ASPECTS OF THE LIFE HISTORY OF THE SOUTHERN BLACK-KNOBBED SAWBACK,

Graptemys nigrinoda delticola Folkerts and Mount

Peter Nicholas Lahanas

Certificate of Approval:

George W. Folkerts
George W. Folkerts
Alumni Professor
Zoology-Entomology

James L. Dobie
James L. Dobie, Chairman
Professor
Zoology-Entomology

John D. Freeman
John D. Freeman, Associate
Professor. Botany, Plant
Pathology and Microbiology

Robert H. Mount
Robert H. Mount
Professor
Zoology-Entomology

Paul M. Estes
Paul M. Estes
Assistant Professor
Zoology-Entomology

Paul F. Parks
Paul F. Parks, Dean
Graduate School

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VITA

Peter Nicholas Lahanas, son of Nicholas S. Lahanas and Elanore (Hienzen) Lahanas (both deceased) was born November 16, 1951, in Fresno, California. He attended T. L. Heaton Elementry (Fresno), Mark Twain Junior High School, and Silverton Union High School (both Silverton, Oregon). In September, 1974, he entered Oregon State University, Corvallis, Oregon, from which he received the degree of Bachelor of Science in Zoology in March, 1978. He entered graduate school, Auburn University, in September, 1978. While attending Auburn University, he held teaching assistantships in both the general biology and physiology programs.

THESIS ABSTRACT

ASPECTS OF THE LIFE HISTORY OF THE
SOUTHERN BLACK-KNOBBED SAWBACK,
Graptemys nigrinoda delticola
Folkerts and Mount

Peter Nicholas Lahanas

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Field studies concerning the life history of *Graptemys nigrinoda delticola* were conducted on and near Gravine Island, Tensaw River, Baldwin Co., Alabama.

Courtship consists of a series of rapid head nods performed when conspecifics face each other snout to snout. The spermatogenic cycle begins in early spring, peaks in September, and is essentially completed by November. Follicles proliferate in September and enlarge during the winter and early spring.

Nesting is nocturnal and extends from mid-May to early August. Optimal nest sites are in open expanses of fine sand, well elevated above the water level and within 50 m of shore. Nests and nesting behavior are described. An average of 5.5 eggs per clutch are deposited, and three to possibly four clutches are laid annually. Natural incubation periods average 62 days.

Hatching begins is mid-August, but emergence from the nest is delayed 3-13 days as hatchlings retract yolk sacs and burrow out. Emergence is nocturnal, individual, and is probably temperature stimulated.

Females grow significantly faster than males and become reproductively mature at a plastron length of about 170 mm (8-9 years); males mature at about 70 mm (4-5 years). Growth is seasonal; initiating in late April, it is 95% complete by September. Sexual dimorphism is pronounced. Most of the features showing allometry are associated either with sexual dimorphism or lengthening of the shell.

Adults and subadults occur primarily in the deep and swift-flowing main river channels, whereas hatchlings and small juveniles occupy the relatively shallow and quiet backwaters of sloughs and bayous. Graptemys n. delticola is the most abundant emydine in the large channels of the delta and made up 41.3% of all turtles collected in traps. Adult and hatchling sex ratios are both essentially 1:1.

Primary food items include sponges, bryozoa, mollusks, and algae. No sexual or age-specfic differences in diet were detected.

ACKNOWLEDGEMENTS

I would first of all like to thank Mr. Boyd Adams of Alco Land and Timber Co., Mobile, who generously allowed me complete and unhindered use of Gravine Island. Without his support, this project could not have been undertaken.

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Jim Godwin, Ken Fahey, and other students offered helpful and enjoyable company in the field.

Members of my graduate committee have been particularly helpful. Dr. George W. Folkerts provided many suggestions and criticisms during all phases of this study. Drs. John D. Freeman and Paul M. Estes offered assistance in the preparation of this thesis over and above what is normally expected. I would also like to offer my sincerest appreciation to Dr. Robert H. Mount for the loan of Auburn University Museum specimens and for his consistent and

enthusiastic encouragement, especially meaningful during some difficult periods, and to Dr. Kirby Hays for his personal and financial support during the latter part of my residency at Auburn.

Finally, I would like to thank my major professor, James L. Dobie, who, by virtue of his uncompromising standards, provided the impetus required to carry this project through to completion.

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I. INTRODUCTION AND REVIEW OF LITERATURE

The black-knobbed sawback, *Graptemys nigrinoda* Cagle, is a member of the testudinate family, Emydidae. It is a medium-sized freshwater species, well adapted to the fluviatile habitat in which it occurs. Distinguishing features in young turtles include strongly serrated carapacial margin and prominent, rounded black vertebral knobs from whence it receives its name. Large adult females may lose these structures. Before the completion of the present study, little data concerning most life history aspects were available (Ernst and Barbour 1972, Mount 1975). This paucity of knowledge, as well as the fact that the black-knobbed sawback is relatively abundant within the rivers of its restricted range, made this species a good choice for study.

From August 1979 through October 1980, field studies were conducted on *G. n. delticola* on and around Gravine Island which is located on the Tensaw River in Baldwin County, Alabama. These field studies were augmented by the examination of preserved material collected from Baldwin County and housed in the herpetological collections of the Auburn University Museum.

Literature pertaining to the black-knobbed sawback is scanty and generally anecdotal in nature. Most of the present information deals primarily with systematics and phylogeny (Cagle 1954a, Tinkle 1958, Folkerts and Mount 1969, McKown 1972, Wood 1977), morphology (Tinkle 1962, Zangerl 1969, Killebrew 1977, 1979, McDowell 1964), or distribution (Shoop 1967, Cliburn 1970, McCoy and Vogt 1980). General accounts providing some information on habitat affinities, reproduction, and food habits are found in Ernst and Barbour (1972), Mount (1975), Conant (1976), and Pritchard (1979). Shoop (1967) provided some information on size at sexual maturity in northern intergrade populations. The observations of Wahlquist (1970), who witnessed feeding behavior in this species on the Coosa River, indicated an insectivorous diet. Waters (1974) examined basking habits in *G. nigrinoda* on the Cahaba River, Perry County, Alabama. Among other findings, Waters reported that thermoregulation is the primary function of basking in this species, but that the elimination of ectoparasites and algae as well as the synthesis of vitamin D are also important. Except for that by Waters (1974) no detailed study on any aspect of life history of the black-knobbed sawback turtle has been made.

The present study was undertaken to help fill some gaps in our knowledge of life history in G. nigrinoda, especially in the areas of reproduction, growth, and food habits.

Systematics

Despite its abundance (Cagle 1954a, Mount 1975, McCoy and Vogt 1980) the black-knobbed sawback was not described until 1954 (Cagle 1954a). This is surprising in view of the fact that this species appeared in the literature nearly a century earlier. Agassiz, in his Contributions to the Natural History of the United States (1857-1873), illustrated this species as a hatchling in plate II, Figs. 10, 11, 12, 12a; displaying ventral, dorsal, lateral, and head views, respectively. As noted by Ewert (1979), these lithographs, drawn by H. J. Clark and A. Sonrel, are "of such high quality as to give the work significant reference value today". The black-knobbed sawback not only can be easily identified in these drawings but is readily referable to the southern subspecies, G. n. delticola (Folkerts and Mount 1969), based on extensive plastral patterns (>60%) and a predominence of dark pigments on the soft parts.

Agassiz mistakenly grouped specimens of G. nigrinoda and G. kohni (Baur) under the name, Graptemys lesueurii, and although he did not distinguish between the former as species, Agassiz admitted that *G. lesueurii* "varys more in form" than other *Graptemys*. *Graptemys lesueurii* Agassiz underwent several taxonomic changes but eventually became *G. pseudogeographica* (Gray 1863) within which *G. kohni* was given subspecific status (Stejneger and Barbour 1917). Just what became of the specimen of *G. nigrinoda* illustrated on plate II of the Contributions is not known.

Concurrently with *G. nigrinoda*, Cagle (1954a) described a closely related species, *G. flavimaculata*, from the Pascagoula River system of Mississippi. Based on similar morphological features, Cagle proposed that these two species, along with *G. oculifera* from the Pearl River system of Mississippi and Louisiana, constituted a closely related allopatric complex which he called the "narrow-headed" *Graptemys* group. That these three species are closely related was subsequently supported by Tinkle (1958), Folkerts and Mount (1969), McKown (1972), Ernst and Barbour (1972), and Killebrew (1979),

Phylogenetically, *G. nigrinoda* appears to be the oldest and most divergent member of the narrow-headed group, (Cagle 1954a, Folkerts and Mount 1969).

Two subspecies are currently recognized within *G. nigrinoda*. The nominate subspecies may be distinguished from the southern race by the presence of a plastral pattern covering less than 30% of the plastron and by soft parts that contain more yellow than black. The southern black-knobbed sawback, *G. n. delticola*, possesses an extensive plastral pattern covering more than 60% of the plastron, and soft parts are primarily black (Folkerts and Mount 1969).

The black-knobbed sawback is retricted to the Alabama-Tombigbee River systems of Alabama and Mississippi (Shoop 1967, Folkerts and Mount 1969, Cliburn 1970, Mount 1975). The northern race occurs in the Tallapoosa, Coosa, Cahaba, and Alabama Rivers from the Fall Line south to near the Wilcox-Monroe County line. The southern subspecies is restricted to the Tensaw and Mobile river systems which form the delta of the Mobile Bay drainage. Populations in all other localities, including Monroe and Wilcox counties on the Alabama River, and the entire Tombigbee-Black Warrior system, are considered intergradient (Mount 1975).

Study Area

Gravine Island. All field studies were carried out in the vicinity of Gravine Island (R1N,T2S; 30° 47'W, 87° 80'N) including the Tensaw, Mobile, and Raft rivers, and their associated channels, sloughs, bayous, and "lakes" (Fig. 1). Gravine Island is approximately 3.2 km long and 1.2 km wide. Topographically, the island is of low relief, generally no more than 1-3 m above the mean summer water level. In 1947

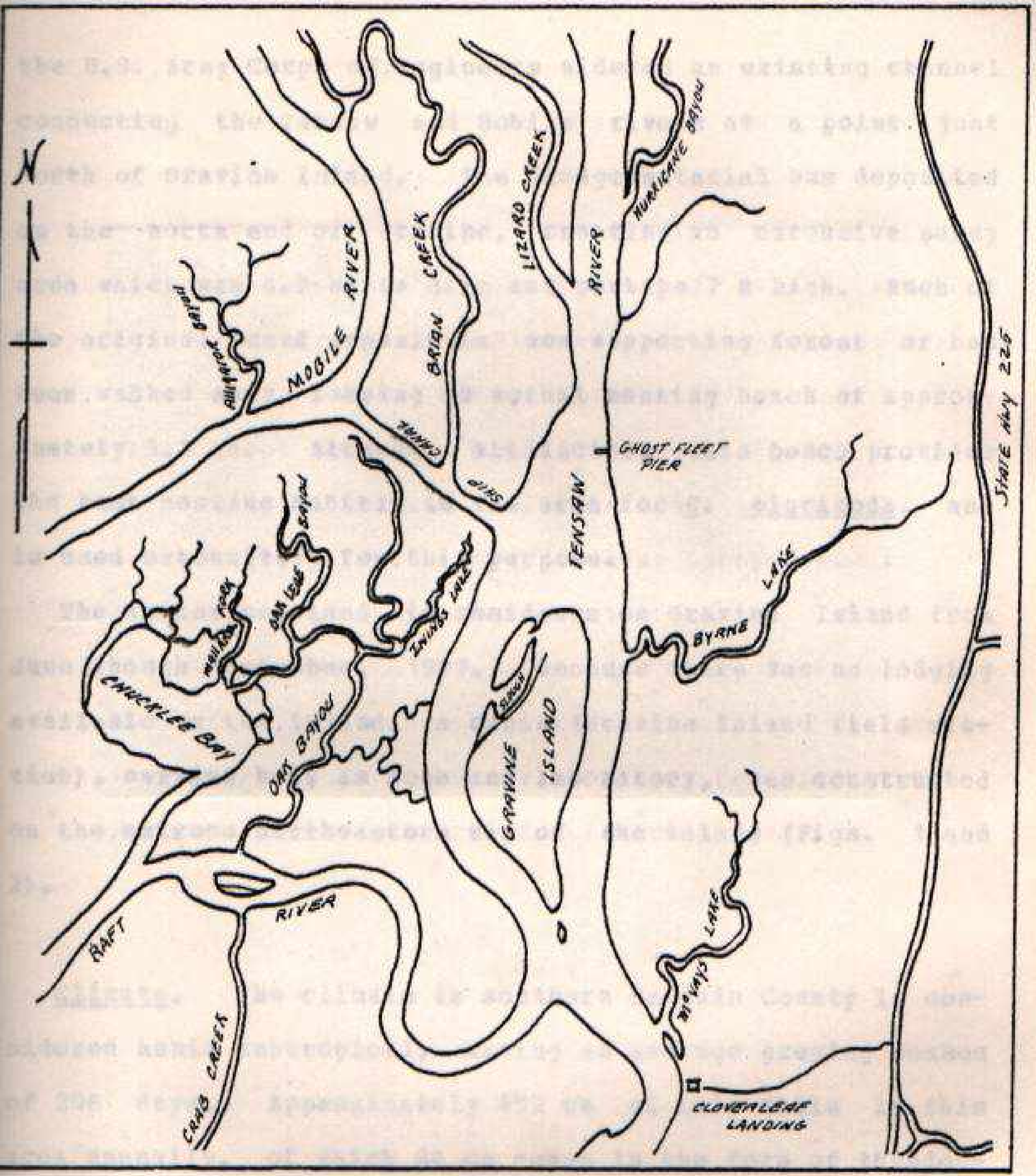


Figure 1. Map of study area centered at Gravine Island, Tensaw River, Baldwin Co., Alabama. Scale: 1 cm equals approximately 0.64 km.

the U.S. Army Corps of Engineers widened an existing channel connecting the Tensaw and Mobile rivers at a point just north of Gravine Island. The dredge material was deposited on the north end of Gravine, creating an extensive sandy area which was 6.2 ha in size and perhaps 7 m high. Much of the original sand deposit is now supporting forest or has been washed away, leaving an actual nesting beach of approximately 3.3 ha. Although artificial, this beach provides the best nesting habitat in the area for *G. nigrinoda*, and is used extensively for this purpose.

The author remained in residence on Gravine Island from June though September, 1980. Because there was no lodging available on the island, a cabin (Gravine Island field station), serving both as home and laboratory, was constructed on the extreme northeastern tip of the island (Figs. 1 and 2).

Climate. The climate in southern Baldwin County is considered humid subtropical, having an average growing season of 298 days. Approximately 152 cm of rain falls in this area annually, of which 84 cm comes in the form of thundershowers during the summer. The mean winter and summer temperatures are 31°C (July) and 13°C (January) (U.S. Dept. Agric. 1941).

Figure 2. Field station on Gravine Island. This structure, located at the extreme northeast tip of the island, served as the authors home and laboratory from June through September 1980.

