excluded the "unusually high" 51 in his average. His largest *G. barbouri* (300 mm CL) had a reproductive potential of 51, and my largest Conecuh River *G. pulchra* (285 mm) had a potential of 71. This implies that *G. pulchra* has a significantly greater reproductive potential than *G. barbouri*.

MATING

I only saw courtship and mating a few times and never a single complete sequence, from initiation of courtship to copulation. Sperm was found to be present in the male tract at all seasons, thus implying year-round mating potential. In both the laboratory and the field, however, mating activity was observed only from September to November. The following account is based on several brief field and laboratory observations, and one may assume that it characterizes the overall sequence of events:

With neck extended, the male would directly approach the cloacal region of the female, who apparently indicated by scent her identity or receptive-

ness. He then swam in front of his potential mate and assumed a face-to-face position in one of several attitudes: slightly to either side, slightly above, or slightly below the female's head. He then rapidly vibrated his head vertically against the side of the female's snout, alternating sides approximately every five seconds. The duration of this phase of courtship was not determined; however, based on several observations this could be as short as 15 seconds. During this display the female apparently withdrew her head slightly, with the eyes partially closed. The male then swam directly to the cloacal region of the female and attempted to appose the cloacae by looping his tail beneath the tail of the female, while maintaining a position on the rear of her carapace. The angle formed between the axes of the shells was approximately 45° . Often the male seemed to "sense" a lack of receptiveness in the female at this stage and returned to the head-to-head posture, possibly repeating the head-to-tail sequence several times before successful copulation. This repetition was observed only in captive specimens, and it may be that stresses of captivity inhibited the females' normal response. In nature, a single courtship sequence may normally be sufficient. Only brief attempts at copulation were observed, and only in the laboratory. Duration of copulation was not determined. This courtship pattern resembles closely that of some other aquatic emydines, including *P. scripta* (Jackson and Davis 1972). The major difference lies in the "titillation sequence," in which the snout of the male *G. pulchra* is vibrated rather than the claws of the forelegs, as in *Pseudemys* spp. *Graptemys kohni* and *G. flavimaculata*, however, have been observed to use claws in courtship (Cagle 1955), and elongate foreclaws are characteristic of mature *G. pseudogeographica* males (Webb 1961).

SPERM STORAGE

If mating occurs chiefly, or entirely, in the fall, then sperm must be stored in the female reproductive tracts, since no ovulation occurs until late April. Oviducal scrapings in March and May contained active and inactive sperm. Sperm storage has been reported in *Malaclemys terrapin* (Hildebrand 1932), *T. ornata* (Legler 1960), and *T. carolina* (Ewing 1943). No concerted effort was made to study sperm storage, since mating may have occurred at any time during the periods of activity and possibly even during the winter months.

From autopsied females I took 104 oviducal eggs that averaged 38 mm by 26 mm in size; 34 eggs from nests averaged 38 mm by 27 mm. This slight difference in width resulted from rapid water absorption, even though the nests were usually less than three days old when found. During incubation, also, the greatest increase was in width, resulting in a more nearly spherical shape at hatching. Cagle (1952) measured five eggs from the oviducts of a female from the Escambia River. Their average measurements (39 mm by 24 mm) fell well within the range of variation observed. On the other hand, his measure-

ments of eggs from a Pearl River female (45 mm by 26 mm) are well outside the range of variation in the eggs of Conecuh River *G. pulchra*. The leathery shell of the egg is of a finely granular texture at oviposition but becomes smoother soon after laying, as water is absorbed and turgor increases.

Ovulation begins in late April and continues through July (Fig. 17). The earliest oviducal eggs were found on April 28 and the latest on July 30. The peak of nesting activity in the study area occurs in June, corresponding to a sharp decline in numbers of enlarged follicles in autopsied females (Fig. 17).

Table 2 shows individual average monthly follicle numbers in three size ranges during the ovulatory season. Since reproductive potential is directly related to body size, both the average carapace length of autopsied females and the calculated reproductive potentials are included in the table. If the total number of enlarged follicles present during each month is subtracted from the estimated reproductive potential, an estimate of the number of ova ovulated prior to autopsy may be obtained. Twenty-five clutches averaged 7.2 eggs per clutch and the average reproductive potential was 29; thus, the average estimated number of clutches would be approximately 4, as confirmed in Table 2. Estimates of numbers of ova ovulated prior to autopsy correspond roughly to one clutch per month from May through July.

TABLE 2.—MONTHLY CHANGES IN FOLLICLE SIZE FREQUENCY IN ADULT FEMALE *G. pulchra* FROM THE CONECUH RIVER, ESCAMBIA COUNTY, ALABAMA*.

Size	May	June	July	August
20-25	13(9-18)	12(4-20)	4(0-5)	1(0-3)
15-20	6(3-8)	5(2-9)	3(0-13)	4(0-7)
10-15	5(2-6)	5(1-6)	2(0-2)	1(0-3)
Total	24	22	9	6
CL	244	254	249	250
RP	30	36	33	33
Ovulated	6	14	24	27
N	8	6	8	5

*Abbreviations: Size = average follicle diameter in mm (range in parentheses); CL = average carapace length in mm; RP = reproductive potential as estimated from the regression line of Fig. 18; Ovulated = estimated number of follicles ovulated prior to autopsy; N = number of females autopsied. The average reproductive potential was 29.3, average clutch size was 7.2, and the average number of clutches per female per year was 4.0.

The number of clutches obviously is correlated directly with size, as is reproductive potential, and autopsies and nesting signs indicate that large females also ovulate earlier and later in the nesting season than small females. A single clutch or two small clutches is characteristic of females in their first reproductive season. At the other extreme, probably six or seven clutches would be laid by the largest female examined, having a reproductive potential of 71 and a single clutch size of 12. However, my findings suggest little

correlation between body size and clutch size (Fig. 19), and if such is the case up to 10 clutches (7 eggs per clutch) might have been laid by this female in a single season. Moll and Legler (1971) reported six clutches for *P. scripta*, the greatest number known for an emydine.

Nearly all follicles over 10 mm in diameter at the beginning of the nesting season were ovulated, and there was no evidence that new enlarged follicles developed during the nesting season. Many, if not all, of the follicles present in late August were in the early stages of development, preparatory to the subsequent nesting season. Although a few may have become atretic, they would not have represented more than 5 percent of the reproductive potential.

Extra-uterine migration of ova has been observed in several species of turtles (Legler 1960) and is probably a phenomenon of general occurrence. Such migration had occurred in at least 67 percent of the female *G. pulchra* autopsied, as determined by lack of correspondence between numbers of corpora lutea and oviducal eggs in respective ovary-oviduct units.

Shelled eggs have been reported in the body cavity of *Deirochelys reticularia* but apparently produced no harmful effects (Cagle and Tihen 1948). In June, 1971, a large female *G. pulchra* was captured, marked, released after being in captivity for over a week, and recovered at the release site several weeks later. It made no attempt to escape, even though approached directly while basking, and was obviously in very poor condition. Subsequent autopsy revealed the presence of a shelled egg in the coelom. The shell of this egg was heavily calcified, as were the shells of the nine eggs in the oviducts. The liver and mesenteries were mottled with yellow, implying widespread infection. Whether the condition arose because egg laying could not take place during captivity is uncertain, but if this were the case, many other marked and released females could have been similarly affected during the study.

NESTING

Field observations of nesting coincided closely with the season of ovulation, as determined by autopsy. The earliest nests and oviducal eggs were found in late April and the latest in late July. Tracks were often seen on nesting beaches well before the nesting season. The purpose of such pre-nesting explorations is unknown, but they probably serve to determine the suitability of potential sites. Because of the unpredictable nature of sand deposition during high water, beaches are subject to wide fluctuation in quality from year to year.

Nesting site situations were variable, but most commonly were on large sandbars associated with sharp bends in the river (Fig. 2). Others were found among areas of moderate undergrowth and heavy canopy along relatively straight river sections (Fig. 1). In order of decreasing importance, factors influencing suitability of nesting sites appeared to be: sand particle size, eleva-

tion above the water level, cover quality, and distance from the water's edge. The characteristic most consistently associated with nesting sites was very fine sand. All normal and complete nests were found in such a substrate. This sand is easily excavated without settling, forms a firm crust when wetted and dried, and retains moisture beneath this crust even when exposed to prolonged dry periods. In a few exceptional cases, nests were found in coarser sand that offered none of these qualities. Such nests were usually incomplete and contained only one or two eggs. Apparently the coarse sand substrate was resorted to by the female only after a thorough exploration of the beach failed to reveal a suitable site or after she had repeatedly failed to scale heavy slopes of coarse sand leading to more favorable sites (Fig. 20). Such "desperation nesting" seemed to be associated with small females, judging from the size of the tracks.

Females rarely wandered far from the water when nesting. Nests were generally situated 3-15 m from the water's edge. This is in contrast to many other aquatic emydines, such as *Pseudemys scripta* and *Graptemys geographica*. The former may move up to half a kilometer overland while nesting (Cagle 1950, Moll and Legler 1971), and the latter also wanders long distances inland in search of nesting sites (Carr 1952).

Assuming suitable substrate, nests were located fairly consistently at elevations of 2-3 m above the existing water level. On gently sloping banks, such elevations were sometimes reached only after a trip of up to 70 m from the water's edge. The greatest distance traveled was 150 m, over apparently suitable substrates. No nest, or even "test holes" were dug along the way, even though the nesting season was at its peak.

A complete nesting sequence was not observed during the study. Six fragmentary observations, when considered together, provided a reasonably complete picture of nesting behavior. Three observations were made at the Conecuh River study area and three at Opintlocco Creek, a small stream in the Mobile Bay drainage in Macon County, Alabama. The earliest observation was made at 7:00 a.m. CST and the latest and 8:00 p.m. CST. Two others were made in the morning, one at noon, and the sixth at 4:00 p.m. Various conditions of cloud cover were present, but at no time was it raining. Temperatures were variable, primarily because of the different times during which observations were made. It seems that nesting may occur at any time, subject to local variations in predator and human activity.