Flora. The shoreline vegetation along the lower Tensaw River is typical Lower Coastal Plain swamp forest, dominated by bald cypress (*Taxodium distichum*), tupelo gum (*Nyssa sylvatica*), river birch (*Betula nigra*), sweet bay (*Magnolia virginiana*), and red maple (*Acer rubrum*), with longleaf pine (*Pinus palustris*) on higher ground. Other trees in this area include tuliptree (*Liriodendron tulipifera*), willow (*Salix* sp.), and sycamore (*Platanus occidentalis*).

Little understory woody vegetation occurs in most areas. It consists primarily of Virginia willow (*Itea virginica*), star-anise (*Illicium floridanum*), galberry (*Ilex glabra*), wax myrtle (*Myrica cerifera*), and black titi (*Cyrilla racemiflora*). Palmetto (*Sabal minor*) forms thick stands in many low-lying areas. The ground cover includes mostly grasses with *Panicum* and *Eragrostis* being the more important genera occurring in the nesting area on Gravine Island.

Aquatic vegetation is abundant in the lower Tensaw River. Common species are yellow pond lily (*Nuphar luteum*), arrowhead (*Sagittaria* sp.), and pickerel-weed (*Pontederia cordata*). Alligator weed (*Alternanthera philoxeroides*), watershield (*Brasenia schreberi*), and water hyacinth (*Eichornia crassipes*) can be found in some sloughs and bayous. (See Lelong (1977) for a more complete list of the vascular flora in this region).

Robert Mount (pers. comm.) informed me that in years past Elodea sp. was abundant in the lower Tensaw, forming dense mats near Cloverleaf Landing (ca. 3 km south of Gravine Island) and elsewhere. This plant is no longer present in appreciable quantities and has all but disappeared from the lower delta region.

During late summer and early fall, 1979, and again during the spring and early summer of 1980, the yellow water lily was a common emergent in the study area, creating extensive beds. One such Nuphar bed, beginning at the Ghost Fleet Pier, (Fig. 1) extended south for approximately 1.5 km. By July, 1980, these lily beds were beginning to thin out and by September of the same year were all but gone. Local fisherman informed me that "the Corps" (U.S. Army Corps of Engineers) had been spraying herbicides upstream to remove aquatic vegetation which might impede barge traffic along the river. Jack Mallory of the U.S. Army Corps of Engineers, Mobile, (pers. comm.) indicated that the herbicide used was 2,4,5-T as the dimethylamine salt, but that little spraying was done in 1980. Mr. Mallory assured the author that spraying was necessary, but, when one considers that these target plants can only grow in water already too shallow for barges to cross, this practice becomes even less understandable. Just what effect the spraying of herbicides will have on the turtles in this area is not known. A detailed study of the effects of this herbicide is urgently needed, especially since there are at least two primarily herbivorous species in this area (*Pseudemys concinna* and *P. alabamensis*).

Tensaw River. The Tensaw is a large, deep, meandering river with a rather strong current. Major river channels average about 0.6 km across at the level of Gravine Island. Water turbidity varies considerably from season to season, but never achieves more than moderate clarity. Water temperatures vary from less than 10°C in winter to 34°C in late summer.

The lower Tensaw, which includes the Gravine Island area, is substantially affected by the tide from Mobile Bay, resulting in a twice-daily fluctuation in water level of about 0.3 m. Water salinity in the vicinity of Gravine Island varies according to tide, season, and amount of recent precipitation.

The river attains its maximum discharge (and therefore, lowest salinity) during the winter and early spring floods. At this time the water level may be 5.0 m above the mean summer level. In most years, much of Gravine Island becomes inundated.

Several marine organisms occur in the study area as a result of tidal influence. Among these are various gastropods and bivalves, barnacles, blue crabs, and several species of fish, of which mullet, flounder, and shark are most conspicuous.

Log jams and emergent branches are abundant along the river bank. These provide necessary basking platforms for the black-knobbed sawback and other turtle species in the area.

II. MATERIALS AND METHODS

Collecting, Preserving, and Data Collection

Adult and juvenile turtles were collected from August through November, 1979, and from April through September, 1980. Trapping attempts in December, 1979, and February, 1980, were unsuccessful.

Turtles were taken in hoop nets which measured approximately 2 m in length and 1 m in diameter. These nets were constructed with 7.6 cm mesh nylon netting supported by steel rings, and provided with two inverted funnels arranged in sequence. A lead net, also of 7.6 cm mesh nylon netting measuring 30 m long and 2 m wide was attached to the mouth of the trap. The upper edge of the lead net was supported with floats and the lower edge contained lead weights. This arrangement kept the lead net oriented vertically in the water when set.

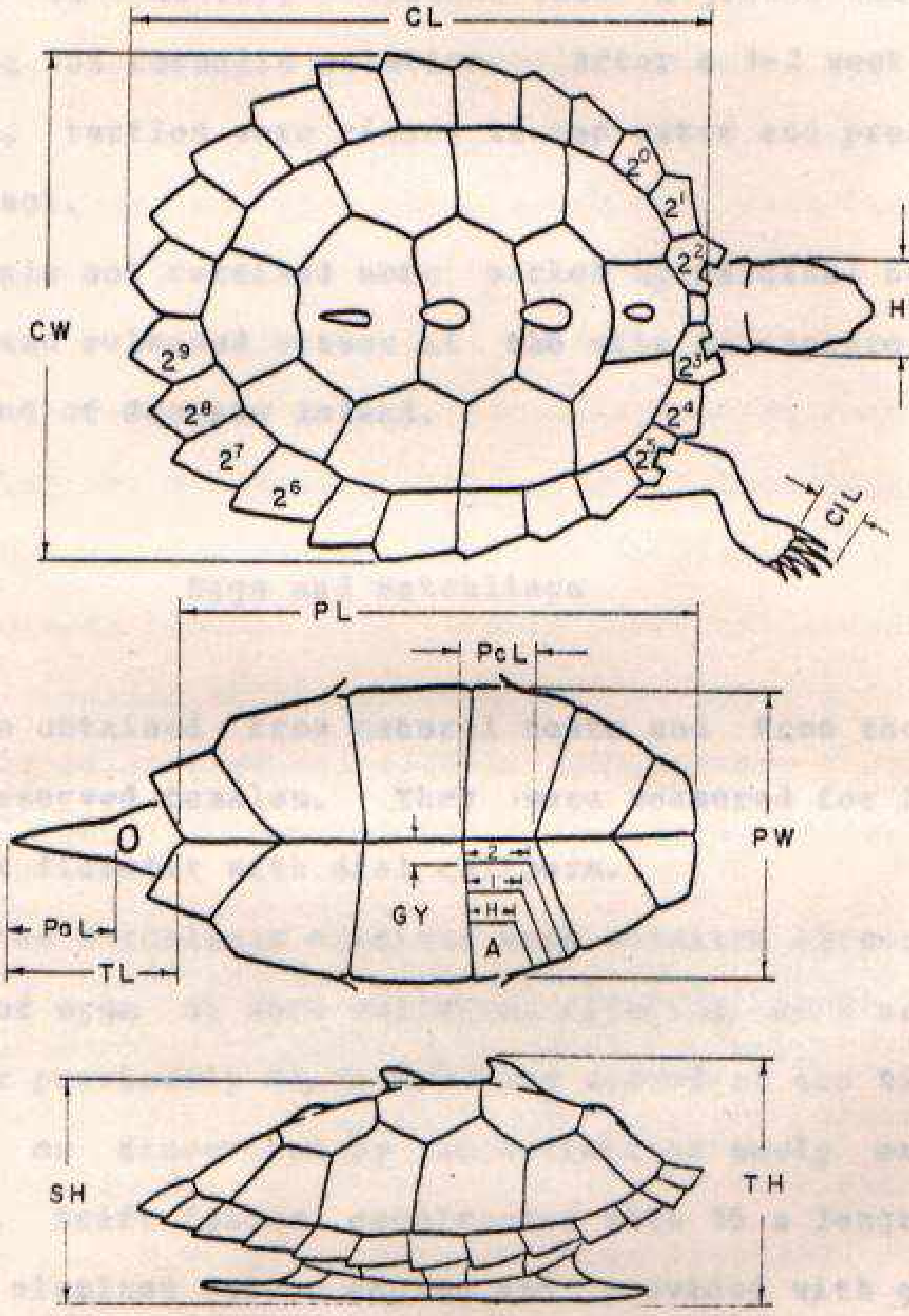
Nets were set from a boat in "likely" situations and were generally attached to emergent logs adjacent to swift, deep water. The hoop nets were oriented so that the mouth faced into the current and were supported by the lead net which was stretched taught in the same direction and secured to another log or to some object on shore. Turtles approaching the logs to bask would encounter the lead net and with the help of the current, would subsequently enter the net. No bait was used to lure turtles to the trap because this practice has been determined useless in collecting other species of *Graptemys* turtles (Chaney and Smith 1950).

Routine data collected from each trapping attempt included the date, locality (plotted on a map), weather, such as sky condition (clear, overcast), and the presence of precipition. Ambient temperature (1 m above ground in shade) and water temperature (5 cm below surface at trap locations and midstream) were recorded with a Yellow Springs Telethermometer (model #44TZ) using disk thermister probes. In addition, notes were made on the local microenvironmental conditions at each trap site including water level, swiftness and turbidity, the presence of emergent logs, vegetation, etc.

A minimum of eleven morphological measurements were made on each specimen collected (Fig. 3). Scute arrangements (illustrated if abnormal), physical condition, sex, and the presence or absence of epizoic organisms were also examined and noted. Absolute or approximate age was determined by counting growth annuli on plastral scutes.

Individuals retained for gonadal, food habits, and parasite studies were killed within 12 hours of capture with a

Figure 3. Standard measurements taken on all *G. nigrinoda* examined. Top: dorsal view. CL, carapace length; CW, carapace width, HW; head width; ClL, claw length. Marking system for released individuals operates on the exponential of the numeral 2, where $2^0 = 1$, $2^1 = 2$, $2^2 = 4$, and so on. The illustrated individual is marked $2^2 + 2^3 + 2^5 = 44$. Center: ventral view. PL, plastron length; PW, plastron width; Pal, post-anal length; TL, tail length; Measurements and abbreviations used in growth analysis are: PcL, pectoral scute length; A, areola; H, pectoral scute length at hatching; numerals, length of pectoral scute at end of 1st and 2nd year of growth; GY, growth of the year. Bottom: lateral view. SH, shell height, TH, total height.


CL
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coelomic injection of 1-5 cc stock solution of sodium pentabarbitol (Uthol) placed near the heart. Upon death (generally within 30 minutes), turtles were injected with and emersed in a 10% formalin solution. After a 1-2 week fixation period, turtles were rinsed in tap water and preserved in 70% ethanol.

Individuals not retained were marked by marginal notches (Fig. 3) and released either at the site of capture or at the north end of Gravine Island.

Eggs and Hatchlings

Eggs were obtained from natural nests and from the oviducts of preserved females. They were measured for length and greatest diameter with dial calipers.

Most of the hatchlings examined were obtained through the incubation of eggs or were collected directly from natural nests either previously discovered and marked at the time of deposition, or discovered by back-tracking newly emerged individuals. Drift fences, constructed with 15 m lengths of 15 cm wide aluminum garden edging and provided with gallon can pitfalls at each end, produced several hatchlings. A few hatchlings were found by randomly searching the nesting beach at night. All hatchlings were measured and preserved in the same way as the adults. Sex was determined by dissection after the method of Yntema (1976).

Reproductive Cycles

Male. A total of 21 male G. p. delticola (2-3 per month) were used in the study of reproductive cycles. Plastrons were removed by first cutting through the bridge with an electric cast saw and then separating the skin from the plastron by working along the plastral margin with a sharp scalpel. The entire reproductive tract, including testes, epididymides, vasa deferentia, and penis, was extracted. Care was taken to remove all extraneous tissues from these organs. To determine seasonal changes in size, testes and epididymides were blotted with tissue paper and immediately weighed individually to the nearest 0.01 gm using a Sartorius-Werke GMBH balance (model #3716). The average testis and epididymis weight was determined and recorded relative to each animal's carapace length.

The right testis and epididymis were used to study the spermatogenic cycle. Tissues to be examined histologically were embedded with paraffin (testis and epididymis together), sectioned to 6 microns and stained with hematoxylin and eosin. Testicular material was examined for the presence and relative abundance of Sertoli cells, spermatogonia, primary and secondary spermatocytes, spermatids and spermatoza. Relative seminiferous tubule size was also noted for each month. Epididymides were examined for the relative abundance of sperm and for thickness of tubule walls. Representative photomicrographs of testis and epididymal morphology during each month examined were prepared.

Female. Fifteen female black-knobbed sawbacks were used to determine the ovarian cycle. Plastrons and reproductive tracts were removed by the method described for males. After extraneous tissues were removed, the ovaries were blotted dry and weighed together to the nearest 0.1 gm using a double beam balance to determine seasonal changes.

Ovarian follicles were counted, measured with dial calipers to nearest 0.01 mm, and grouped into four more or less natural size classes. Class I follicles (< 5.0 mm) were too numerous to count but their relative abundance was noted. The remaining three classes were designated as follows: Class II (5-10 mm), Class III (11-16 mm), Class IV (> 17 mm). Class IV follicles were considered preovulatory as determined through the measurements of yolks in shelled oviducal eggs. Oviducal eggs were counted and measured.

Nesting and Nest-site Selection

Nest-site preferences were determined through the analysis of microenvironmental conditions at each nest location. Turtle nests were located either by following turtle tracks until a concentrated ground surface disturbance was found (generally done each morning) or by following the turtle itself until a nest was dug and eggs deposited. Data recorded for each nest site included:

1) Date.
2) Time: (If turtle observed in the process of nesting).
3) Location of Nest: (If one was constructed).
4) Distance In: The length of the path taken by the turtle traveling from shore to the nest. This, and the following lineal measurements were estimated by "stepping off" the distance.
5) Distance Out: The length of the path taken by the turtle traveling from the nest back to shore.
6) Actual Distance: The straight-line distance from the nest to the shore on which the turtle stranded.
7) Substrate Type: Three major types were distinguished as determined by the parameters outlined in Table 5.
8) Substrate Slope: Its presence and direction facing.
9) Height Above Water: Estimated.
10) Associated Vegetation: The nest was considered associated if it was in contact with a clump of vegetation or deposited in a vegetated area and not more than a meter from the nearest plant.

11) Test Nests: The number and location along the turtle's path.

12) Incidence of Predation: Recorded as: not visited, visited but did not find eggs, and, nest destroyed.

Other data not taken routinely at every nest due either to unavoidably severe disturbance to the nest or because their importance was not discovered until late in the nesting season, include:

13) Test Sctatches: The number and location along the turtle's path.

14) Moisture Content of the Substate: Determined in terms of percent weight (to the nearest 0.01 gm) for each major type and measured nearly simultaneously using a triple beam balance.

15) Nest Temperature: Determined either by opening up the nest and immediately inserting a disk thermister into the nest cavity or by excavating another hole to the same depth as and 0.25 m from the actual nest and measuring its temperature.

16) Substrate Temperatures: Sand surface temperature was determind in all instances by placing the thermister on the surface of the sand in direct sunlight immediately above the nest. Sand surface, nest (13 cm deep) and ambient temperatures were measured

simultaneously and continuously for 24 hours in each of the three major nest-type situations (see Table 8). All of the above temperatures were taken using the instrument described earlier.

17) Nest Dimensions: Six nests were carefully excavated and the eggs removed before recording total depth, depth to cavity, cavity diameter, and neck diameter.

Hatching, Hatchling Emergence and Orientation

Hatching, hatchling emergence from the nest, and hatchling orientation were in part investigated simultaneously, and in three ways: 1) through observations of natural, undisturbed nests, 2) through the use of natural and artificial nests within enclosures, and 3) through observations of one glass-enclosed nest. Nests that were missed during the nesting season were located by methods previously described. When such a nest was found, the number and direction of hatchling tracks radiating from the nest as well as much of the information normally secured at the time of deposition, were recorded. Any hatchlings still remaining in the nest were removed and their position in the ground and developmental condition noted.

An attempt was made to enclose natural nests at about halfway through their incubation period. Each enclosure was constructed of the same materials as the drift fences, and measured 1 m in diameter. In order to trap emerging hatchlings and secure orientation data, these enclosures were provided with 4 #303 metal cans sunk level with the substrate, and placed equidistant along the inside perimeter. The 6 nest enclosures erected, along with the eggs contained therin, were subsequently destroyed by human vandals.

Later, a larger enclosure was constructed of the same materials. It measured 3 m in diameter and was provided with #303 metal can pitfalls every 30 degrees along the inside perimeter.

To investigate the possiblity of temperature acting as a cue stimulating nocturnal emergence, ambient, sand surface, and nest temperatures were monitered hourly throughout the experiment and were recorded as described before. Pre-emergent individuals, post-emergent individuals, or less than four day old hatchlings were buried at a depth of 13 cm in the center of the nest and allowed to emerge at will.

Hatchling orienting ability was determined in the same way as from natural nests. Each morning during the emergence experiment, the various paths taken by hatchlings emerging the night before were duplicated on paper. Hatchlings were tested for orienting ability both on level and sloped (ca. 10 degrees) substrates.

Growth and Sexual Dimorphism

Growth in _G. n._ _delticola_ was estimated using the method developed by Sergeev (1937). Only animals having a complete set of clearly distinguishible growth rings were employed. Sexual dimorphism and allometric growth were determined through the analysis of the eleven morphological features measured in each individual.

Food Habits and Parasites

Diet in the southern black-knobbed sawback was determined through the examination of gastro-intestinal contents exposed through dissection. All food items were identified to the lowest possible taxonomic rank. Most were identified to generic level. Food items were recorded both as percent occurrence and percent volume. If more than one type of food was present, individual volumes were measured volumetrically when possible, or by estimation when not. Because some _Graptemys_ species display sexually dimorphic food preferences (Wahlquist 1970, Shealy 1976, Vogt 1980, 1981a), the diets of each sex were analyzed separately. Food habit studies were augmented with observations of feeding behavior in captive individuals.

All captured animals were examined for external parasites. The entire gastro-intestinal tracts of dissected individuals were examined for the presence of internal parasites. When found, the genus of parasite, as well as its relative abundance were recorded.

Statistical Analyses

Because the statistical analyses employed are as varied as the subjects treated, details of proceedures are provided within the sections to which they directly apply. Methods used for the analysis of variance, linear regression, and the various types of hypothesis testing are those of Zar (1974). Means followed by the standard error are sometimes inserted directly into the text.

III. RESULTS AND DISCUSSION

Reproduction

Courtship and Mating

Courtship and/or mating has been described in eight species of Graptemys (Table 1). Courtship in G. oculifera and G. caglei has not been reported. Two very different behavioral patterns are exhibited, depending of the species, and in at least one species, G. p. pseudogeographica some aspects of both patterns occur (Vogt 1980). Most Graptemys display a courtship pattern wherein the male approaches the female, and while facing her, extends his forelimbs, and with rapid vibrations of his foreclaws "titillates" her nasal region. In addition to G. p. pseudogeographica (Ernst 1974, Vogt 1980), this type behavior has been reported with only slight variations in G. o. ouachitensis (Vogt 1980), G. p. kohni (Cagle 1955), G. barbouri (Wahlquist 1970), and G. flavimaculata (Cagle 1955, Wahlquist 1970). Within the genus Pseudemys the titillation type of courtship pattern is highly developed. Correspondingly, males of this genus have developed extremely elongate foreclaws which are probably

Table 1. Known courtship patterns within the *Graptemys*.

Species	Type	Observed in	Source
G. pseudogeographica	Head bob & Claw titillation	lab	Ernst, 1974 Vogt, 1980
G. p. kohni	Claw titillation	lab	Cagle, 1955
G. o. ouachitensis	Claw titillation	lab	Vogt, 1980
G. versa	Head bob	lab	Ernst and Barbour, 1972
G. geographica	Head bob	lab	Vogt, 1980
G. barbouri	Claw titillation	lab	Wahlquist, 1970
G. pulchra	Head bob	field	Shealy, 1976
G. flavimaculata	Claw titillation	lab	Cagle, 1955
G. nigrinoda	Head bob	lab	This study

useless for any function other than courtship. The presence of elongated foreclaws in male emydids may therefore be suggestive of this type of courtship pattern.

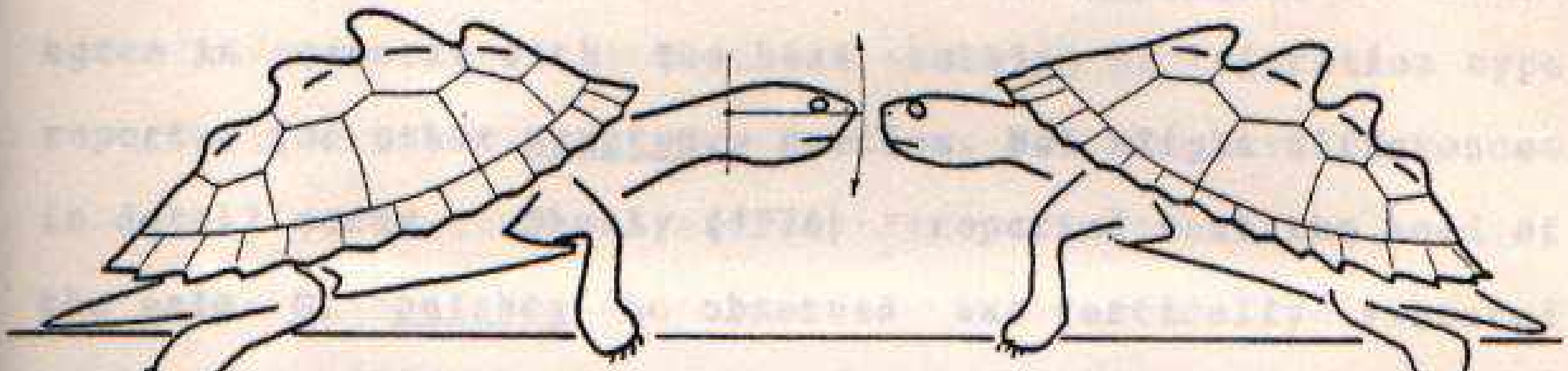
The other courtship pattern, peculiar only to some *Graptemys* species, does not include use of the forelimbs. Rather, the head is extended and vibrated (rapidly nodded) against or near the snout of the female. This pattern of courtship has been reported for *G. geographica* (Vogt 1980), *G. pulchra* (Shealy 1976), and may occur in *G. versa* (Ernst and Barbour 1972).

Observing courtship and mating in most aquatic turtles under natural conditions is difficult. Consequently, most workers have relied heavily on observing this behavior under laboratory conditions (Table 1). Courtship behavior has been reported in hatchling and juvenile turtles. In some instances these observations represent the only source of information available on courtship in these species (Cagle 1955). Whereas courtship, as displayed in young turtles, may not be as refined as in adults, it probably represents a good approximation of the adult behavior.

Courtship and mating in *G. nigrinoda* were not observed under field conditions. However, specific behavioral patterns easily recognized as courtship were observed in yearlings maintained together in a ten gallon aquarium. This tank was supplied with a gravel substrate, aquatic plants (*Elodea* sp.), rocks, and a basking limb illuminated with flourescent lights. Water was maintained at 24°C and kept clean with a standard air pump and filter. Food, in the form of raw beef, pork, chicken, and fish was provided daily. Both individuals had been hatched and reared in captivity in isolation from any adult turtles.

On 6 January 1981 at 2210 h these two turtles swam toward each other just above the substrate and on meeting, they ceased swimming motions and settled to the bottom of the tank. The head and neck of both individuals was extended towards each other to within 1.0 mm. Simultaneously the forelimbs were extended downward, raising the anterior portion of the shell off the substrate (Fig. 4). With its neck slightly arched, one turtle was observed to vertically nod its head rapidly, 5-6 times in the course of one second. After a two-second pause, nodding was again repeated. A total of three head nod sequences occurred before they parted.

Courtship behavior in these juveniles was observed again at approximately 2420 h and at 1500 h on 7 January 1981, with orientation, pattern, and duration being essentially the same as before. Carey Chrestensen (pers. comm.) observed this same behavior during December 1980 and January 1981 in her captive *G. nigrinoda* hatchlings. The only



COURTSHIP PATTERN

Figure 4. Courtship pattern in G. n. delticola as exhibited in laboratory reared juveniles. The head of one individual is rapidly nodded (5 times per second) in a vertical plane, pivoting at the level of the axis, as conspecifics face each other snout to snout.

difference she noted is that both animals involved displayed head nodding and that sometimes their snouts actually made contact. With my specimens, only one animal was observed to nod in any single confrontation. The sex of the individuals was not known, nor was it known whether the same turtle performed the head nodding behavior in both instances.

Courtship patterns as displayed in G. nigrinoda yearlings agree in general with the head bobbing or vibration type reported for other Graptemys species, but slight differences in detail occur. Shealy (1976) reported that the head of the male G. pulchra he observed was vertically vibrated against one side, and then the other of the females snout, alternating every five seconds. In G. nigrinoda, the head of the "male" is nodded directly in front of the "female's" head. In this respect the behavior is quite similar to that of G. geographica (Vogt 1980). The rapidity of head nodding was not reported in G. pulchra or G. geographica, but in G. versa it occurred at a rate of approximately five times per second (Ernst and Barbour 1972). Unlike the head bobs and related movements reported for various testudinids, in which both head and neck are moved together (Auffenburg 1965, 1966, 1969), G. nigrinoda nods only the head, the neck remaining motionless.

Generally, the closer two taxa are phylogenetically, the more similar are their courtship patterns. One would expect, therefore, that among various species of Graptemys, those most closely related would share at least generalities in courtship patterns. Such is not the case (Table 1). Within both the broad-headed and narrow-headed Graptemys groups, both general courtship patterns occur. Courtship in distantly related G. pulchra much more closely resembles that shown in G. nigrinoda than does one of the black-knobbed sawback's closest relatives, G. flavimaculata. Why such an incongruous relationship exists between phylogeny and courtship pattern within the Graptemys is not at all clear, and is further confounded by the fact that males of certain head-nodding species such as G. nigrinoda have significantly longer foreclaws, relative to carapace length, than do females. Others, like G. geographica (Vogt 1980), do not. It is interesting, and perhaps important to point out again that G. pseudogeographica, which is thought to most closely approximate the ancestral form (Folkerts and Mount 1969) has elogate foreclaws and displays both types of courtship behavior (Ernst 1974, Vogt 1980). Other Graptemys species may also be found to display both courtship patterns if further research is done.

Male Reproductive Cycle

The spermatogenic cycles of North American and Neotropical emydines for which data are available, are essentially identical (Moll 1979). Slight variations occur only in the timing of each particular phase depending on the species, latitude, and seasonal conditions (Atland 1951, Legler 1960, Moll and Legler 1971, Moll 1973, 1979).

Except for the present study, the spermatogenic cycle has not been investigated in any species of Graptemys.

A total of 21 male G. nigrinoda were examined for testicular activity. Of these, 16 were considered reproductively mature as evidenced by the presence of mature sperm in the epididymus or testis.

From April-June seminiferous tubules are regressed and somewhat compressed in form. Except for cellular debris remaining from the previous reproductive season (Moll and Legler 1971, Moll 1979), lumina are empty (Fig. 5). Spermatogonia and Sertoli cells are abundant along the basement membrane during this period, and epididymides are full of mature sperm (Fig. 6).

Spermatogenesis begins in June as differentiation of the spermatogonia leads to the formation of primary and secondary spermatocytes. All early stages of spermatogenesis (spermatogonia and spermatocytes) are now abundant (Fig. 7).

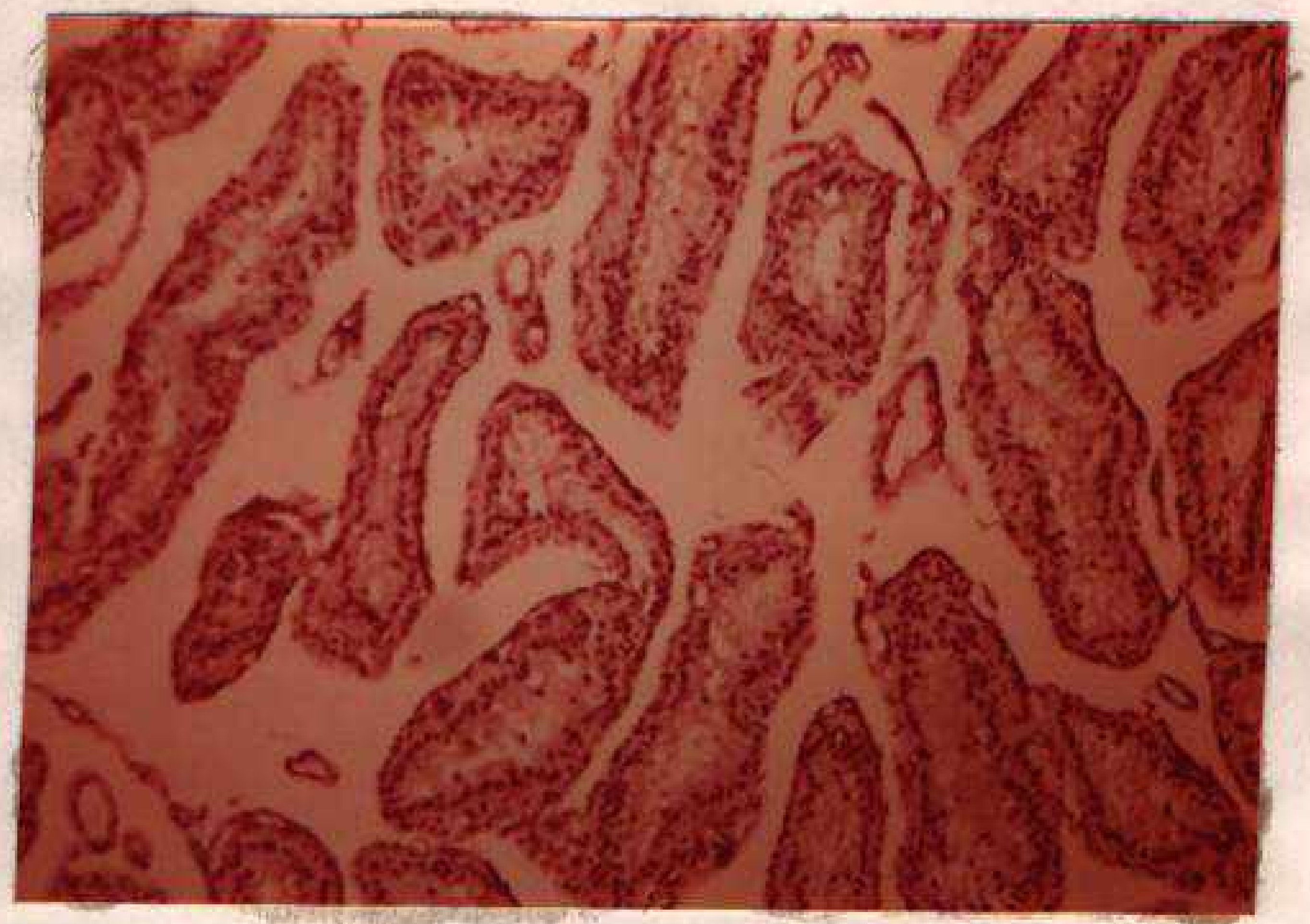


Figure 5. Testis section, 48x. May. Seminiferous tubules collapsed, spermatogonia and Sertoli cells present.