The following account of nesting behavior is a composite of the six fragmentary observations. The female, with head elevated, lingered at the water's edge for several minutes, during which time she surveyed the area by rotating her head approximately 45° to each side, pausing about 15 seconds at each point of maximum rotation. With head lowered and extended, she then left the water and ambled at a seemingly invariable and mechanical pace (about one



Figure 20. Sandbar heavily used in 1971 by nesting female *Graptemys pulchra* (see Fig. 2), Conecuh River, Escambia County, Alabama. Note trail in the foreground with shallow "test holes." Apparent difficulty in scaling sandy slope is shown by horizontal and back-sliding trails at center. All nests were located on the upper level and many were at the edges of vegetation (background).

step per second) directly onto the sandbar. Occasionally she would pause and raise her head, perhaps to look for possible predators, or perhaps to search for a suitable nest site. Otherwise she appeared oblivious to potential terrestrial threats.

On one occasion a large female was easily captured within 2 m of the water during such a nesting journey. She made no attempt to enter the water, but withdrew her head and legs into the shell. Another time a female, surprised at night approximately 2 m from the water, made a frenzied dash for the water, barely being overtaken at its edge.

Between pauses, the head was kept lowered. Periodically, the nose was pressed close to the substrate, as if seeking olfactory clues. At variable intervals the consistency of the sand was tested with the front legs by an alternating sweeping motion, creating furrows from 1 to 5 cm deep. Occasionally, deep holes were dug, apparently with the hind legs, but were not completed (Fig. 21). Such "test holes" were often found to have stones, leaf litter, roots, or other obstacles at the bottom. When the site was selected, excavation was carried out by alternating sweeps and scrapes of the hind legs. The resulting nest was a flask-shaped cavity about 15 cm deep, having a lower spherical chamber about 10 cm in diameter and a neck about 4 cm in diameter. The eggs were seemingly deposited with no regard to position and covered completely by alternating sweeping movements of the hind legs. No "plug" was formed, as in *Pseudemys* spp. As sand was drawn into the nest, each leg was forced into the entrance to pack its contribution to the filling, this continuing until the cavity was filled. This was followed by lateral movements of the body that served to smooth the sand over the nest entrance. The route leading to the nesting site could have been quite tortuous, whereas that leading back to the water was invariably direct (Fig. 21). The behavior observed by Cahn (1937) in *G. pseudogeographica*, in which the nesting female described a complete circle during oviposition, was not evident in *G. pulchra*.

INCUBATION

Artificial nests were maintained as closely as possible to field conditions, being constructed of concrete blocks filled with sand and placed outdoors where they received approximately a half day of sunlight and a half day of shade. Temperatures were also maintained close to those of natural nests. Sand from a natural nest site, or a similar site, was used as the nest medium.

Incubation periods ranged from 74 to 79 days (av. 76) in nine artificial nests. This compares reasonably with 65 to 80 days in *Chrysemys picta* (Ernst 1971), 61 to 79 days in *Pseudemys scripta* in the Temperate Zone, and 71 to 83 days in neotropical *P. scripta* (Moll and Legler 1971). Field observations showed an average period of 95 days (79 to 110) between the peak of nesting and the peak of emergence. These observations were considered much less reliable than those based on artificial nests as indicators of incubation period.



Figure 21. "Test hole" dug by nesting female *Graptemys pulchra* at the Conecuh River, Escambia County, Alabama. Note narrow groove made by the tail between footprints, distinguishing *G. pulchra* tracks from those of *Trionyx* spp., which makes broad tail grooves.

Inasmuch as most nests were destroyed by predators, observations of hatching or hatchlings were scarce. Also, hatchlings remained in the shells within the nest until yolk absorption was complete, requiring at least several additional days.

Eight determinations of nest temperatures were made in the field, ranging from 23 to 31°C (av. 29°C). The lowest temperature observed was in a nest located in a shallow depression in complete shade, whereas the highest was in a comparatively shallow exposed nest in sand darkened slightly by humus.

Egg mortality apparently exceeded 90 percent in each of the three nesting seasons during the study period. Such mortalities have also been observed in *P. scripta* (Moll and Legler 1971), *T. ornata* (Legler 1960), and *C. picta* (Ernst 1971). Cagle (1950) found only one undisturbed nest out of 500 on a nesting bank in Louisiana.

Mortality may have been somewhat less during the 1970 nesting season than in the following two seasons, as evidenced by the relatively large number of hatchlings appearing in the fall of 1970. Nest predation near areas of human population, such as East Brewton, seemed to be less than in more remote areas. In the Conecuh River study area, only 10 intact nests were found during three nesting seasons, whereas several hundred destroyed nests were found in the same period. All of the intact nests were fresh, and it is unlikely that they would have escaped predation. The fish crow was the major diurnal egg predator and the raccoon the major nocturnal predator.

Although the effects of egg submersion was not studied, it was observed that at least some nests survived following periods of temporary inundation. During the 1972 season one nest, from which at least six hatchling *G. pulchra* had emerged, had been beneath the water line for a week or more during early incubation.

Several cases of presumed infertility were found, both in individual eggs and in entire clutches. Infertility appeared to be more common in populations from small Mobile Bay drainage streams in Macon County (Cubahatchee Creek, Opintlocco Creek) than in the Conecuh River population. Since population density was much lower in these smaller streams, it is possible that the greater frequency of infertility resulted from less opportunity for successful mating. Of 64 eggs from the Conecuh River population incubated in 1972, one entire clutch (8 eggs) and one egg from another clutch failed to develop. One entire clutch of ten eggs at Cubahatchee Creek was apparently infertile. Several other clutches incubated in 1969 and 1970 from these Mobile Bay drainage streams contained eggs that were undeveloped or entirely inviable.

An unidentified fungus, which was found only on the surface of infertile eggs, was initially blamed for much egg mortality. No embryo was found in any egg supporting fungal growth. To determine if fertile eggs were susceptible, eggs from several clutches were placed in sand where an entire clutch had been infested by fungus. No fungal growth on the eggs was evident after two

months, even though the sand was heavily infiltrated with hyphae. One egg was found to lack an embryo and the yolk was dehydrated, presumably resulting from an earlier rupture of the shell. All other eggs hatched normally.

Soon after deposition the eggs increased rapidly in size and turgidity, presumably as a result of water absorption. One clutch of eggs averaged 29.5 mm by 43 mm just prior to hatching, as compared to the average of 26 mm by 38 mm for all measured eggs at oviposition. Water absorption by eggs of *T. ornata* was reported by Cunningham and Hurwitz (1936). Pores have also been shown to be present in the shell of emydine turtle eggs (Young 1950).

During incubation, the upper half of the egg shell changes from translucent pink to white within a few days after laying. The lower half of the shell remains pink nearly until hatching. The white area indicates the position of the dorsal surface of the developing embryo and, if the egg is undisturbed, the hatchling is in an upright position at hatching.

HATCHING

Normally the hatchling is in an upright position within the egg, with the long axis of the body corresponding to the greatest length of the egg. Hatching begins with a minute puncture of the shell in the head region, which probably occurs as a result of penetration by the caruncle. The hole, (Fig. 22A) is located at, or slightly dorsal to, the apex of the egg. Amniotic fluid flows freely out of the puncture, causing rapid collapse of the shell. Within 15 to 30 minutes a vertical or horizontal enlargement of the puncture results in one or several straight slits about one cm in length (Fig. 22B). This is followed by a crossing of slits, often in an asterisk pattern, forming an opening through which the head can be extended. Rupture of the shell and pulmonary respiration before yolk absorption is perhaps made necessary by a decreased allantoic capacity for adequate gas exchange. Lynn and von-Brand (1945) demonstrated that late turtle embryos require as much oxygen as hatchlings, and that turtles in the process of hatching require more.

Exposed hatchlings remain in the shell about four days, during which time the remaining yolk is resorbed. The yolk sac decreases in size from 12 to 15 mm at hatching to nearly complete absorption after three days (Fig. 22E). In natural nests, greater lengths of time may be spent within the shell, presumably delaying emergence until conditions are more favorable. Thus, nests left undisturbed often contained hatchlings with all yolk absorbed and with tightly closed and healed umbilical scars. In artificially exposed hatchlings, yolk absorption and umbilical scar formation occurred within 5 to 8 days. The caruncle (Fig. 22F) is shed generally within two weeks after hatching.

No signs of hatchlings overwintering in the nest were observed. This is in contrast to the findings of Cagle (1944b) for *P. scripta*; Ernst (1971), Sexton (1957), and Hartweg (1946) for *C. picta*; and Newman (1906) for some other species of *Graptemys*. All hatchlings found in the spring had heavily

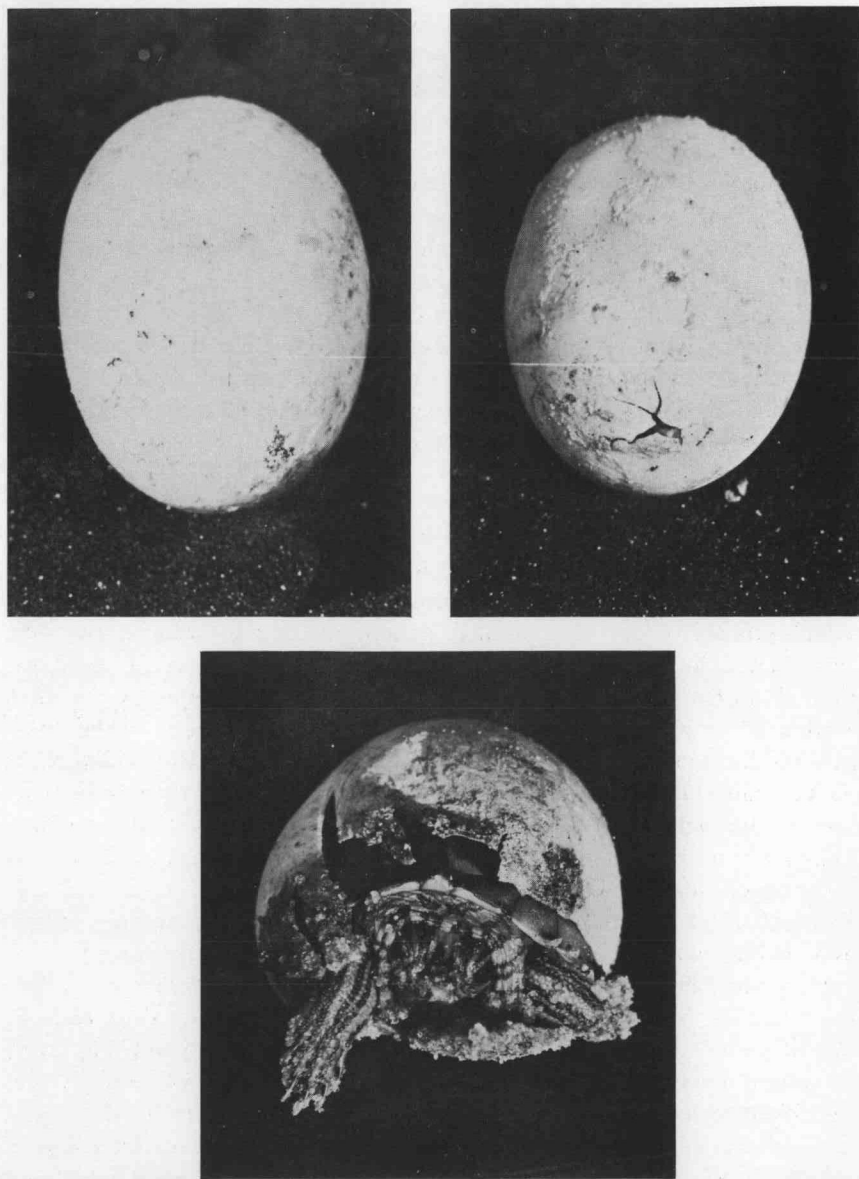
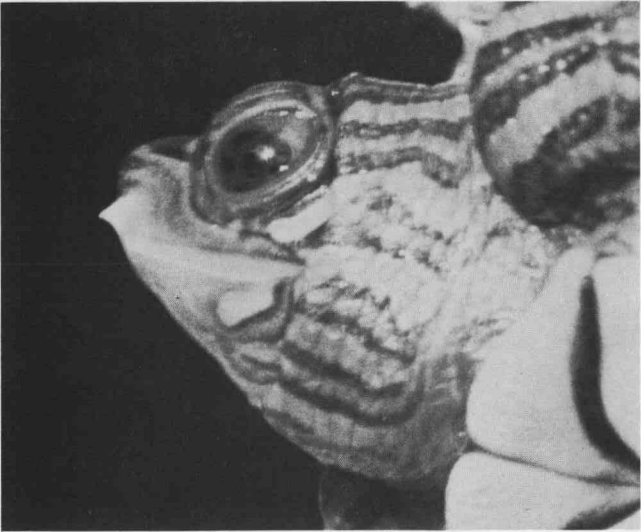
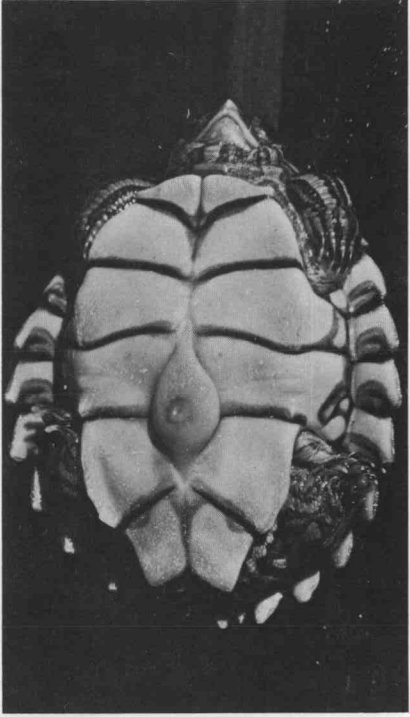
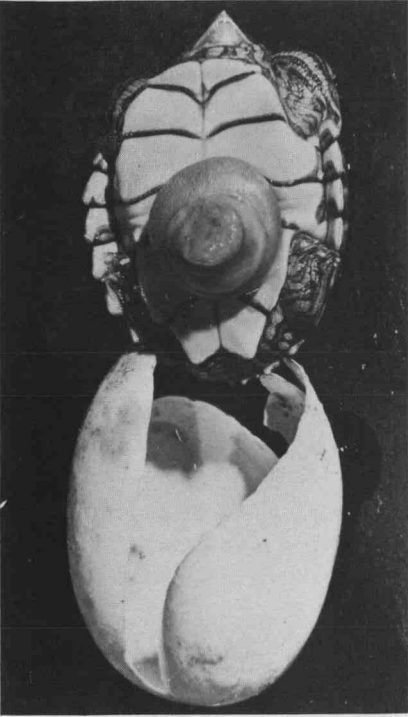


Figure 22. Representative stages in hatching in *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama. The initial puncture made by the caruncle is enlarged to an asterisk-shaped opening. The head and forelegs enlarge the opening further and emergence is normally arrested at this stage for the several days required for yolk absorption.



stained plastra, indicating prolonged exposure to a muddy substrate. No nest was found in such a substrate, but bottoms in slow-moving river sections preferred by hatchlings were usually composed chiefly of fine silt. Also, no hatchling tracks were seen on nesting beaches in the spring.

Movement to the water by hatchlings was consistently direct. This is in contrast to the behavior of *Trionyx* hatchlings, which left the nest in apparently random directions, some traveling a hundred meters to reach water that was less than 10 m away and visible from the nest.

HATCHLINGS

Fecal samples from newly hatched *G. pulchra* indicate that they begin feeding shortly after reaching the water. The tendency to bask is apparently greater in hatchlings than in older individuals. Often only hatchlings or yearlings were found basking during comparatively unfavorable weather conditions in the fall. They also displayed a greater reluctance to enter the water and could often be directly approached and captured with no regard for cover on the part of the captor. A greater need for pre-hibernal growth or food storage may have prompted such activity. Hatchlings were found to feed as late as November, while older individuals generally stopped feeding in October.

Mortality of hatchlings after entering the water was apparently low, because yearlings seemed to be as numerous in the spring as hatchlings were the preceding fall. Fecal samples from several specimens of a large aquatic predator, the alligator snapping turtle *Macroclemys temmincki*, caught in the study area, showed only mussel remains. No stomach samples were taken from other potential predators, the most important of which may be several species of gar and the Great Blue Heron. Although a single alligator (*Alligator mississippiensis*) was observed, it was not considered to be a significant predator of *G. pulchra* in the study area.

POPULATION DYNAMICS

POPULATION DENSITY

The highly variable and discontinuous distribution of individuals along most sections of river in the study area made estimates of population density difficult to substantiate. Use of a "Lincoln Index" under these circumstances greatly overestimated population size. For example, use of an unmodified index would result in an estimated density of over 500 individuals of *Graptemys pulchra* along the 500-meter segment of river immediately downstream from the East Brewton bridge, assuming unbiased sampling. Such estimates are highly untenable; therefore direct observations and collecting data were relied upon for more reasonable estimates of population density.

Two methods of estimating population density were used. For long,

straight stretches of river with a relatively homogeneous bottom, counts of basking individuals were made during periods of maximum basking (high water levels). On winding segments of river, consisting of shallow runs with gravel bottoms alternating with deep silted or sandy pools, individuals usually concentrated in the pools during periods of low water level. Diving under these conditions often yielded large numbers of individuals, even though small sizes often were not well represented. The scarcity of smaller sized individuals may have been due to differences in feeding habits (see pp. 94-99). The numbers of individuals in such concentrations at favorable sites, when expressed as a function of the distance between such sites, resulted (with some modification) in a more or less workable estimate of population density.

Population estimates using both methods are listed in Table 3. I believe that in both cases true numbers are underestimated significantly, and at best probably represent no more than 75 percent of the true density. The density of *G. pulchra* in the study area was estimated to be approximately one turtle per 3-4 m of river length. Other estimates of population density in aquatic emydine turtles are one adult *Pseudemys scripta* per 6 m of river (Moll and Legler 1971), one *P. scripta* per 3.3 m of river (Tinkle 1958), and 239 *Chrysemys picta* per acre (Ernst 1971).

TABLE 3.—ESTIMATES OF POPULATION DENSITY OF *G. pulchra* AT THE CONECUH RIVER, ESCAM-BIA COUNTY, ALABAMA*.

Location	U. S. 29	Co. # 4	E. Brewton
Date	April-May, 1970	September, 1970	September, 1969
Method	Surface	Diving	Diving
Juveniles	16	0	18
female, immature	10	23	14
female, mature	5	8	17
male, mature	4	15	16
Total	35	46	65
Area	500 m	300 m	500 m
Number per 100 m	7	15	13
Validity	25%	50%	50%
Balanced estimate per 100 m	28	30	26

*Area is in meters of river channel (longitudinal). Validity is the estimated percentage of turtles counted by the method used. Balanced estimate is the observed density plus the estimated number of turtles not counted by the method used.

COMPOSITION

Frequency of size classes is illustrated in Figures 23 to 25. Among females (Fig. 23) and juveniles, pronounced peaks are evident for size classes 50 to 75 mm CL and 225 to 250 mm. The first peak includes both males and females

during at least the first two years of growth. Development of sexual maturity in males over 75 mm eliminates them from remaining classes, thus accentuating the decline in numbers to the 75 to 100 mm class. A further, less radical decline continues to the 150 to 175 mm class. Studies of released and recaptured females reveal that the period of maximum growth may accelerate removal of individuals from the intermediate size classes into larger classes. Relative scarcity of members of the 150 to 175 mm class was observed throughout the study.

The second peak in abundance at the interval 225 to 250 mm is associated with attainment of sexual maturity in females (at around 220 mm) and a sharp decline in growth rate. Growth has virtually ceased in most females over 250 mm; thus members of this size class probably accumulate as new individuals mature and growth ceases. The size at which growth essentially ceases, however, varies, as indicated in Figure 24, where there are only slight differences in frequency of size classes between 230 and 265 mm.

In males (Fig. 25), a more "normal" distribution centering around the size class 90 to 95 mm is evident. Growth declines, though less sharply than in females, after attainment of sexual maturity (80 mm CL). There is less variation in the size at which growth in males essentially ceases. More than half (58%) of mature males were between 85 and 100 mm in length.