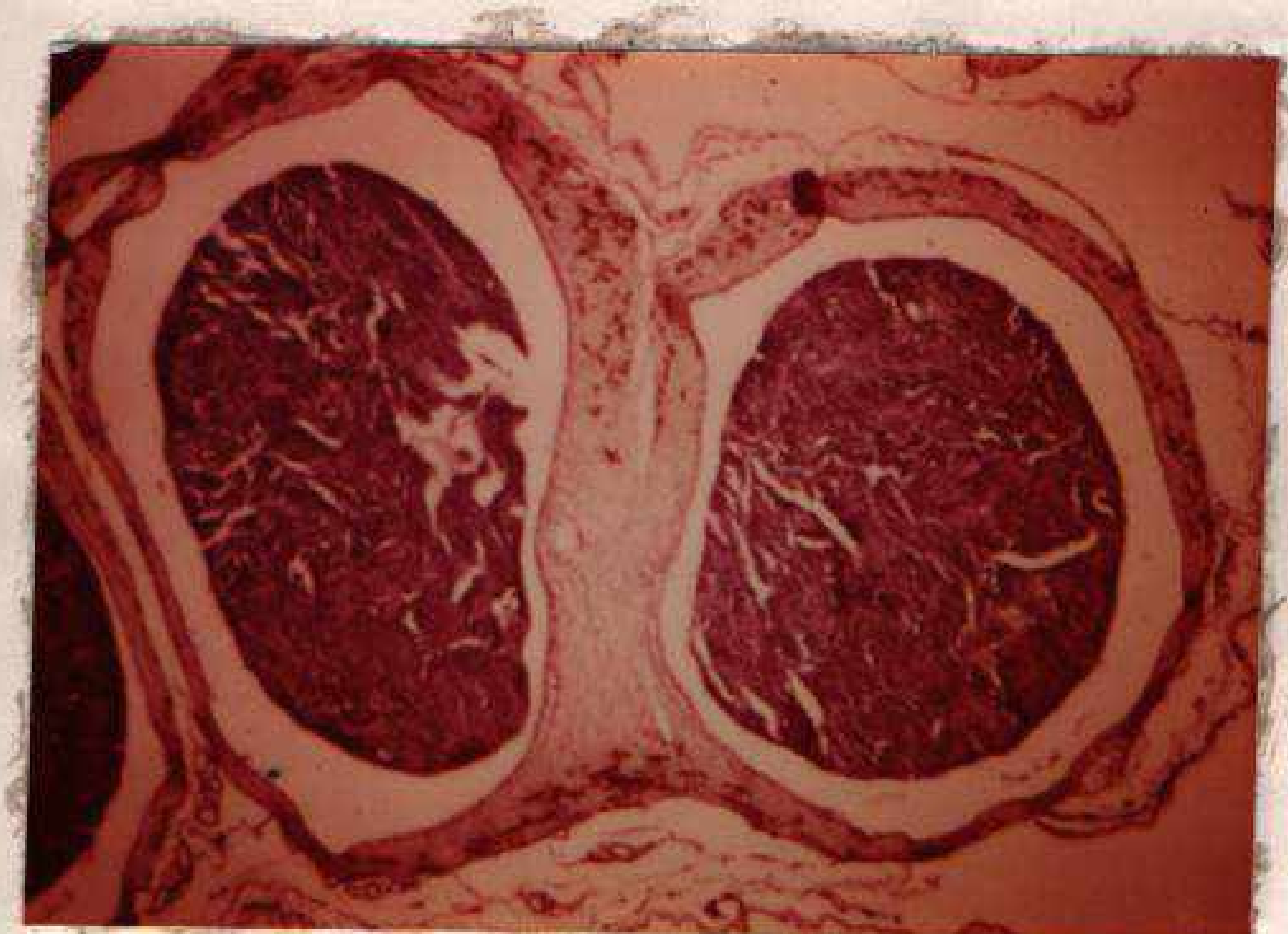


Figure 6. Epididymis section, 48x. May. Spermatozoa abundant.

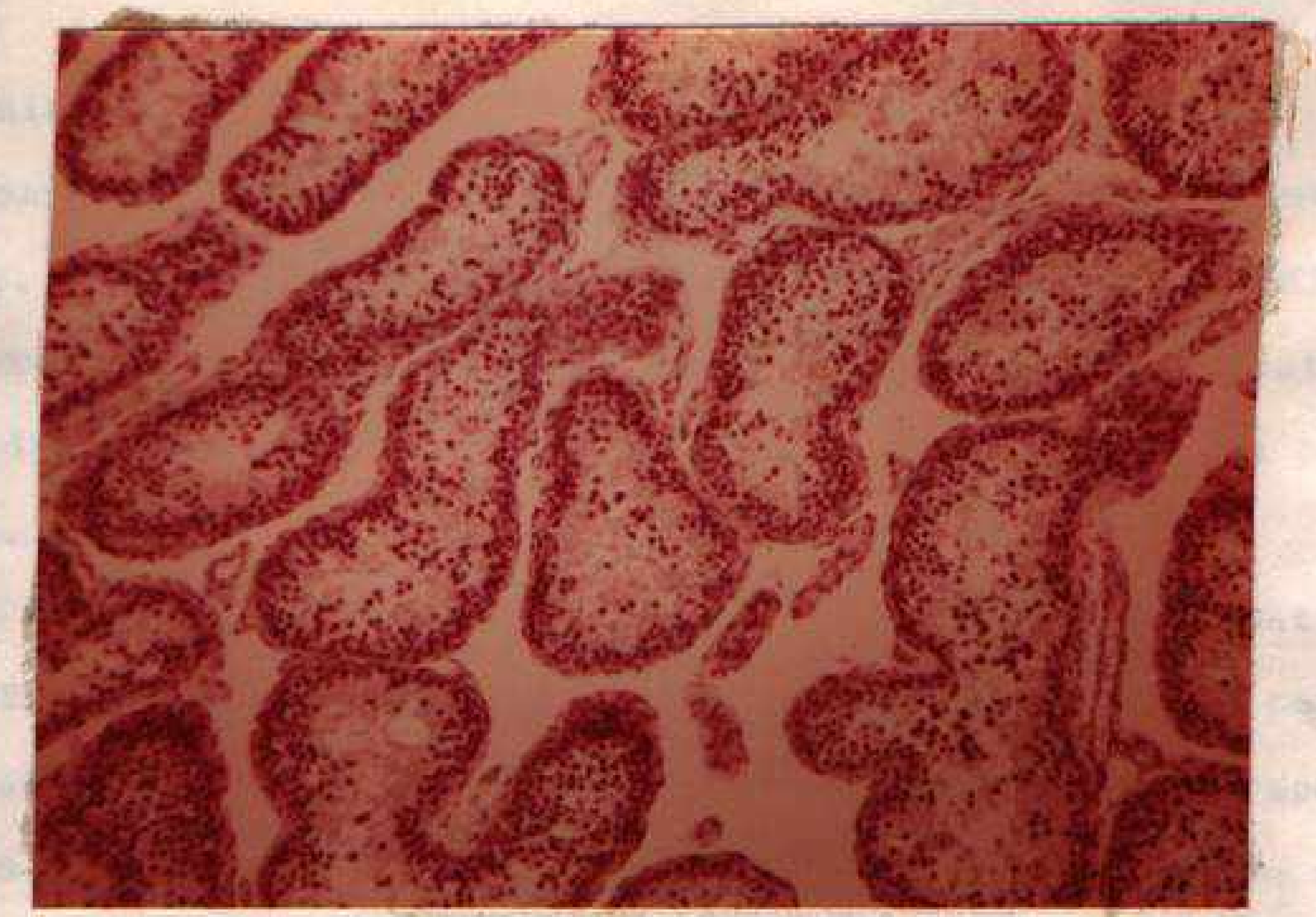


Figure 7. Testis section, 48x. July. Seminiferous tubules expanding, 1° and 2° spermatocytes present.

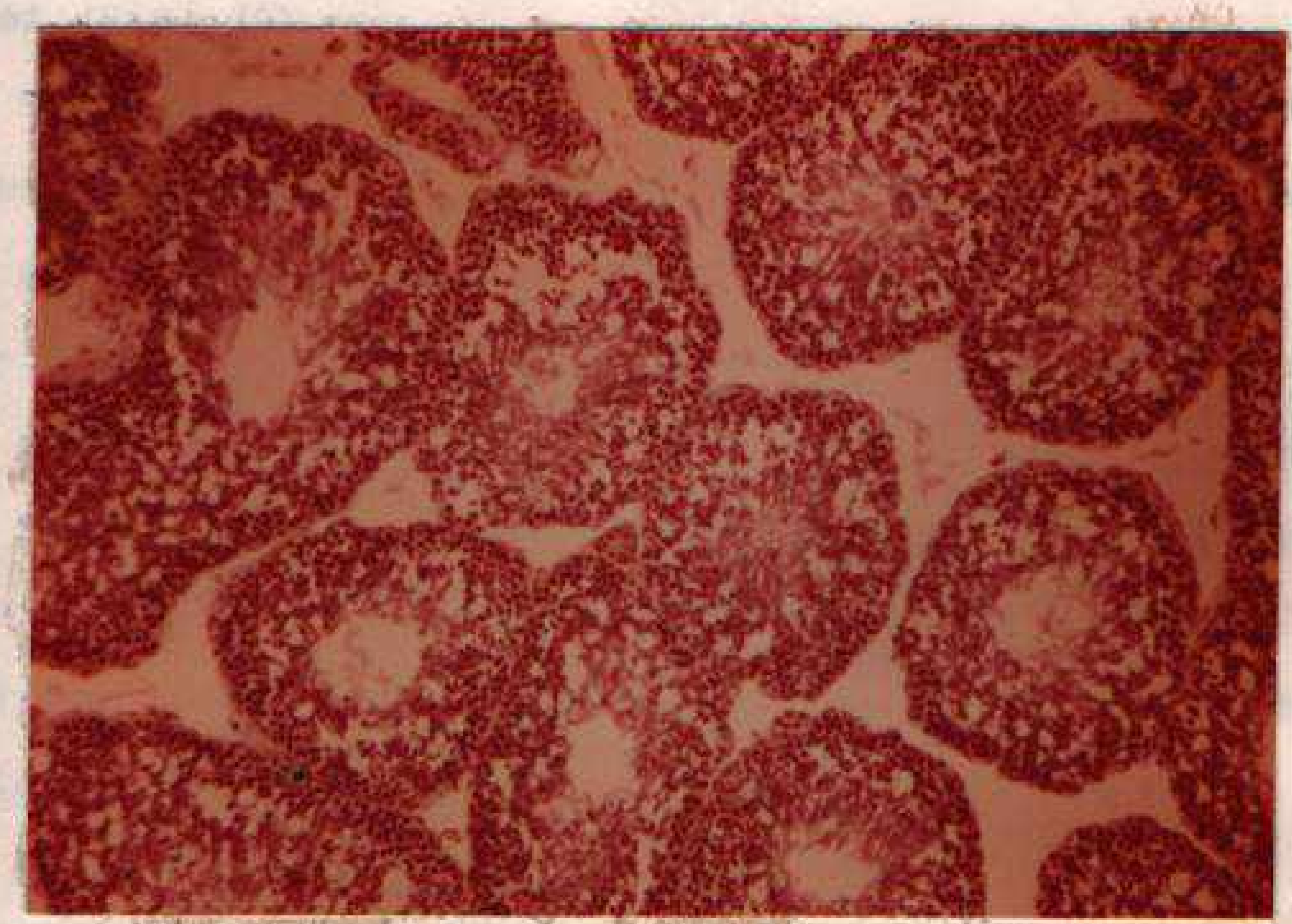


Figure 8. Testis section, 48x. August. Spermiogenesis begins, spermatids and spermatozoa present.

Seminiferous tubules are beginning to expand as is, concomitantly, the testis itself, but the lumina remain empty. Mature sperm are still present in the epididymides but are fewer in number than during the preceeding months. Epididymal walls are beginning to thicken as the tubes contract.

By August, the seminiferous tubules are approximately threefourths expanded as spermatogenesis reaches its peak. Spermatogonia, spermatocytes, and, for the first time, spermatids are abundant. Spermiogenesis begins at this time and the previously empty lumina begin to fill with mature sperm (Figs. 8 and 9). There are essentially no sperm in the epididymids at this time, and the tube walls are highly contracted (Fig. 10).

In September, the seminiferous tubules are fully expanded and testes are at their maximum size. Spermiogenesis is at peak production with mature sperm completely filling the lumina. Numbers of spermatogonia and spermatocytes become fewer as spermatogenesis declines and is completed in October. Spermatids are still fairly abundant, and mature sperm can be seen clustered around Sertoli cells (Fig. 11). The epididymides again contain mature sperm and are expanding rapidly.