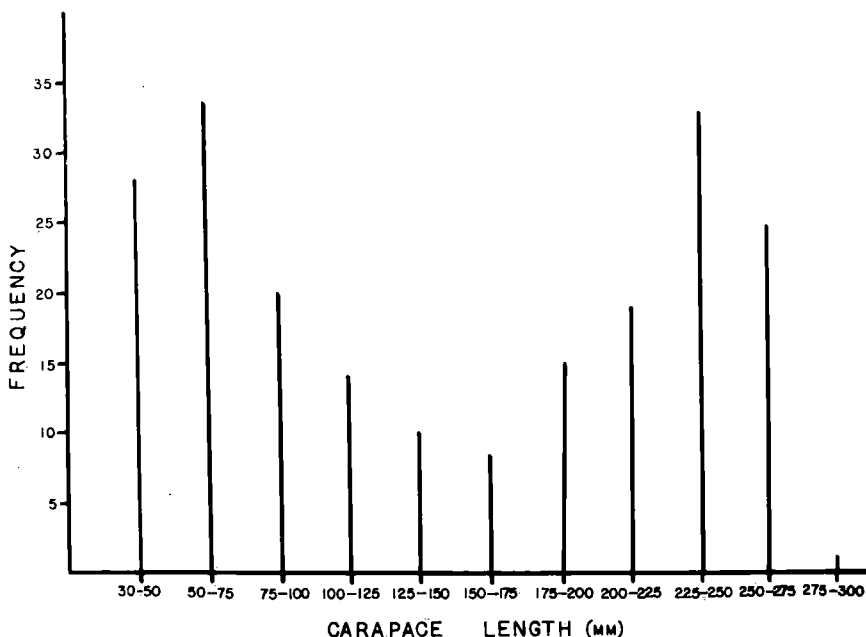


Figure 23. Relative abundance of size classes of juvenile and adult female *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama.

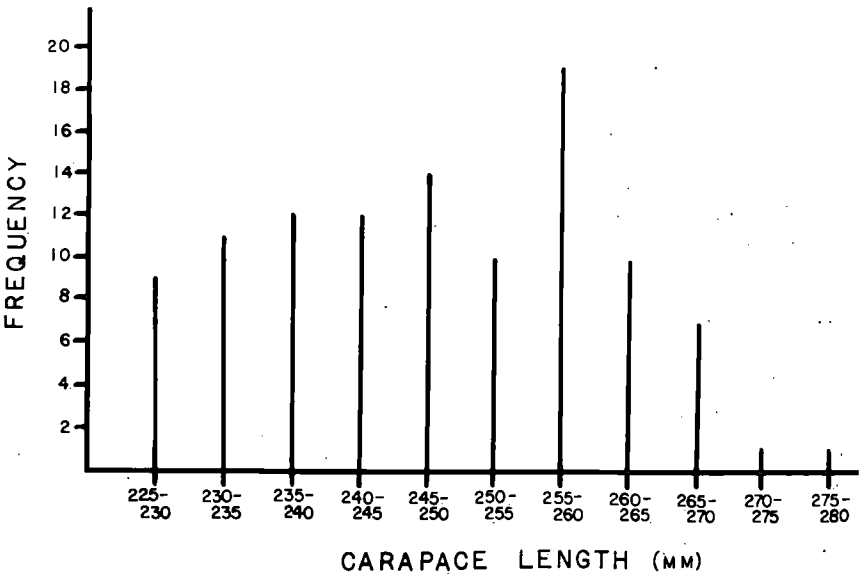


Figure 24. Relative abundance of size classes of adult female *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama.

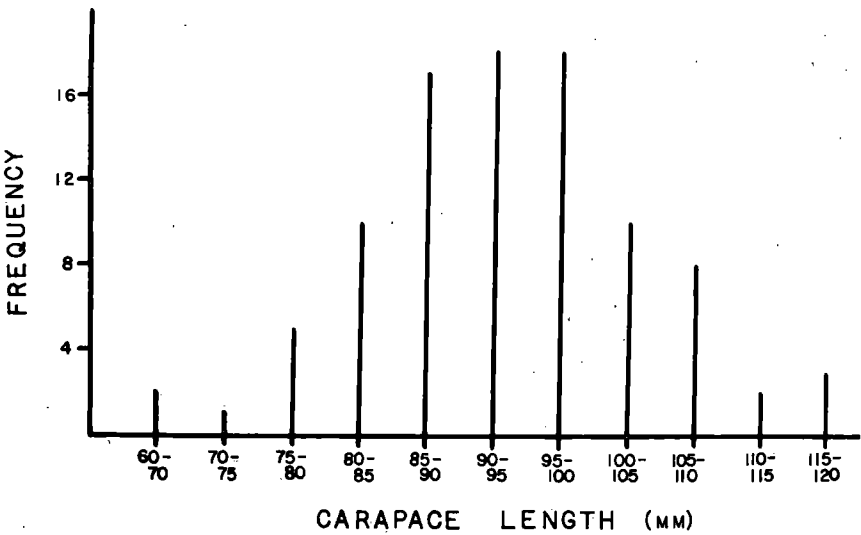


Figure 25. Relative abundance of size classes of adult male *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama.

MORTALITY

Field observations of nests indicate that nest destruction probably exceeds 90 percent in most seasons, *i.e.* very few eggs develop and contribute hatchlings to the population. These observations are consistent with those of other workers (Allen 1938, Cagle 1950, Gibbons 1968, Moll and Legler 1971), who found egg mortality to be as high as 99.8 percent. Numbers of hatchlings added to the study area population per year appeared to vary somewhat during the study period. For example, during the late fall of 1969 and spring of 1970 hatchlings were relatively abundant but were scarce during the following three seasons.

POST-NATAL MORTALITY

Few instances of natural post-natal mortality were observed; one juvenile female, several young adults, and several old adults were found dead of unknown causes during periods of rapidly dropping water level. These observations occurred during early spring and summer. On a nesting beach a freshly killed young adult female was found, surrounded by raccoon tracks (Fig. 26).

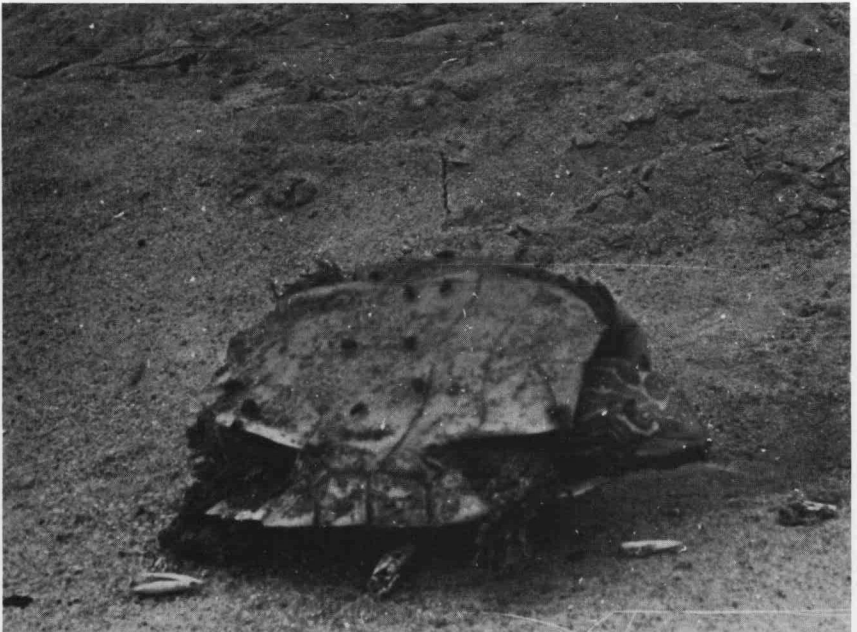


Figure 26. Freshly killed nesting female *Graptemys pulchra* (AUM 21973) at the Conecuh River, Escambia County, Alabama (sandbar of Figures 2, 20, and 21). Note egg shells in foreground. Predator was probably a raccoon.

Under laboratory conditions hatchlings and very small individuals were especially delicate. Thus, it is assumed that very small individuals would be most susceptible to natural stresses. The data in Figure 23 support the conclusion that significant mortality after hatching occurs in size groups under 175 mm in carapace length. Ernst (1971) likewise found a significantly higher mortality among juvenile *C. picta* than among adults, but Gibbons (1968) found a lower mortality in juveniles.

During the first few years of growth the shell is comparatively soft and offers little resistance to injury. At this time very young individuals probably direct nearly all food resources toward growth rather than energy storage during most of the year. Thus, with even a brief decline in food quantity or quality, a lack of metabolic reserves may result in decreased vigor and increased susceptibility to disease and injury. Among adults such stresses are probably detrimental only if prolonged or extreme. The observed adult mortality is attributable to shooting by man, to unknown diseases, or to some unknown predator. Occasionally individuals collected during periods of flooding had freshly eroded, bleeding, and evidently infected areas on the plastron.

HOME RANGE AND HOMING

Definition of home range within a habitat that undergoes drastic changes annually or seasonally is necessarily tenuous. Populations of *G. pulchra* were found to congregate in particularly favorable areas. Although apparently subtle, changes associated with seasonal fluctuations in water level, especially sand and silt distribution, often resulted in major redistributions of individuals. Sexton (1959b) found that *Chrysemys picta* emigration coincided with high water levels.

In areas less subject to seasonal changes distribution was consistent and predictable to the extent that certain logs and trees would be expected to serve as basking sites for a specific number of individuals of each species. Chaney and Smith (1950) and Cagle (1952) also noted such behavior in *G. pulchra* with respect to home range.

Variation in home range was most pronounced from year to year. At the close of a period of intense marking efforts in the fall of 1969 in a moderately stable area near East Brewton, it became difficult to find unmarked individuals, and the next year only 10 of the original 62 marked individuals were recovered. In the following two years, I recovered 12 and 4 members, respectively, of the original group. Thus, even though the area apparently remained the most favorable one within the immediate vicinity (a km in either direction) and the population density remained stable, significant movement had occurred. The distance between favorable areas was generally several hundred meters, depending on river channel characteristics, and most individuals probably did not often move between these areas during a single season. Although a quantitative estimate of home range size was not made, it is prob-

able that the area involved was similar to Moll and Legler's (1971) estimate of 278 m of river for *P. scripta*.

Homing ability has been demonstrated in many emydines (Cagle 1944a, Legler 1960, Moll and Legler 1971). Distances in excess of 2000 m have been traversed, upstream and downstream, in returning to a home range. Such movements may also be quite rapid. One sonically tracked female *P. scripta* moved 1000 m in 90 minutes after being displaced from its point of capture (Moll and Legler 1971).

To determine homing tendency in *G. pulchra*, 47 marked individuals (13 males and 34 females) were released 24 channel km upstream (6♂, 15♀) or downstream (7♂, 19♀) from capture sites. Release and recapture data on eight displaced and recovered individuals are shown in Table 4. All recovered individuals were females, implying either less adherence to home range or less homing ability in males. On the basis of similar data, Cagle (1944a) reached the conclusion that males of *P. scripta* move randomly when displaced. However, other available data for *G. pulchra* show that males may be responsive to home range, for of 53 non-displaced males 42 percent were recaptured near the point of release (Table 5). Since more non-displaced males than females were recovered, movements of males may be regulated by other factors, such as food availability.

Half the recovered females returned to the point of capture, while half remained at the point of release (Table 4). Because of the great distances involved (approximately 24 km) and the small size of the collecting areas (1 to 4 km), it is not likely that either homing ability was absent or that random movement occurred from the point of release. The same proportion (24%) of females was recovered both in displaced and in non-displaced groups, indicating that individuals either returned to the original point of capture (home range) or remained in the areas of release, but did not wander randomly (Table 5).

As shown above (Moll and Legler 1971), such returns may be accomplished in comparatively short periods of time. It is unlikely that any recovery failure resulted from lack of sufficient travel time.

Of the four displaced individuals that returned, two returned to an upstream home range and two returned downstream (Table 4), indicating that homing ability may be unaffected by direction of stream flow. Downstream return in this case implies that olfaction was not involved. Channel characteristics, with associated factors such as current velocity, stream width, and bottom structure, are perhaps the most likely qualities used as cues for navigation in this case.

No signs of territoriality were detected in *G. pulchra* during this study. Cagle (1944a) stated that territoriality was evidently non-existent in the genera *Pseudemys*, *Chrysemys*, *Chelydra*, and *Sternotherus*.

TABLE 4.—RECOVERY OF DISPLACED FEMALE *G. pulchra* AT THE CONECUH RIVER, ESCAMBIA COUNTY, ALABAMA*.

No.	C.L. (mm)	Date, points of Capture-release	Date, point of recapture	Interval (months)	Return
23	257	Aug., 1969; 29-4	Aug., 1970; 29	5	Up
264	253	May, 1971; 4-29	June, 1971; 29	1	
258	206	May, 1971; 4-29	Mar., 1972; 29	5	
19	239	Aug., 1969; EB-4	June, 1972; EB	13	Down
19	239	June, 1972; EB-4	Sept., 1972; 4	3	
256	61	May, 1971; 4-29	June, 1972; 4	5	Down
249	94	May, 1971; 29-4	Sept., 1972; 4	9	
234	264	May, 1971; 29-4	Sept., 1972; 29	9	Up
259	221	May, 1971; 4-29	Sept., 1972; 29	9	

*Abbreviations: No. = individual marking number; C.L. = carapace length in millimeters; 29 = U. S. Highway 29; 4 = Escambia County Highway 4; EB = East Brewton. Interval is in months of growth between release and recapture. Return is direction of movement from point of release, if movement occurred. Distance between points is approximately 15 river channel miles.

TABLE 5.—RECOVERY OF DISPLACED VERSUS NON-DISPLACED *G. pulchra* AT THE CONECH RIVER, ESCAMBIA COUNTY, ALABAMA.

	Number Released	Number Recovered	Percent Recovery
DISPLACED			
Males	13	0	0
Females	34	8	24
Total	47	8	17
NON-DISPLACED			
Males	53	22	42
Females	111	27	24
Total	164	49	30

FOOD AND FEEDING

Food of *Graptemys pulchra* in the study area falls into two general categories: arthropods (especially insects), which were important to males and to juvenile females during the first few years of growth; and molluscs (bivalves and gastropods), essentially the only food source for older juveniles and adult females. Cagle (1952) found a similar situation in Pearl River specimens. Some other *Graptemys* may be omnivorous (Cahn 1937), and others are primarily molluscivorous as adults (*G. barbouri*, Carr 1952).

As indicated in Figure 27, individuals less than 100 mm in carapace length are almost entirely insectivorous. In 36 fecal samples having identifiable arthropod remains, including samples from adult males, the following groups and frequencies were found: Trichoptera (as sclerotized larval fragments and cases), 27; Coleoptera (mostly terrestrial adults), 18; Odonata (nymphs and adults), 11; Hymenoptera (adults), 5; and millipedes (Diplopoda), 3. Webb (1961) found case-building Trichoptera, as well as Odonata, Coleoptera, and crayfish to be important food items of *G. pseudogeographica*.

A dietary shift to molluscs occurs in females at 80 to 100 mm CL, with insects occasionally being represented in larger juveniles (Fig. 27). The most important molluscan food item by far is the imported oriental mussel, *Corbicula maniliensis* (Fig. 28). This mussel probably represents the predominant macrozoic biomass in the study area. It was so abundant in some bottom situations that a sample of the top 3 cm of substrate often yielded equal volumes of *Corbicula* and sand. During some periods of rapidly dropping water level, shells were deposited on sandbars in concentrations of several hundred per square meter. *Corbicula* represented at least 95 percent of all food consumed by adult females. Some correlation was found between carapace length and

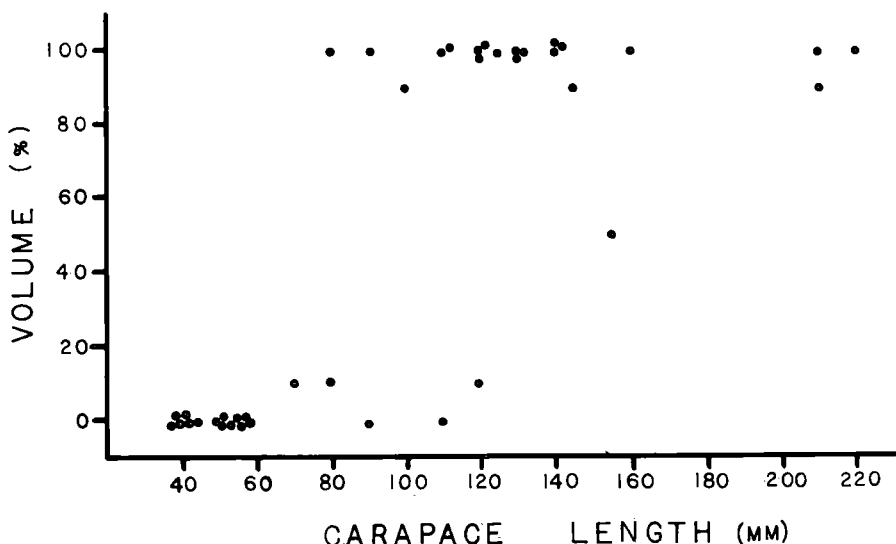


Figure 27. Ontogenetic dietary shift in female *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama. Importance of molluscs is expressed as percentages of fecal remains. Arthropods constitute the alternate food item.

size of *Corbicula* eaten (Fig. 29). Individuals under 150 mm CL fed mostly on mussels from 2 to 12 mm in length, while individuals over 150 mm CL fed on all sizes of mussels, particularly those from 5 to 20 mm in length. Adult females (over 220 mm CL) fed mostly on mussels from 15 to 25 mm long. Figure 29 does not show the relative importance of various mussel size classes, however.

The remaining 5 percent of the adult female diet in the study area included native mussels (generally under 50 mm, the largest *Corbicula* were 30 mm long), common aquatic snails, and crayfish (one sample). Fecal samples of adult females from the Mobile River drainage, where *Corbicula* was not found, contained mostly native mussels from 30 to 50 mm in length. One fecal sample from a Mobile Bay drainage specimen contained fish vertebrae, implying that carrion may be an occasional food source. Captive hatchlings seem to prefer fish to insects and crayfish.

Adult males, although primarily insectivorous, fed occasionally on small mussels and snails. Small aquatic snails represented about 15 percent of the volume of fecal material among 11 adult males. This figure may overestimate the importance of molluscs as a food source, however, since proportionately much less digestible material may be present in snails than in insects. Small numbers of minute *Corbicula* shells were frequently found in male fecal samples, but did not constitute an important item.

Some individuals in their first few seasons of growth contained highly





Figure 28. *Corbicula maniliensis* from the Conecuh River, Escambia County, Alabama. Left, representative shells from fecal samples of adult female *Graptemys pulchra*. Right, shells stranded by receding water near East Brewton, Alabama.

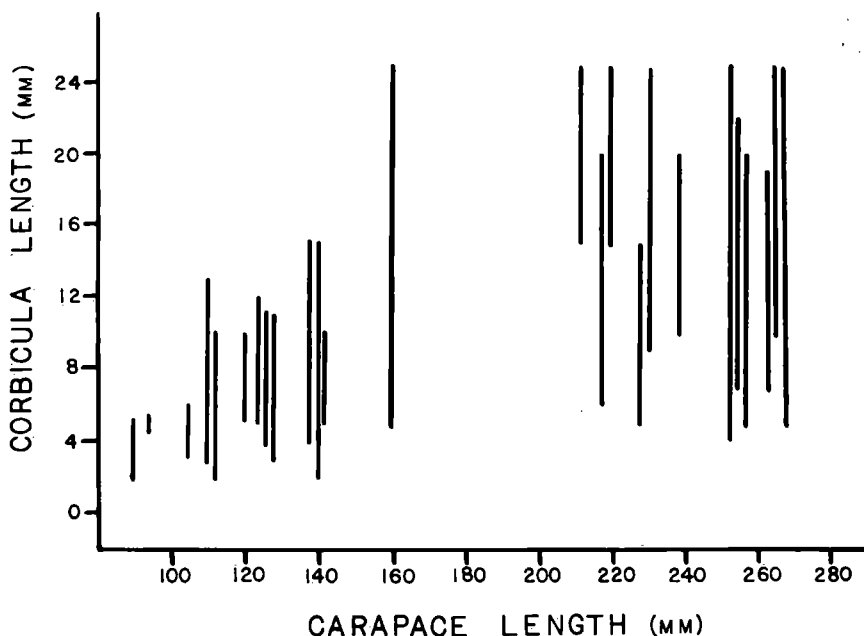


Figure 29. Size of *Corbicula* ingested as a function of carapace length in female *Graptemys pulchra* from the Conecuh River, Escambia County, Alabama.

eroded fragments of large *Corbicula* shells, much larger than could possibly have been crushed by turtles of such small size. This, combined with the facts that only incomplete shells were found, and that fragments were not greatly eroded by a single passage through the digestive tract of large individuals, led to the conclusion that fragments expelled by large individuals were ingested by small individuals. The reason for this cannot be determined, but it may be related to the obtainment of calcium salts for shell development or other needs. Moll and Legler (1971), speculating on the occurrence of snails in the diet of *Pseudemys scripta*, believed that "females may feed heavily on snails prior to the nesting season to build up stores of calcium for egg shell production."