By November, seminiferous tubules are beginning to contract as spermiogenesis ends and spermiation begins. Some

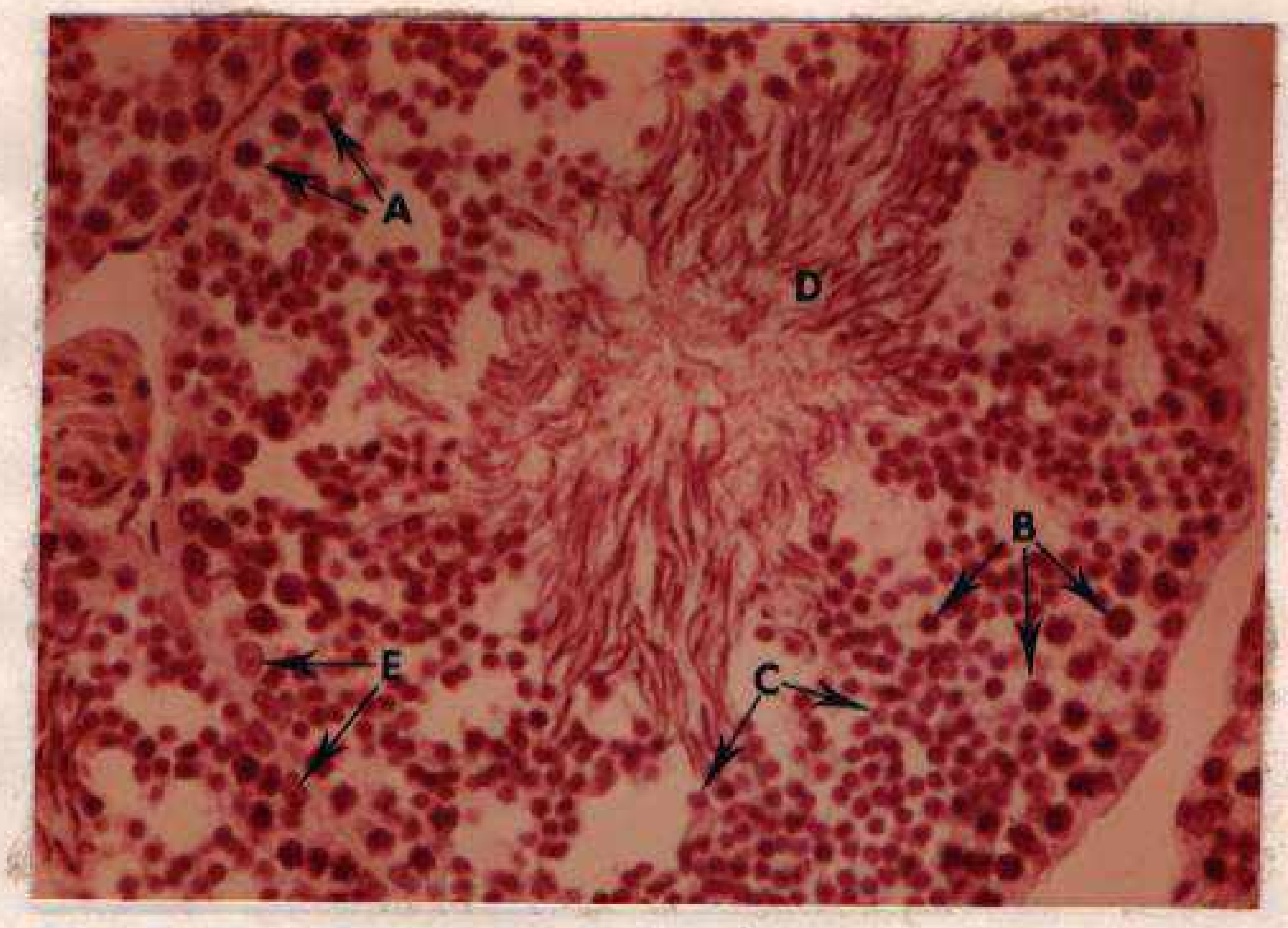


Figure 9. Testis section, 400x. August. A, spermatogonia; B, spermatocytes, C, spermatids; D, mature spermatozoa; E, Sertoli cell nuclei.

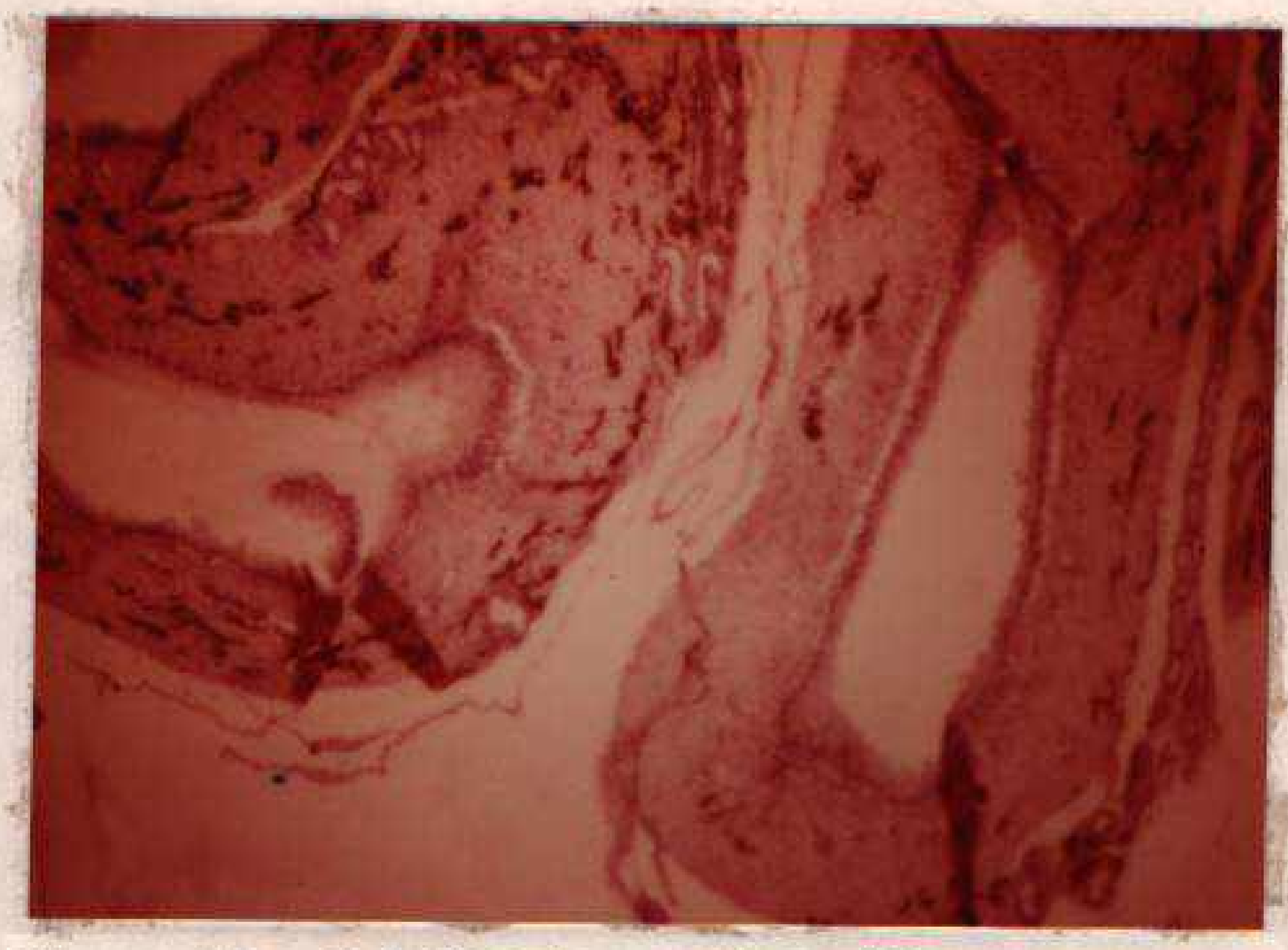


Figure 10. Epididymis section, 48x. August. Epididymal walls highly contracted, no sperm present.

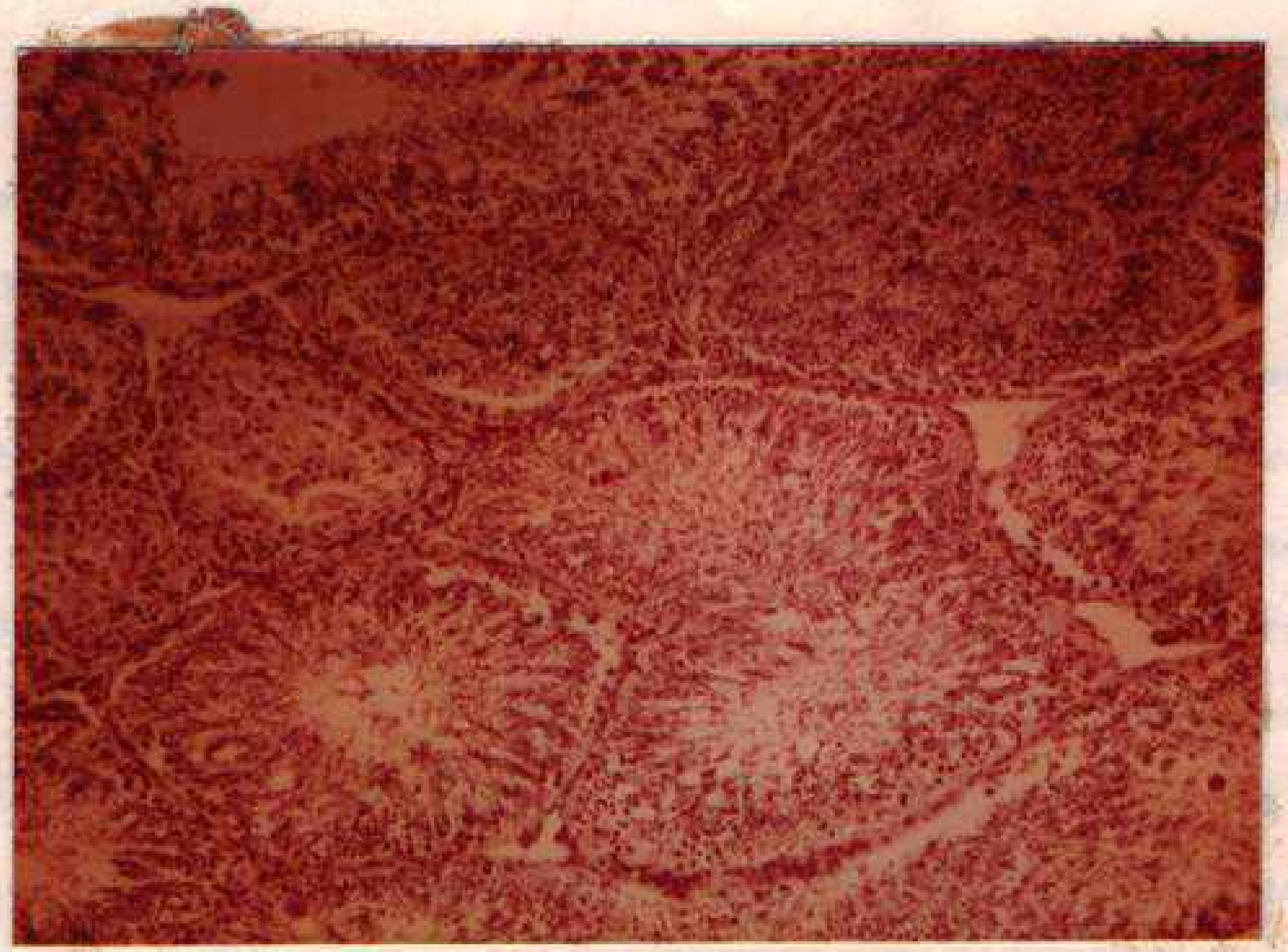


Figure 11. Testis section, 48x. September. Seminiferous tubules fully expanded, spermiogenesis in peak production.

Figure 12. Testis section, 48x. November. Spermatogenic cycle essentially completed.

sperm remain in the testes, but except for cellular debris lumina are essentially empty (Fig. 12). Epididymides are packed with mature sperm.

In *G. nigrinoda*, the spermatogenic cycle is intimately tied to seasonal changes in testicular and epididymal weight (Fig. 13). Spermiation begins in September, filling the epididymides to capacity. The epididymides remain filled until spring when the amount of sperm begins a steady decline becoming essentially absent in August. This suggests that mating occurs in late spring and early summer. Mating, however, should be possible anytime mature sperm are abundant within the epididymides (Shealy 1976). Vogt (1980) concluded that the potential for mating in *G. pseudogeographica* and *G. o. ouachitensis* occurs in both spring and fall, based on mating behavior exhibited by captive individuals at these times. No corresponding decrease in the amount of sperm contained within the epididymides is observed in the fall because it is being continually replaced via spermiation. Autumn matings in *Graptemys* have been reported in *G. pulchra* (Shealy 1976) and *G. pseudogeographica* (Vogt 1980). By December, spermiogenesis has ended but at the same time, water temperatures have dropped to below the minimum required for activity in *G. nigrinoda* (Waters 1974). Therefore, no decrease in sperm concentration is evident until spring when matings resume.

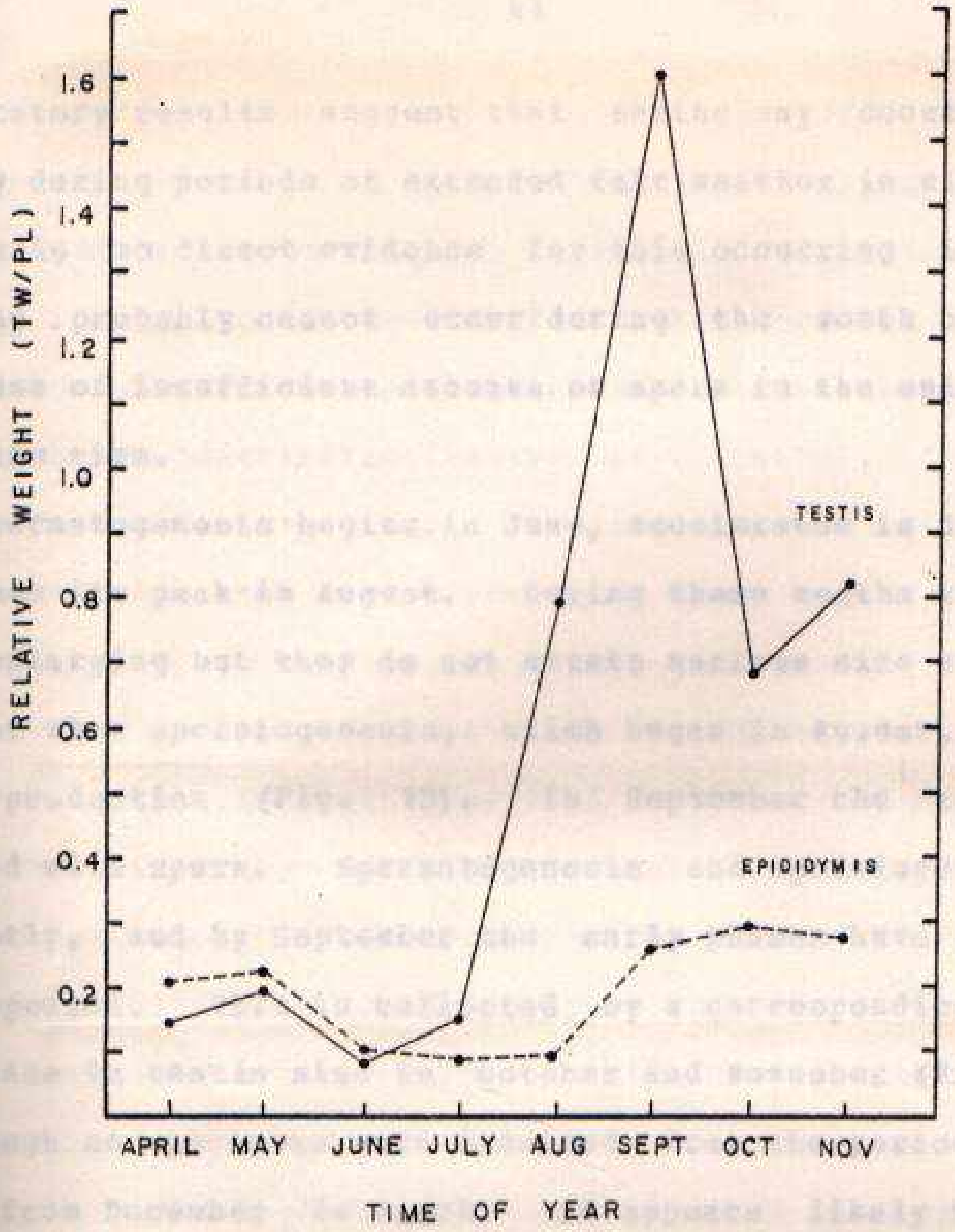


Figure 13. Seasonal weight changes in testes and epididymides of G. n. delticola from the Tensaw River, Baldwin Co., Alabama.