Captive adult females kept in artificial pools (about 4 m in diameter and 50 cm deep) fed on crayfish almost exclusively, even though mussels were made readily available. Although crayfish were abundant in adjacent swamps and lowlands, the scarcity of crayfish in the Conecuh River (only one seen in four years) precluded their significance as a food item. It seems unlikely that *G. pulchra* could regularly catch healthy crayfish, even if they were available.

It is likely that mussels were eaten by grasping them with the jaws, pulling them out of the sand, and crushing them with the broad lateral alveolar surfaces of the jaws. Large females often showed pronounced erosion on the

lateral alveolar surfaces and none on the mandibular apex, resulting in a hooked condition of the lower jaw. This prevented the mouth from being sealed when closed. Small mussels and snails were occasionally swallowed entire, as evidenced by the presence of unbroken shells in the feces. The front feet were probably not used as extensively in feeding on molluscs as on arthropods, since mussels were not torn apart before being eaten.

Presumably because of the low food value to weight ratio of molluscs, fairly large quantities of mussels were consumed. The small intestine of an adult female is about 10 mm in diameter when empty, but many intestines were found distended to 30 mm in diameter for as much as 15 cm along their length, totaling 106 cc in volume. Usually within a day or two after capture all of the intestinal contents were expelled, implying that such a quantity represents no more than a single daily feeding.

Small individuals frequently were seen browsing in shallow water near sandbars or heavily sloping banks, or more commonly among drifts of floating debris that harbored large numbers of insects. Feeding on caddisfly larvae, the most important food source, was not seen. Case-building caddisflies are probably found in areas not visible from the surface. Also, feeding is probably inhibited by the presence of a diver. Young turtles and adult males seemed equally adept at feeding on floating prey or on submerged items. As in other emydines, the claws of the front feet are commonly used as an aid in tearing food into bite-sized morsels.

Very few data are available to elucidate the diel aspect of the feeding cycle. Captive specimens fed at various times. Large individuals observed while diving during the day were generally inactive and among submerged cover. Surface feeding by individuals of various sizes was observed only during early morning hours. The remainder of the day, especially during the spring and most of the summer, was spent basking and among cover. Boyer (1965) remarked that the stomachs of basking *Graptemys* often were packed with food items. Basking has been shown to be linked with feeding in other aquatic emydines (Moll and Legler, 1971). Regal (1966) showed that in certain Squamata, digestion may depend on thermoregulation to the extent that prolonged maintenance of suboptimal temperatures following a meal may be fatal.

In adult females heavy feeding began in May and essentially ceased in October. Small individuals and males apparently fed as late as November. Feeding coincided rather closely with the annual activity cycle (see pp. 99-100).

ACTIVITY

SEASONAL ACTIVITY

The major determinant of seasonal activity is water temperature. In the study population feeding essentially ceased and general activity sharply declined as water temperatures fell below 19°C (66°F). This was in contrast

to temperature relationships of some other aquatic emydines. Ernst (1971) reported *Chrysemys picta* "active" at water temperatures as low as 10°C; Cagle (1950) reported a similar minimum temperature for activity in *Pseudemys scripta*. *Pseudemys concinna* in the Conecuh River study area was never found inactive, even though the water temperature dropped to 11°C. Carr (1952) observed similar differences between *G. barbouri* and *P. floridana* with respect to temperature relationships.

Water temperatures below 19°C, coupled with changes in feeding and activity in *Graptemys pulchra*, occurred regularly in early to mid-April and in late October to early November. During the summer months when water temperatures reached 30°C (86°F), little correlation was observed between water temperature and either basking or underwater activity. Boyer (1965) found this to be true for aquatic turtles generally. However, during times of extremely hot weather, high water temperatures, and low water levels (August and September) in the study area, there was a marked decrease in basking.

Some basking activity was observed during all months, even during warm periods in winter months when the water temperature was as low as 11°C. When both water and air temperatures were low (November to February), long periods of inactivity resulted. Prolonged inactivity was evidenced by an accumulation of silt on torpid individuals found resting on the bottom in deep, silted pools, usually wedged among limestone boulders or sunken trees. Such individuals were reluctant to move when disturbed and when they did move, they were extremely lethargic. Carr (1952) noted similar behavior in *G. barbouri*. The head and appendages were normally somewhat withdrawn into the shell, a pose never observed during months of activity.

A sharp peak in basking activity regularly occurred in March and April and was associated with high water levels caused by spring rains. Basking remained extensive from May through July but normally declined from July to October.

Other species of turtles in the same habitats with *G. pulchra* showed different activity patterns. *Macrolemys temmincki*, observed on several occasions during the winter, was always found deeply imbedded headfirst in the bottom mud, with the tail either exposed or close to the substrate surface. *Pseudemys concinna* showed no reduction in underwater activity during winter months. Swimming speed remained high and response to approach by a diver was rapid, even at minimal water temperatures. It was not determined whether feeding continued through the winter in *P. concinna*, but it is unlikely that the sharp growth rings observed in this species in the study area could have resulted if feeding had been continuous.

DIEL ACTIVITY

Basking was the most conspicuous daily surface activity, and it occurred at all times of day. The basking habits and requirements of *G. pulchra* were essentially the same as for turtles studied by Boyer (1965).

The basking drive in *G. pulchra* is obviously intense. Individuals kept indoors for several weeks with no opportunity to bask were seen mounting basking sites immediately after being released. On one occasion, a large female climbed onto a sandbar, the closest exposed surface, within minutes after being released. As a rule, individuals of this species strongly avoid such exposure, except while nesting. Moll and Legler (1971) found an increased tendency to bask in *P. scripta* when sites were unavailable for long periods of time.

Although the functions of basking are probably manifold, Auth (1975) concluded that thermoregulation is the primary function in *Chrysemys scripta*. Both he and Boyer (1965) state that basking is dependent upon the interaction of several factors, of which ambient water and insolation temperatures are most important.

In *G. pulchra* two functions of basking appear paramount: (1) to provide a mechanism for increasing body temperature, and (2) for maintenance of a healthy integument through inhibition of fungal and algal growth, ectoparasites, and bacterial infections. Captive individuals that are unable to bask, especially if small, are highly susceptible to infestation by an unidentified fungus. Growth of the fungus usually begins between the toes or in the inguinal or axillary pits, eventually affecting the entire skin. When the infestation reaches the latter stage, the turtle is not likely to survive, even with treatment. Small individuals and males are much more susceptible than adult females.

The only ectoparasite observed during the study was the aquatic leech, *Placobdella* sp., which apparently could survive nearly as much exposure as its host. During basking, a leech normally contracts its body into a spherical shape, thereby reducing the surface area and thus its susceptibility to desiccation.

Environmental factors associated with increased basking in the field included high water levels, warm air temperatures, and bright skies. Basking did not occur in *G. pulchra* or in any other species on cloudy days when water temperature exceeded air temperature. This implies that the function of basking is primarily thermoregulatory, and is not principally associated with drying of the integument. The same conclusion was reached by Boyer (1965) and Auth (1975).

Basking behavior supports the hypothesis of thermoregulatory function.

The turtles often spent several hours out of the water, during which they presumably maintained a high body temperature and a correspondingly high metabolic rate. Partially shaded basking sites often seemed to be favored, especially during late summer. Such sites perhaps allowed prolonged high body temperatures without exceeding maximum tolerances. Individuals that have been basking for some time (as evidenced by a completely dry shell) often exhibited a "panting" behavior. Whether such behavior was in response to excessively high temperature is uncertain, but it characterized individuals that had been basking for long periods in mid-day sunlight. Boyer (1965) and Moll and Legler (1971) showed that gaping was associated with temperatures approaching the "critical maximum." Such individuals were unusually sensitive to disturbances. They were approached with great difficulty, often dropping off the basking site over a hundred meters in advance of a swimmer who had only the top half of the head exposed above the water. Probably because of the effects of heating, surface collecting was generally much more productive during morning hours. On the other hand, members of the genus *Graptemys* are well known for their extreme wariness while basking, which seemingly is independent of high body temperature. Newman (1906) noted that startled birds flying from the shore or frogs jumping into the water caused abrupt reentry by *Graptemys*.

Basking in covered and shaded situations was observed frequently during periods of high water, when such sites were the only ones available. Most individuals, especially very large females and hatchlings, seemed to prefer covered basking sites. Presumably hatchlings tend to use such sites because of the protection they offer. Large females may have been selectively favored by offering less conspicuous targets for "plinkers." Carr (1952) suggested that the extreme wariness of *Pseudemys rubriventris* might be due to its long-time persecution by man, "who has been weeding out the unwary individuals for a century or more." An additional, and perhaps overriding, advantage to such sites may be that they provide for a less radical body temperature increase that does not exceed requirements for digestion and metabolism.

Adults were particularly conservative in their selection of basking sites. Freshly fallen trees seemingly offered ideal sites but were generally not used by adults during the same year, unless other basking sites were extremely scarce. Even when other sites were scarce, however, turtles would generally prefer to travel several hundred meters to apparently more familiar sites. Moll and Legler (1971) found that *P. scripta* would not bask on artificially anchored sites, even though the sites were constructed of logs that were identical to those at their familiar sites.