Laboratory results suggest that mating may occur sporadically during periods of extended fair weather in winter, but there is no direct evidence for this occurring in nature. Mating probably cannot occur during the month of August because of insufficient amounts of sperm in the epididymides at this time.

Spermatogenesis begins in June, accelerates in July, and reaches its peak in August. During these months the testes are enlarging but they do not attain maximum size until September when spermiogenesis, which began in August, reaches peak production (Fig. 13). In September the testes are packed with sperm. Spermatogenesis and spermiogenesis end abruptly, and by September the early phases have virtually disappeared. This is reflected by a correspondingly rapid decrease in testis size in October and November (Fig. 13). Although no specimens were examined from the period extending from December to March, it appears likely that the testes continue to regress at a rate correlated with reduced metabolism during the winter months, reaching their minimum size in April and May. Sometime prior to April (March ?) the germinal epithelia begin producing spermatagonia as the testes prepare for a new spermatogenic cycle.

As noted above, cellular debris in G. nigrinoda accumulates among the spermatozoa within the lumina of the seminiferous tubules, and remains until spring. This phenomenon has also been reported in the neotropical slider P. scripta (Moll and Legler 1971) and in the lizard Xantusia vigilis (Miller 1948). The fate of this cellular material is not known, but Miller suggests that Sertoli cells, which are most abundant during the early stages of the cycle, are responsible for eliminating it.

Female Reproductive Cycle

As with the spermatogenic cycle in males, female reproductive cycles in North American emydines are essentially similar, differing only in timing. Follicular development may be completed before brumation, or afterwards, and some species display both patterns depending on latitude (Gibbons 1968, Ernst 1971a, Moll 1973, Christiansen and Moll 1973).

Few data are available on female reproductive cycles of Graptemys. Shealy (1976), observed that in G. pulchra, the ovarian follicles were enlarging from September to November, during which time feeding and activity ceased. Vogt (1980) reported a similar period of follicular development in Wisconsin Graptemys (a general description which I assume included G. geographica, G. o. ouachitensis and G. pseudogeographica) but indicated that feeding occurs at this time.

The ovarian cycle has not been investigated in any narrow-headed Graptemys.

Reproductive tracts of 15 supposedly mature *G. nigrinoda* females collected in all months from April to October were examined for ovarian activity. Of these, only 7 were determined to be sexually mature based on the presence of enlarged ovarian follicles. Fortunately, these include individuals collected in April, May, June, July, September, and October. The description and conclusions on the ovarian cycle in *G. nigrinoda* are drawn from these data, and from information available on other North American emydines as well.

The ovarian cycle can be conveniently be separated into four phases: follicular enlargement, ovulation, nesting period, and the latent period (Moll 1979).

Follicular Enlargement. In *G. nigrinoda*, vitellogenesis begins in late summer (August and September) after the final clutch has been deposited. No preovulatory and few Class III follicles are present in the individuals from September and October. The smaller size classes, I and II, are more abundant in these months than at any other time (Fig. 14). Ovarian weight probably becomes minimal during this period. It cannot be ascertained from the present data whether these small follicles become preovulatory before the onset of brumation, or afterwards, but by April they have attained their maximum size. Probably, during the comparatively warm months of October and November, the first clutch complement

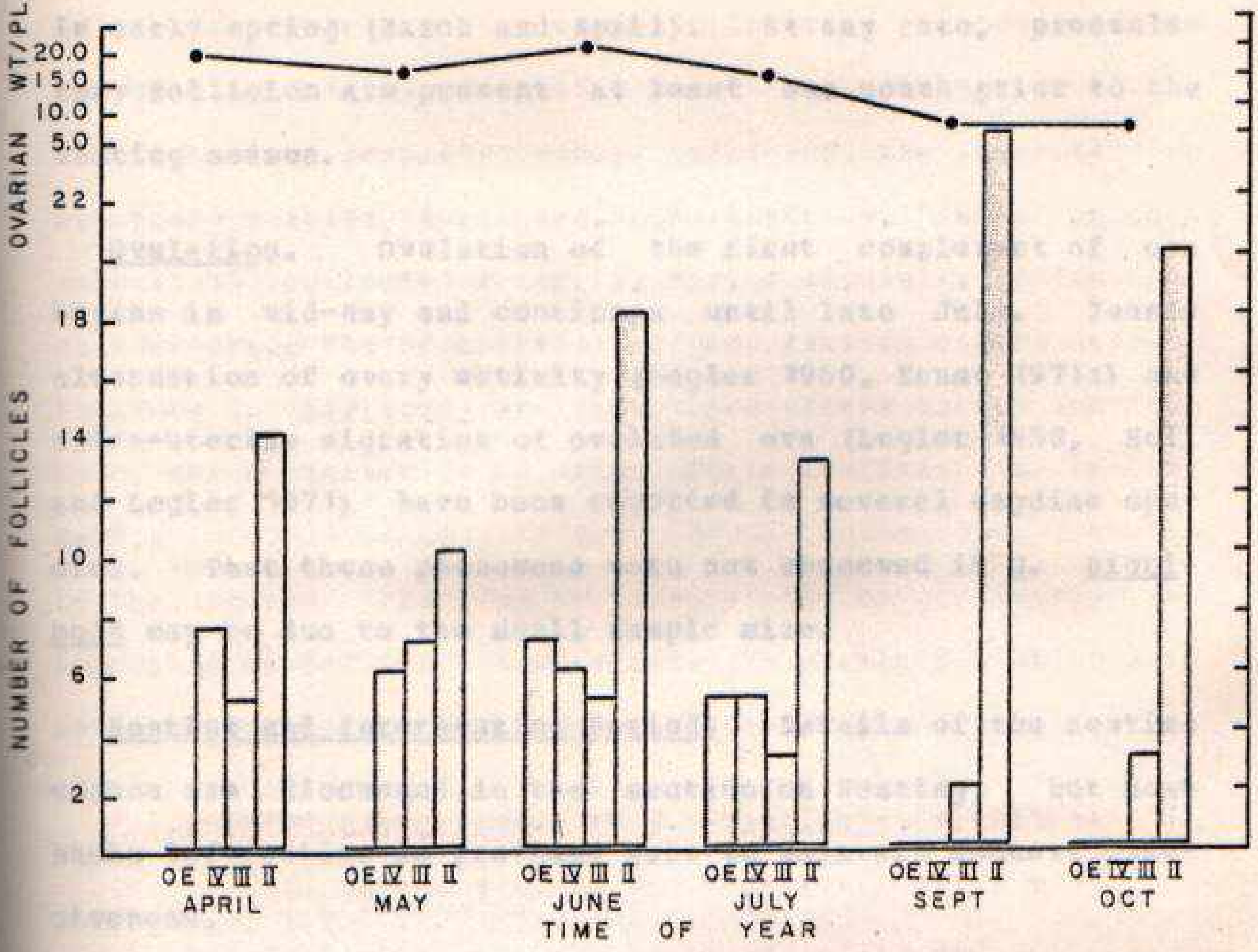


Figure 14. Seasonal changes in relative ovarian weight (upper scale) and abundance of ovarian follicles and oviducal eggs (OE) in 7 G. n. deltícola females from the Tensaw River, Baldwin Co., Alabama. Values for April represent the average from two individuals. Follicle size categories are as follows: Class II, 5-10 mm; Class III, 11-16 mm; Clas IV, (preovulatory) >17 mm.

reaches size Class III before winter and finishes developing in early spring (March and April). At any rate, preovulatory follicles are present at least one month prior to the nesting season.

Ovulation. Ovulation of the first complement of ova begins in mid-May and continues until late July. Yearly alternation of ovary activity (Legler 1960, Ernst 1971a) and extra-uterine migration of ovulated ova (Legler 1958, Moll and Legler 1971) have been reported in several emydine species. That these phenomena were not observed in *G. nigrinoda* may be due to the small sample size.

Nesting and Internesting Period. Details of the nesting season are discussed in the section on Nesting, but some basic information is provided here to maintain context cohesiveness.

Nesting begins on Gravine Island in late May, peaks from mid-June to mid-July, and ends in early August. The earliest known nesting occurred on 20 May 1980 and the latest nest was deposited 5 August in the 1980 season. The internesting period was not determined directly but can be extrapolated from the known nesting period when the number of clutches deposited annually is known. In the individuals examined from June and July, size Class III, preovulatory, and oviducal eggs were present simultaneously. The simultaneous occurence of several size classes of enlarged follicles may be used to estimate the approximate number of clutches an individual would deposit that year (Moll 1979). The fact that no preovulatory and few Class III follicles are present in September suggests that, unlike _G. pulchra_ (Shealy 1976), most of the follicles within these two size classes are ovulated in the same year that they become preovulatory. Therefore, at least three clutches, and possibly four, are indicated for _G. nigrinoda_ annually. The nesting season is approximately 72 days long, but nesting activity is concentrated only for 60 days. If three clutches are deposited during this period with the first one being laid at the begnning of the season, the internesting interval could be as long as 30 days. Internesting intervals reported for other North American emydines are approximately 14 days (Moll 1973, Christiansen and Moll 1973) and 14-21 days (Gibbons 1968) in _C. picta_, and 15-24 days in _G. barbouri_ (Wahlquist and Folkerts 1973).

Latent Period. No latent period was observed in the ovarian cycle of _G. nigrinoda_. Follicular proliferation or enlargement was evident in all months for which specimens were examined. It is likely that for perhaps one month subsequent to depositing the final clutch of the season (such as in late July and August, for which no specimens were avaialable), a latent period exists. The examination of specimens from this period is required before any definitive conclusions can be drawn.

Nothing resembling atretic follicles was observed.

Reproductive Potential

Clutch size in _G. nigrinoda_ was determined by counting complements of enlarged follicles (Classes III and IV) and by counting numbers of shelled eggs, both oviducal and those deposited in nests. No substantial difference was found between the results of these two methods. Using oviducal and nest eggs, clutch size averages 5.5±0.43 eggs per clutch (n=9, range=3-7). Assuming a minimum of three clutches annually with an average of 5.5 eggs per clutch, _G. nigrinoda_ would have an average annual reproductive potential of 16.5. This value is comparable to that for _G. barbouri_ with 17.0 (Cagle 1952) but is considerably less than in other _Graptemys_ investigated: _G. pulchra_, 29 (Shealy 1976), _G. o. ouachitensis_, 21, and _G. pseudogeographica_, 28.2 (Vogt 1980). The annual reproductive potential for any narrow-headed _Graptemys_ has not been previously reported. Cagle (1953) reported that a small _G. oculifera_ female collected 4 June, contained 3 shelled oviducal eggs and 4 enlarged follicles, indicating that two clutches or a total of 7 eggs would have been deposited by this individual.

Nesting Season

Based on follicular and nesting activity data, the nesting season extends at least from mid-May to early August. The earliest nest discovered on Gravine Island was on 20 May 1980, but the island had not been visited since mid-April of the same year. Thus, clutches could have been deposited prior to this without being observed. In addition, old turtle tracks were present on Gravine on 20 May, indicating earlier activity. On 12 April 1980, for example, three sets of tracks, but no nests, were found. These "wanderers" have been reported in other emydines. Shealy (1976) believed that wandering individuals are making prior visits to determine the suitability of possible nesting habitat. It may also be that motivated by hormonal changes associated with follicular development, nesting appetite causes female turtles to wander onto nesting beaches prematurely. Wandering may occur repeatedly in some individuals with each new set of enlarging follicles as evidenced by the fact that wandering <u>G. nigrinoda</u> were discovered (via turtle track analysis) not only prior to, but thoughout the nesting season. Of 32 sets of tracks traced between 19 June and 5 August 1980 15.2% represented wanderers. This hypothesis concerning wandering may account for the presence of adult females on the island, but fails to explain why tracks of smaller turtles, some of which may have been made by male turtles, may occasionally be found crossing beaches.

The last nest of the 1980 season was deposited on 5 August. The latest nesting activity prior to this date occurred on 29 July when two nests were deposited. Peak nesting activity occurred from mid-June through mid-July during which 6-7 _G. nigridoda_ came ashore nightly.

Nesting always occurs after dark with periods of highest activity between 2100-2400 h as determined from nightly track counts and observations. Few _Graptemys_ species have been observed in the process of nesting. Shealy (1976) reported that _G. pulchra_ nests during the day. Similarly, Vogt (1980) found that _G. pseudogeographica_ and _G. o. ouachitensis_ were diurnal nesters, having peak periods of activity between 0630 and 1000 h. Cagle (1953) observed a _G. oculifera_ nesting in late afternoon. Generally, turtles nest either by day or by night, but rarely during both periods (Moll 1979).

There are two obvious benefits to nocturnal nesting: 1) females are less conspicuous and consequently less suseptable to predation, and 2) by nesting at night, turtles avoid high and possibly lethal daytime sand temperatures. While the increased risk of predation may be a consequence of diurnal nesting, I agree with Moll and Legler (1971) and Vogt (1980) that lower temperatures are the significant factor limiting nesting to night. Sand surface temperatures become warmer than 50°C (Table 8; Fig. 32) in the early afternoon on Gravine Island. It usually requires a minimum of one hour for G. nigrinoda to complete nesting and return to the water. On a clear summer day a nesting individual may not have time to complete a nest before reaching her critical thermal maximum. Critical thermal maxima average 41.6°C in semi-aquatic emydids (Hutchison 1979).

No evident environmental correlations with nesting activity were observed, except that nesting was not initiated during heavy thundershower activity. If, however, a nest was already under construction when precipitation began, the female appears to complete the nest before returning to the water. This was observed in one occassion and was inferred in several other instances from turtle track analysis. On three occasions, nests were discovered along with only the track from nest to shore, being evident, the incoming track having been erased by the rain. In addition, no unfinished nests that were more than half constructed were ever found.

Nesting activity was reduced drastically on weekends when human activity (camping, picknicking, boating, etc.) on and near Gravine was heavy. For example, seven nests were deposited the night of 3 July 1980, a Thursday, whereas only one nest was found during the next three days. During the July 4th weekend, more than 100 people visited the island. On 7 July, six nests were discovered.

Some authors have noted a strong correlation between night temperature and nesting activity (Moll and Legler 1971). No such relationship was observed in G. nigrinoda probably due to the absence of cold nights during the period in which I resided on Gravine Island.

Nest-site Selection

Studies investigating the environmental parameters regulating nest-site selection in emydines are few. Anderson (1958) found that G. oculifera and G. pulchra on the Pearl River of Mississippi and Louisiana nested on sand bars as far away from the river as possible. Conversely, Shealy (1976) found that Conecuh River populations of G. pulchra from Alabama nested near the shore. Except for the studies Burger and Montevecchi (1975) and Burger (1977) who examined nest-site selection in Malaclemys terrapin, all present knowledge of nest-site selection in emydines results from causual observation.

A total of 59 turtle nests were located on Gravine Island during 1980. Of these, 38 (64.4%) were determined to be G. nigrinoda mostly through the direct observation of nesting females and resulting hatchlings. In some cases the size of eggs, clutch size, width of nesting females' track and location of the nest, were also used (Table 2). The remaining

Table 2. Criteria for the differentiation between nests of *G. nigrinoda* and *P. alabamensis* on Gravine Island, Tensaw River, Baldwin Co., Alabama.

Criterion		*G. nigrinoda*	*P. alabamensis*
Egg length	$\bar{X}$ ± SE (n) (R)	37.03 ± 0.33(42) (32.8 - 41.7)	40.26 ± 0.59(7) (37.3 - 42.0)
Egg width	$\bar{X}$ ± SE (n) (R)	23.78 ± 0.17(42) (20.0 - 26.0)	28.73 ± 0.73(7) (25.5 - 30.8)
Clutch size	$\bar{X}$ ± SE (n) (R)	5.50 ± 0.43(8) (5 - 7)	10.50 ± 1.44(4) (7 - 14)
Largest track width		187 mm	279 mm
Smallest track width		171 mm	203 mm
Nest location (n)		91.6% > 6.0 m from shore (36)	98.1% < 6.0 m from shore (15)

nests were that of *P. alabamensis*. Although James Dobie (pers. comm.) has found *Trionyx spiniferus*, *Kinosternon subrubrum*, *Chelydra serpentina*, *P. scripta*, and *P. concinna* nests on Gravine in the past, none were located here during the 1980 season.

Only nests discovered on the main nesting beach, which was divided into four quadrats (Fig. 15) were used in nest-site selection analysis. Information collected elsewhere will be interjected where appropriate.

Nest Location

Of the 34 nests for which location data were taken, Quadrat I contained the greatest number of nests, accounting for 61.8% of all the nests located. Quadrat IV had the second highest number of nests (20.6%), whereas Quadrats II and III were rarely used, both including only 8.8% of the nests.

The location of nests appears to depend more on where turtles came ashore than as any preference for a particular area of beach. All nests in Quadrats I, II, and IV were deposited by individuals emerging from the river on the north side of the island. Thus, 91.2% of the sawbacks nesting in the main study area on Gravine island entered form the north. There are at least two plausible explanations. First of all, as Figure 16 illustrates, the water is deeper along much of the north shore's length. Deep water offers

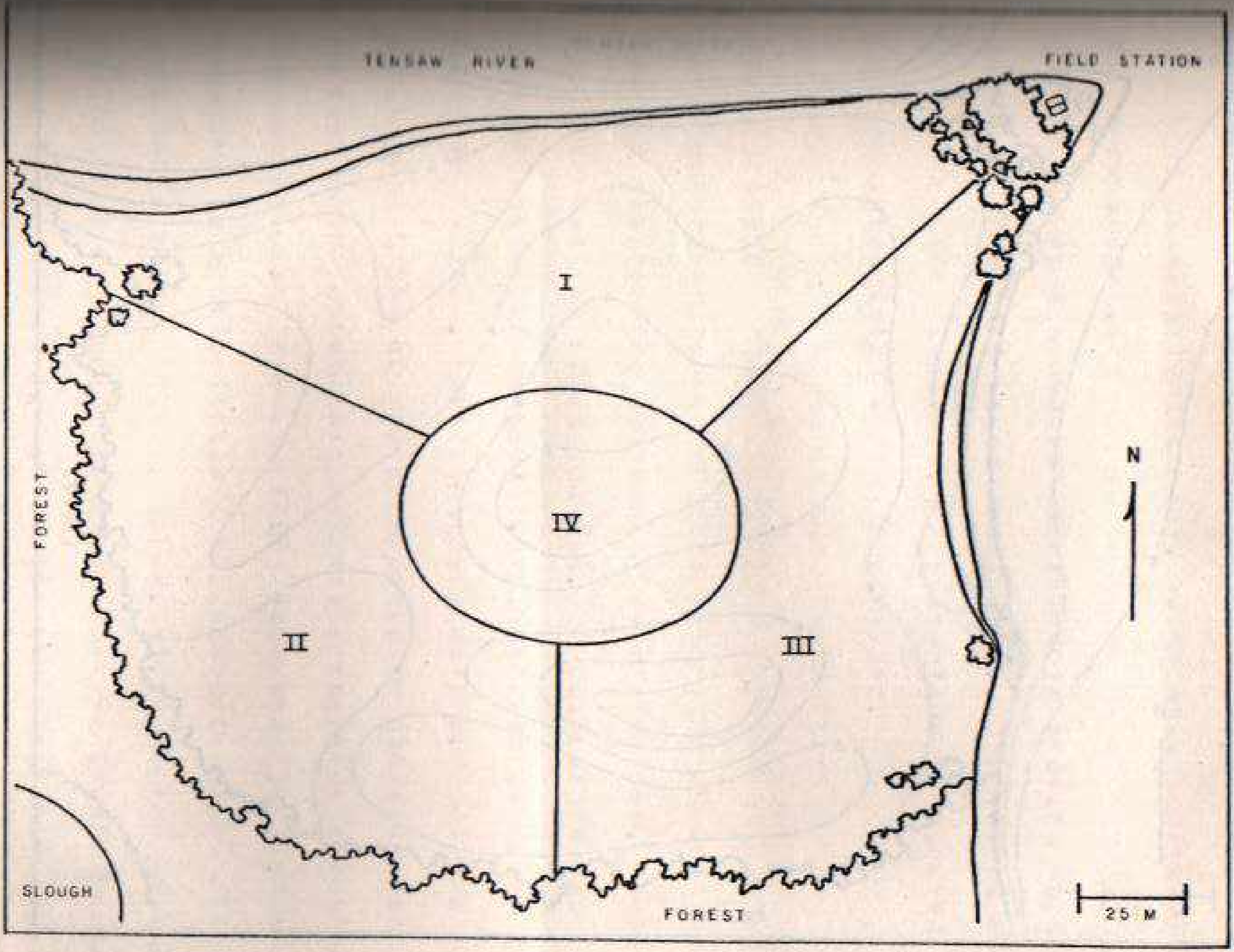


Figure 15. Map of the main nesting beach located on the north end of Gravine Island. Roman numerals indicate quadrats.

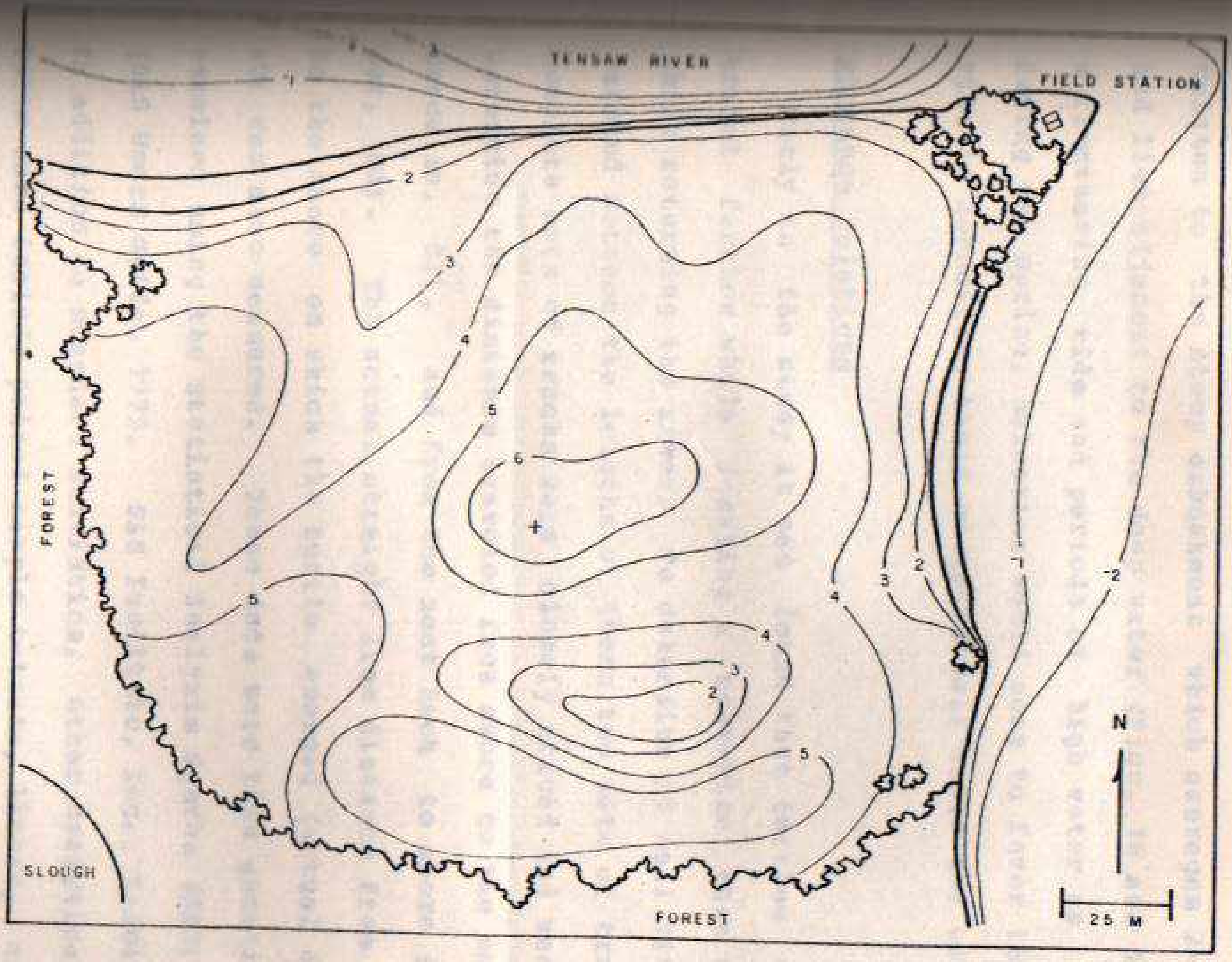


Figure 16. Topographic map of the main nesting beach located on the north end of Gravine Island. Elevations are in meters.

greater protection to turtles approaching the beach, and approximately 80% stranded here. The other explanation relates to the steep embankment which averages 2-3 m high and lies adjacent to the deep water (Figs. 16 and 17). With a fluctuating tide and periods of high water as is common during the spring, selection would seem to favor those individuals depositing their clutches well above the water line.

Distance Relations

Early in the study it was found that turtles tended to travel farther while locating a nest-site than they did while returning the river. To determine if real differences existed between the lengths of these two sets of tracks, 28 complete sets of tracks were closely traced and measured to determine the distance traveled from shore to the nest (distance in, DI), and from the nest back to shore (distance out, DO). The actual straight line distance from the nest to the shore on which the turtle emerged (actual distance, AD) was also measured. These data were then quantitatively examined using the Statistical Analysis System (SAS) program (SAS Users Guide, 1979. SAS Institute, Inc., Raleigh, NC). In addition to standard statistics, other analytical procedures used include paired sample t-tests, linear, and quadratic regression.

Figure 17. Nesting beach on the north end of Gravine Island (looking east) used extensively by G. n. delticola. Approximately 80% of the turtles nesting here came ashore in the area of the embankment.

Typically, nesting <u>G. nigrinoda</u> traveled farther to the nest ($X=59.6\pm15.9$ m) than away from it ($X=43.3\pm8.20$ m). Distance in was significantly greater than AD ($t=4.80^*$, $P<0.05$) or DO ($t=3.84^*$, $P<0.05$). Distance out however, was similar to AD ($t=1.94$ NS, $P>0.05$). To further clarify distances relationships between DI and DO, each of these distances were lineally regressed with AD, and their resulting slopes compared. The slope of the regression line was almost twice as steep for DI ($Y=-15.2+1.98X$) as for DO ($Y=2.9+1.06X$) and their slopes differed significantly ($F=46.34^*$, $P<0.05$). Thus, turtles travel almost twice as far to reach the nest as to return to the water. To determine whether DI or DO increases exponentially as a function of AD, both DI and DO were quadratically regressed with AD, and their resulting curvatures compared. It was found that as AD increases, DI became proportionally larger to a slight but significant degree ($Y=9.47+0.746+0.0074X^2$, $t=5.11^*$, $P<0.05$) whereas DO was essentially similar to AD at all distances ($Y=1.21+1.153-0.0005X^2$, $t=0.95$ NS, $P>0.05$). Infact, 25% of the DO tracks were the same distance as AD.

An extreme case exemplifying the above pheromenon occurred 18 July 1980. After stranding on the north side of the island, an individual crawled 445 m inland before constructing her nest. When nesting was completed she traveled 208 m north and re-entered the river only a few meters west of where she had originally emerged. The AD was 193 m.

In all 28 instances, nesting females returned to the same beach they entered from. Appearently, *G. nigrinoda* females have the ability to orient successfully not only when the shore line is visible, but also where it is obscured by topographic features. By what method these individuals are able to orient is not known. Moll and Legler (1971) found that nesting *P. scripta* also had orienting ability but that this ability was lost after two weeks in captivity or if vision was impared by blindfolding. Both memory (of the incoming path?) and vision may be important, but how an individual determines direction from the bottom of a dune trough, as was often the case on Gravine Island, is not known.

Nests were constructed anywhere from 4.3 m to 193 m from shore. Sixty-one percent were within 35 m of shore, or less. One clutch of hatchlings was discovered approximately 1.5 m from and 1 m above the water level, but was located outside the main nesting area. Shealy (1976) reported that *G. pulchra* rarely travels far inland to nest. The great distances sometimes traveled by female *G. nigrinoda* may simply be a reflection of the large nesting area available.

From the above analysis and observations, nesting females obviously expend more time and energy traveling from shore to where the nest is eventually excavated than from the nest back to shore. This perhaps suggests searching on the part of the female for proper nesting conditions. Observations similar to these were noted for *G. pulchra* (Shealy 1976).

Elevation Above Water

Of 29 nests examined, estimated height above mean water level averaged 4.2 m and varied anywhere from 0.2-9.0 m. No preference for any particular elevation was evident. In most cases, elevation of the nest seemed to be a function of how far inland an individual nested. In no instance was a clutch deposited at or below the mean summer water level as was observed in *G. ouachitensis* or *G. pseudogeographica* by Vogt (1980) or in *P. alabamensis* as observed by the author on several occasions.