In the Conecuh River, basking sites were usually parts of trees that had been undercut and had fallen into the stream. The sites most frequently used had several qualities in common. Most importantly, a site did not have an exposed continuity with the shore, a feature also noted by Boyer (1965) and by

Moll and Legler (1971). Trunks and branches of overhanging willows, which were favorite basking sites during high water, were strictly avoided when the water level dropped sufficiently to cause the exposed trunk to be continuous with the shore. As little as 30 cm of open water sufficed to make such a site acceptable. As noted by Cagle (1952), sites associated with deep holes and swift currents were preferred, as were trees that had lost most of the smaller branches. Other qualities being equal, sites providing the greatest field of vision seemed to be preferred. Given time, basking individuals habitually moved to the highest possible point on the site. Boyer (1965), who observed the same behavior in Louisiana *Graptemys*, considered its purpose to be the gaining of an improved vantage point.

While basking, the fore feet are normally used to maintain position, while the hind feet are often extended with the toes spread, allowing exposure of maximum surface area. If a point of balance is achieved on the basking site, the fore legs are also extended. The head and neck are invariably extended, perhaps as much for surveillance as exposure. Identical behavior has been observed in *P. scripta* (Moll and Legler 1971) and in emydines generally (Boyer 1965).

Basking adults were occasionally observed to wave the forelegs repeatedly against the sides of the head, as if brushing away some source of irritation. This behavior may have been caused by gnats or mosquitos, which were attracted to the eyes.

Various species of turtles dropping from basking sites commonly alerted basking individuals of *G. pulchra*. *Trionyx* spp. were especially sensitive to disturbances, and its hasty reentry often alerted other turtles. *Pseudemys concinna* also served a "sentry" function among basking groups. The resounding splash of a large female *G. pulchra* or *P. concinna* dropping several meters from an overhanging tree, under conditions of concentrated basking, often initiated a chain of plunges extending for several hundred meters along the river. As a result, it often happened that fewer individuals were collected when basking was extensive than otherwise. It was noted that splashes caused by fishes, kingfishers, or even occasionally swim fins did not normally alert basking turtles.

Very little information on nocturnal activity in *G. pulchra* was obtained. A few individuals were found at night lingering close to the surface among exposed branches and roots, as was also reported by Chaney and Smith (1950) in the Pearl River. No individuals were found feeding or located in hiding places favored during the day. Thus, the nature and extent of nocturnal activity in the field remains essentially unknown.

Specimens kept in outdoor pools were consistently observed at night actively searching the bottom. Feeding was observed only at night among adults, but at all times among small individuals. In the field adults were usually found hiding during the day, but small individuals were found both in

hidden and in exposed areas, presumably feeding. One may surmise from this that adults feed principally at night and bask or remain hidden during the day, whereas immature individuals follow a much more flexible routine.

PREDATORS AND PARASITES

PREDATION

Nest predation is by far the most significant inhibiting factor on population growth in *Graptemys pulchra*. As indicated in the discussion of reproduction, at least 95 percent of all nests found at the study area were destroyed by predators. Similar rates of predation in other species have also been cited by Allen (1938), Cagle (1950), and Moll and Legler (1971).

Cagle (1950) found the most important predator of *Pseudemys scripta* nests in the populations he studied to be skunks, raccoons, and snakes. The major diurnal predator of *G. pulchra* nests was the fish crow, which evidently patrols the beaches regularly looking for nesting females. Tracks on nesting beaches indicated that crows may follow a nesting female to the nesting site. Whether crows waited for the completion of the nest before eating the eggs is unknown, but nests destroyed by crows characteristically showed signs of excavation. Eggs were normally carried away from the nest before being eaten, as evidenced by the absence of shells at the nest site and the scattered occurrence of shell fragments (Fig. 30).

The major nocturnal predator on nests was the raccoon. Some nests may have been destroyed while under construction, but raccoons easily found nests several days after laying, unless signs of the nest had been removed by rain. Moll and Legler (1971) found that most nests were destroyed within 12 hours after laying and were located by the odor of turtle urine. Raccoons excavated the nests, as did crows, but unlike crows, they ate the eggs at the site, since the shells of most or all the eggs were found near the nest (Fig. 31).

In small streams (Opintlocco Creek, Cubahatachee Creek) of the Mobile Bay drainage in Macon County, Alabama, predation seemed to be less intense. Approximately 50-75 percent egg mortality was apparent in these populations. The much smaller populations of *G. pulchra* resulted in a relative scarcity of nests in these areas. Since considerable energy would be required to locate nests, predators may have directed efforts toward more lucrative sources of food.

Early in the study I had anticipated that the opossum would be an important predator, but such was not the case. Even though opossums were common in the area, no tracks were seen on the nesting beaches. Another possible predator of nests was skunks. Presumably skunks would leave signs similar to those of raccoons, and some instances of predation may actually have been due to skunks. Other potential predators of infrequent occurrence on the

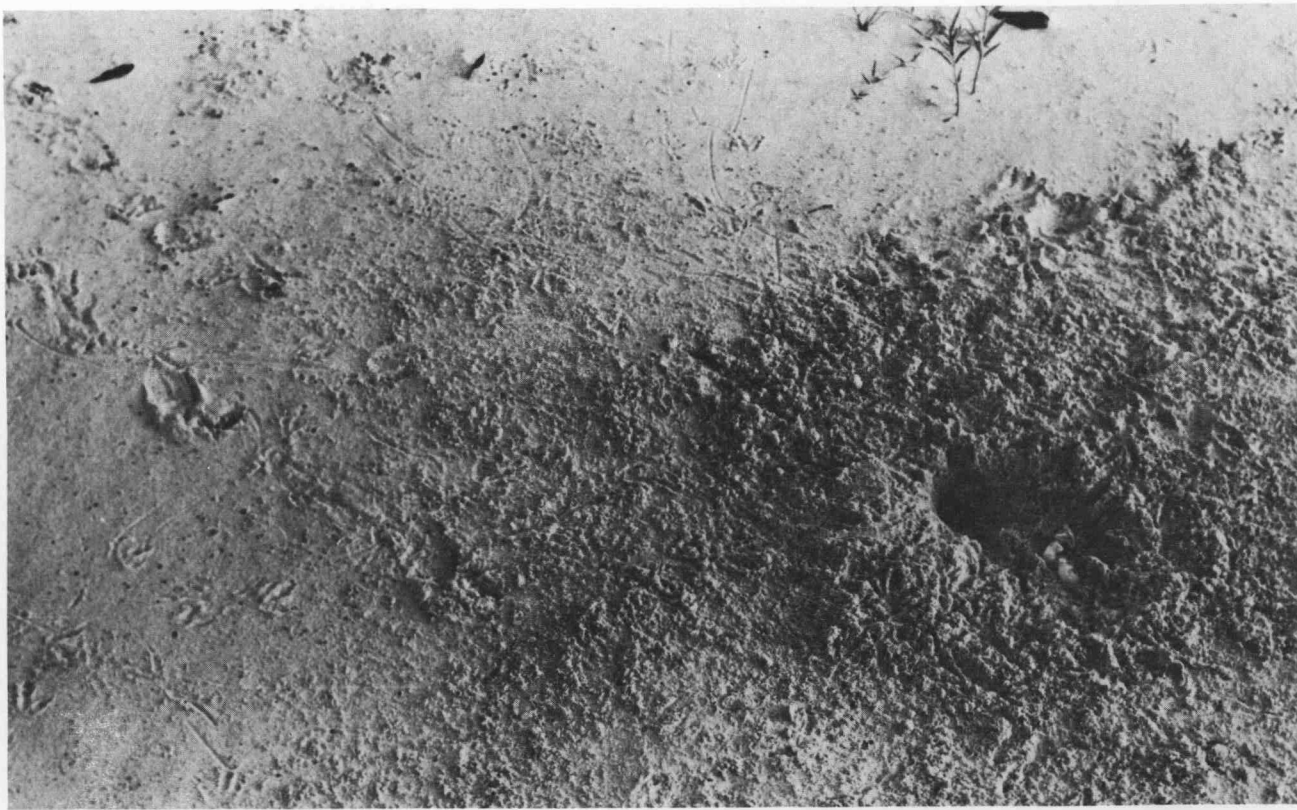


Figure 30. Nest of *Graptemys pulchra* destroyed by the fish crow, Conecuh River, Escambia County, Alabama. Note crow tracks at lower left, turtle tracks at upper left, and egg shell at nest entrance.

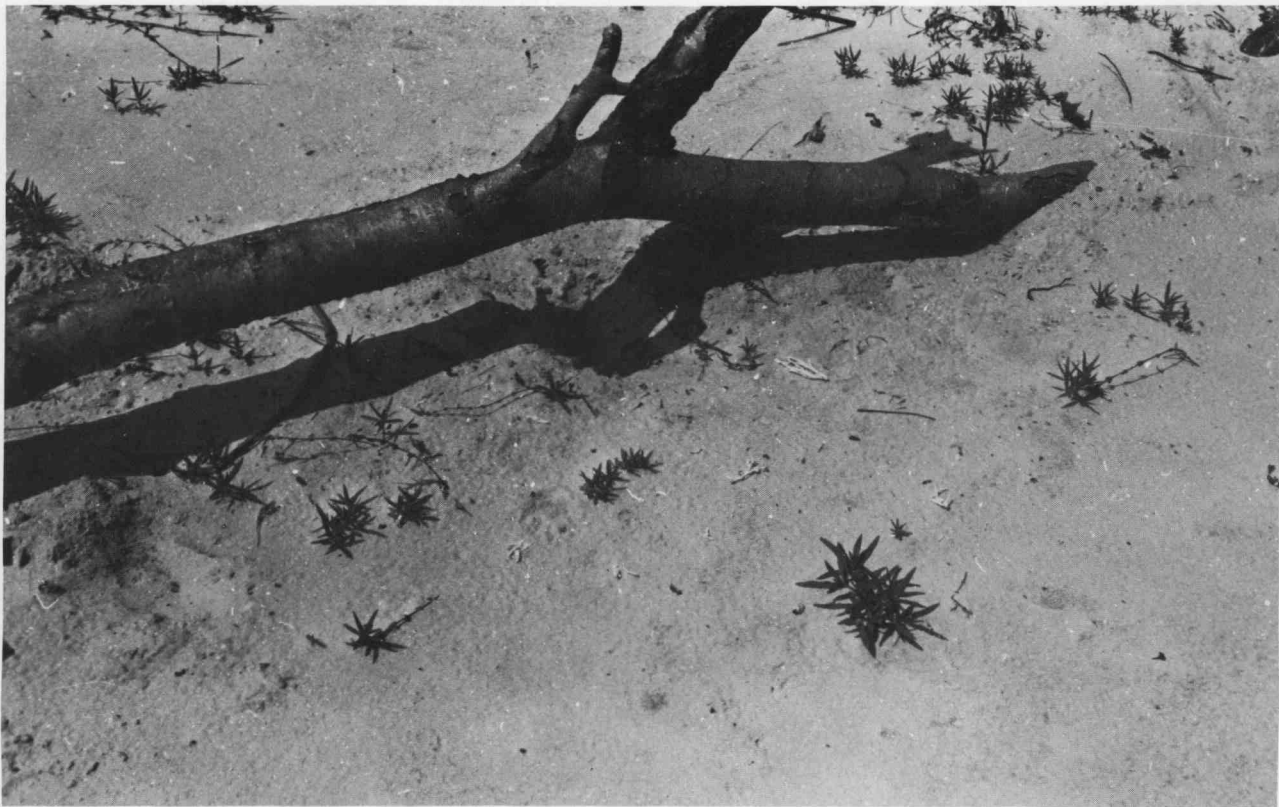


Figure 31. Nest of *Graptemys pulchra* destroyed by the raccoon, Conecuh River, Escambia County, Alabama. Note crushed egg shells scattered around the nesting site and the wide excavation of the nest.

nesting beaches were bobcats and otters, but no instance of nest predation was attributable to them.

Nests located in otherwise "suboptimal" sites among vegetation or on shaded banks seemed not to be destroyed as frequently as those in exposed situations. An increased effort by the nesting female to conceal the nest may have resulted from heavy predation of both nests and nesting females in the study area.

No instance of hatchling predation was seen. It is likely that large predators, such as gars, herons, and alligator snapping turtles, feed at least occasionally on hatchlings, but the extent of such predation remains unknown. Many larger individuals were found with posterior portions of a rear leg, tail, or carapace missing. Such wounds may have been made by alligator snapping turtles, but fecal samples of several snappers failed to show turtle remains. James L. Dobie (pers. comm.) found that the stomach samples of alligator snappers often contained the remains of other turtles.

One instance of predation on adults was seen. A nesting female was found, freshly killed, with the rear legs mangled and small holes torn in the inguinal pit (Fig. 26). The injuries corresponded closely with those in an incident described by Cagle (1950), in which crows had turned a female turtle over and pecked holes in the inguinal pits. In the present instance there was no nest cavity, but fresh egg shells were scattered around the site. Since the torn holes were probably not large enough to allow extraction of the eggs, the female probably extruded the eggs under stress. The only tracks in the area were those of a raccoon.

The only significant predator of adults is man. Conversations with local fishermen revealed that turtles were thought of as vermin, or at least as competitors for the fish. Some residents, while drifting downstream or wandering along the banks, used turtles for rifle targets. Several adult females had wounds which may have been made by bullets. In one example, a projectile had penetrated the upper neck region and the supraoccipital bone of the skull. Carapace wounds were often recognized as having resulted from shooting.

Basking turtles were not normally alarmed by boats moving upstream under power, however noisily, and were often literally washed off the basking sites by the wake. On the other hand, boats drifting downstream generally alarmed nearby basking turtles. Thus, a boat drifting downstream could rarely come within 30 m of basking turtles, while a boat driven rapidly upstream could often approach to within a few meters. Possibly there was, on the part of the turtles, an association of drifting boats with "plinkers." From such observations it seems that the state of wariness in individuals of *G. pulchra* is not based so much on fear of threatening objects as on familiarity with harmless objects or situations. Similarly, during periods of high water levels and re-

sultant extensive drifting debris, basking turtles were much less easily alarmed by drifting swimmers or debris than during periods of low water and slight debris.

PARASITES

Although a complete survey of parasites was not made, no instances of deleterious degrees of parasitism were found during the study. A single ectoparasite, *Placobdella* sp. (a leech), was seasonally abundant in the study area. It was commonly found on turtles during the spring, at which time the leeches were often carrying many young.

The most common intestinal parasite was an acanthocephalan belonging to the genus *Neoechinorhynchus*. It was never found in great numbers and probably infected less than 25 percent of the adult population. A fluke, *Telorchis* sp., was also found in the small intestine of one adult female. Ernst and Barbour (1972) listed a sporozoan, *Myxidium chelonarum*, in the bile duct and gall bladder of *G. pulchra*.

INTERSPECIFIC INTERACTIONS

Graptemys pulchra was the most abundant turtle found in the study area. Other species, in order of decreasing apparent abundance, include *Trionyx spinifer*, *Pseudemys concinna*, *T. muticus*, *Sternotherus minor*, *Macrolemys temmincki*, and *P. scripta*. Very little effective competition among these species was evident; probably the only situations in which this might possibly occur involve young *Pseudemys* sp. and young and male *G. pulchra*, all of which are insectivorous. Since food presumably was not a limiting factor, probably little or no significant competition occurred. Competition for basking sites may have been significant in some areas, but it was probably not important at the population level.

Predator-prey interactions may be important between *M. temmincki* and the young, and some adults, of other species. Specimens of *Trionyx* and *Pseudemys*, as well as of *G. pulchra*, were often found with a portion of a leg, tail, or carapace missing. Such wounds were often smooth-edged and wedge-shaped and could have been made by the shearing beak of *M. temmincki*. James L. Dobie (pers. comm.) found other turtles to be an important food item for Louisiana *M. Temmincki*; however, as previously indicated, the feces of several isolated alligator snapper specimens captured at the study area contained no turtle remains.

The most significant interaction observed was associated with basking. Even though a slight tendency toward species uniformity in basking groups was observed, interspecific "cooperation" was evidenced when alarmed individuals fell off basking sites, which in turn would cause similar reactions among other members of the aggregation, regardless of species. The turtles

most sensitive to noise and disturbance were *Trionyx* sp., and these acted as "sentinels" for the other less sensitive forms. Congregations of basking turtles, regardless of species composition, were much more difficult to approach than isolated individuals.

LIMITING FACTORS

Species of the genus *Graptemys* occur in the extreme northern United States. This, together with the fact that *G. pulchra* is found in the upper (*i.e.* northern) portions of river drainages within its range, makes it unlikely that latitude or altitude per se are important limitations to its distribution. Likewise, suitable annual temperature regimes occur well outside the present range of the species. Consequently, it seems likely that its limitation to particular drainages results primarily from drainage isolation and absence of overland migratory behavior. Ecological barriers are effective, however, as evidenced by the absence of the species from certain major streams within its range (*e.g.* Blackwater and Perdido rivers).

The physical and chemical characteristics of the medium- and large-sized streams favored by *G. pulchra* presumably are major factors affecting the species' distributions. Although the degree of adaptability to pond or lake situations has not been determined, the species seems to survive at least marginally in such situations. There are no reports of its occurrence in artificial impoundments of small streams or in natural (except oxbow) lakes, although apparent stable populations have been observed in impoundments of large streams, such as Gantt Reservoir (Conecuh River) in southern Alabama and Weiss Reservoir (Coosa River) in northeastern Alabama.

The requirement of fine sand at nesting sites, if exhibited by populations throughout the range, may be a limiting factor both within and outside the species' range. Females within the study area were observed consistently selecting nesting sites based on the degree of sand coarseness (see pp. 77-78). Nest predation, which exceeded 95 percent during the study period, conceivably might reach 100 percent in some areas. Differential predation pressure and vulnerability of the nests can alter the mortality rates.

Atmospheric basking probably is necessary for health, if not survival, in *G. pulchra* (also see Auth 1975). Thus, the availability of basking sites may be limiting in some situations, such as lakes, where these sites may be limited.

Within the study area, apparently two types of stresses on the general population occur annually. These are the periods of winter inactivity (hibernation?) and spring flooding. Shells of several dead individuals were found after periods of flooding, although the precise time and cause of death were uncertain. Moll and Legler (1971) found that tropical *Pseudemys scripta* examined during such periods showed reduced vigor and resistance to disease, although the many specimens of *G. pulchra* collected during periods of high

water showed no reduction in fecal volume. Adult females with infected plastra were occasionally found during periods of high water levels. *Graptemys pulchra* may thus be somewhat more limited in abundance in areas subject to very frequent or extensive flooding, although this is thought to be less important than certain other factors, particularly food availability.

It is unlikely that males of the species are limited by food availability, since they are insectivorous. Females, on the other hand, are highly adapted to feeding on molluscs, and thus may be restricted to areas where these animals are found. It seems likely that the potential ecological range of the species is restricted by mollusc distribution, since within the range of *G. pulchra* the effects of mollusc distribution are apparent. The greatest density of turtles observed, which was in the study area, was associated with an extreme abundance of molluscs, including several species of pelecypods and at least one species of gastropod. Fecal samples of females from other areas (Mobile Bay and Yellow River drainages) contained nowhere near the abundance of mollusc remains as those of Conecuh River females. Few *G. pulchra* were found in those streams supporting scant mollusc populations, and none at all were found in streams in which molluscs were entirely absent. Conversely, no stream within the range contains large mollusc populations and no *G. pulchra*. Molluscs were consistently absent from brown-stained, probably acidic, coastal plain streams, such as the Perdido and Blackwater rivers, and the absence of *G. pulchra* from these systems likely is best explained on this basis. It is tempting to speculate that a study of these and other streams from which *G. pulchra* is absent would show that chemical factors preventing calcium availability exclude both molluscs and *G. pulchra*.

Since no other "broad-headed" *Graptemys* occur with *G. pulchra*, competitive exclusion from *G. barbouri* to the east, *G. geographica* to the north, and *G. kohni* to the west may be limiting.

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