Nest Type

Five types of nest-sites were recognized on the main nesting beach (Table 3). The most common site chosen was open, flat ground devoid of any vegetation or objects (Type A, Figs. 18, 19; and see also 31) and was represented in 30% of the 30 nests examined. Type B nest-site is identical to Type A, except that the ground surface sloped. This type included 20% of the nests. Thus, half of all nests examined were constructed in open, unvegetated areas. However, nests were more easily located in these situations (though not greatly so), therefore introducing a slight bias. Also, it

Table 3. Utilization of available nesting situations by G. n. deltícola on Gravine Island, Tensaw River, Baldwin Co., Alabama.

Nest type	Description	No. (%) of nests
A	Open, flat, without associated vegetation.	9 (30%)
B	Open, sloped, without associated vegetation.	6 (20%)
C	On hillock grown to well spaced clumps of Panicum sp.	8 (26.6%)
D	Level ground grown to well spaced clumps of Panicum sp.	3 (10%)
E	Sloped ground grown to well spaced clumps of Panicum sp.	2 (6.7%)
F	Level ground densely grown to Eragrostis sp.	2 (6.7%)

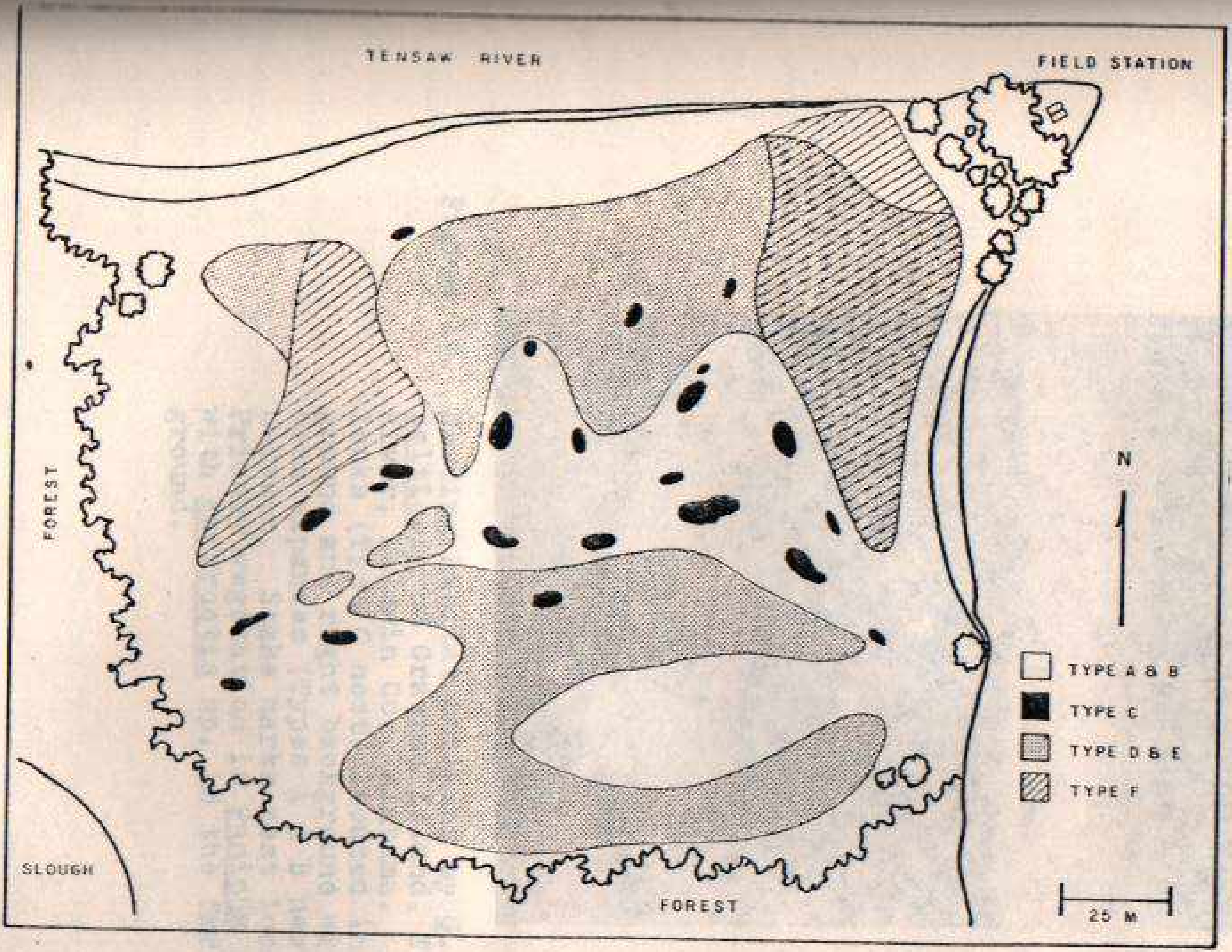


Figure 18. Map of the vegetation and substrate type zones of the main nesting beach located on the north end of Gravine Island. Primary vegetational components are: A&B, none; C-E, *Panicum* sp.; F, *Eragrostis* sp. Substrates I&II are associated with zones A-E; type III is found in hatched zones.

Figure 19. Nesting habitat utilized by G. n. delticola on Gravine Island, Tensaw River, Baldwin Co., Alabama. Hillocks (Type C nest) located in foreground and right background with open expances (Types A & B nests) between. Stake marks nest location. Primary vegetation is Panicum sp. with Eragrostis sp. in the far background.

was impossible to accurately estimate the total area of each nest-site type, due to complicated and extensive overlapping between types. As a result, many Type A and B nests were well within vegetated zones but were either greater than one meter from any vegetation itself or were obviously within an "island" of another type. Type C sites represented the second most utilized, accounting for 26% of the nests examined. These nests were located on top of small, vegetated hillocks which appear as islands rising abruptly from less densely vegetated or barren expanses (Figs. 18 and 19). These hillocks are created by the sand stablizing affect of rooted vegetation; in this case, Panicum sp. Female G. nigrinoda appear to be preferentially selecting this habitat over others. This is indicated not only by the relatively large number of clutches deposited in hillocks, but by an individuals nest-site searching behavior as well. Often a turtle seeking a nest-site will travel to one of these hillocks or similar vegetated rise, and after crawling all over it, will leave it for another some distance away which is similarly investigated. For example, on 18 June 1980 an individual, as determined by DI track analysis, examined two such hillocks before ultimately depositing her clutch in a third. That hillocks were preferred for nesting finds additional support in the fact that this type was the least abundant nesting situation available (Fig. 18). Although a few hillocks were larger, most were less than 10 m across.

Exactly why hillocks are preferred for nesting is problematical. Extrinsic abiotic factors such as substrate type, moisture content of the sand, temperature relations, and elevation are essentially identical or can be found in other situations elsewhere in the main nesting beach, as are their vegetational components (Fig. 3). One explanation is that there may be an inherent tendency to deposit eggs as high above the water line as possible. While generally there were areas higher, these hillocks offered the highest point in any immediate area.

Flat and sloped ground with short vegetation (types D and E) (excluding hillocks) were used 10.0% and 6.7% of the time, respectively. It is perhaps more illustrative to group all open nest sites (A and B) and all short grass nest-sites (D and E) together, because slope did not appear to be one of the more important parameters for nest-site selection in G. nigrinoda (slopes of various inclinations and directions were utilized with about the same frequency). If Type C is also included, as seems appropriate considering that except for smaller area this nest type situation is identical to the other two short grass types, the black-knobbed sawback nests in open and short grass situations with about equal frequency: 50.0% and 43.3%, respectively. As Figure 18 illustrates, both situations were approximately equal in abundance. Nest-sites, excluding hillocks, appear to be chosen at random with respect to the two major nesting situations available.

Other nesting situations were rarely encountered. One nest was discovered beneath a willow tree (*Salix* sp.). Shealy (1976) reported that *G. pulchra* oviposits in shaded situation regularly. Similarly, Anderson (1958) found that *G. oculifera* often nests adjacent to or within the forest canopy bordering sandbars. Another nest of *G. nigrinoda* was located in a dense stand of tall grass (*Eragrostis* sp.). Under these shaded conditions, incubation periods would undoubtedly lengthen, but it could not be determined exactly what effect shading has on the development of these clutches because both nests were ultimately destroyed by vandals.

Substrate Type

Three major substrate types were available to *G. nigrinoda* on Gravine Island for ovipositon. These three types are described in Table 4 in terms of relative availability, sand particle size, degree of homogeneity, and moisture content. Table 8 provides information on temperatures in each type. A general overview of how these substrate types are distributed on the main nesting beach is illustrated in Figure 18.

The substrate type most often chosen by nesting sawbacks was Type I, accounting for 83.3% of the 30 nests examined.

Table 4. Charactoristics of three substrate types utilized for nests by *G. n. delticola* on Gravine Island, Tensaw River, Baldwin Co., Alabama. Samples were taken from typical nesting situations.

Parameter	Type I	Type II	Type III
Approximate availability on Gravine	75.0%	20.0%	5.0%
General description	Homogeneous quartz. Little organic matter. No pebbles. On level or slope. May be grown to *Panicum* sp.	Heterogeneous quartz. Little organic matter. Pebbles. High ground and slopes. May be grown to *Panicum* sp.	Heterogeneous quartz. Highly organic. Pebbles. Low lying basins. May be grown to *Panicum* and/or *Eragrostis* sp.
Sand particle size. $\bar{X}$ ± SE (R) n = 25	0.48 ± 0.21 mm (0.22 - 1.26)	0.43 ± 0.28 mm (0.14 - 1.40)	0.42 ± 0.23 mm (0.05 - 0.86)
Pebble size*	--	5 - 15 mm	4 - 25 mm
Moisture** content	3.51%	4.03%	1.80%

* Values represent most abundant size range.

** Determined by weight using a double beam balance. All samples taken from 10-15 cm deep within five minutes of each other on 9 September 1980.

This substrate type represented approximately 75% of the total area available. This coincidence is unfortunate in that it tends to disguise the importance of Type I substrate as possibly optimal nesting medium. Few obstructions are found within this fine, homogeneous sand. It is easily worked, holds position well, and remains moist even under drought conditions.

Type II substrate was also utilized fairly extensively, accounting for 13.0% of the nests. While it has high moisture content, its heterogeneous composition causes it to be slightly more difficult to work.

Only 3.4% of the nests were located in Type III substrate. This type is relatively rare, representing only about 5.0% of the nesting beach, and was the most difficult type in which to locate nests. Regardless of this bias, I believe that Type III substrate was mostly avoided by G. nigrinoda females because it: 1) becomes hard when dry, making excavation difficult, 2) is heterogeneous in composition, containing large pebbles that might impede excavation, 3) has a relatively low moisture content which could result in egg desiccation, and 4) it is often shaded by dence vegetation, which could result in unusually long incubation periods.

It was also noticed that although Type III was usually encountered by nesting turtles first, it was often observed (via DI track analysis) that individuals would crawl completely through it and nest in Type I or II substrate.

Optimal Nesting Habitat

Optimal nesting habitat appears to be on beaches fairly high above the water line (2-4 m), in open, sunny situations that may be grown to well separated clumps of short grass, and within 50 m of shore. Nests are constructed in fine, clean, homogeneous quartz sand which becomes wind blown when dry but maintains a relatively high moisture content at 13 cm deep. More than 50% of the G. nigrinoda nests-sites examined on Gravine Island fit all of the above criteria.

It has been noticed by several observers that turtles often crawl over seemingly suitable nesting sites and eventually select a spot that appears identical to those passed (Pope 1934, Carr 1952, Shealy 1976). This was also observed in G. nigrinoda. Suitable and virtually identical nesting conditions are to be found within 5 meters of shore yet turtles often traveled 50 meters inland before ovipositing. As turtles move along the beach prior to nesting they often behave in a way which suggests that they are testing the substrate for nesting suitability. Yet just what they are testing for remains for the most part a mystery as those measurable parameters fail to turn up significant differences between the nest-site and areas passed. Perhaps, in addition to various cue receptors (vision, olfaction, tactle, thermo, etc.) there is a hormonal component involved which not only stimulates substrate testing behaviors, but actually operates as a positive feedback mechanism with these behaviors. Environmentally stimulated hormonal feedback mechanisms modifying reproductive behavior are known to occur in some birds (Lehrman 1961, Erickson 1970). With this in mind, the following hypothesis was postulated. Forced onto the nesting beach by hormonal changes resulting from follicular enlargement or ovulation, _G. n. delticola_ females begin to receive a series of repetitive stimuli which,as mediated by the hypothalamus, alter existing hormonal levels or composition and in turn elicits sand testing behavior. Possible stimuli might be anything in the immediate environment such as the appearence of the substrate, temperatures, odors, etc., or perhaps simply the act of crawling about on land, an activity performed in these thoroughly aquatic emydines only by females during nesting. Lehrman et al. (1961) found that nest construction in ringed doves (_Streptopelia risoria_) could, in part, be stimulated by the presence of nesting material. In _G. nigrinoda_, individual variation in hormonal levels or in response to them, would readily account for the tremendously large variation in nest distance relations and "wanderers", as well as explaining why suitable nesting habitat is passed up. The act of continual sand testing, then, in turn acts positively to enhance endocrine levels which increase nesting appetite until the urge to nest becomes so great that actual nest excavation begins. This supposition finds some support in the observation that test nesting (see below) generally becomes intensified near where the actual nest is ultimately constructed. Sometime during this period (again a result of positive feedback elicited in responce to cavity excavation) uteran contractions begin and cannot be reversed at will. This would explain why once a nest cavity is near completion female turtles of many species will usually continue to nest even when being closely observed (Ehrenfeld 1979).

Nesting Behavior

The following description of nesting behavior results from the observation of 16 partial and 1 complete nesting sequences and from turtle track analysis. Nesting activity was divided into seven categories which are represented by distinctly different behaviors.

Offshore and Stranding Related Activity

Female *G. nigrinoda* begin congregating on the north side of Gravine Island (Fig. 17) from 30-50 m off shore about an hour before dark, and continue to move closer to the shore line as daylight receeds. When making a final approach to the beach, individuals move to within 10 m of shore, slowly swimming and constantly looking about. Of 4 turtles observed continuously during this period of activity, time spent "swimming and looking" ranged from 15-25 min. Any movement along shore will frighten incoming turtles into diving and swimming off. It is not known whether frightened turtles will return the same night, or whether they ultimately select another location for nesting. Disturbances in the water, such as mullet jumping, are seemingly ignored by the turtles.

On emergence from the water, turtles generally paused briefly before making a slow but deliberate ascent onto the beach which, depending on the location, may involve scaling the aforementioned embankment. Similar stranding behavior has been reported in nesting Trionyx sp. (Webb 1962), Clemmys guttata (Ernst 1970), and G. pulchra (Shealy 1976).

Because the embankment area provided better cover for observation, my observations during this period of activity include only those from the embankment area. In view of the fact that 80% of the black-knobbed sawbacks which nested on Gravine came ashore below the embankment, behavior displayed by turtles in this area can be considered typical for the population as a whole.

If the embankment cannot be scaled at the stranding point, individuals usually move along the base of the embankment until encountering a cleft, through which they could climb. If the embankment could not be scaled soon after stranding, turtles usually return to water. This was determined by both track analysis (in no instance was an individual observed to travel more than a few meters down the beach before either scaling the embankment or returning to the water) and through direct observation. On two occasions when turtles were observed to return to the water, they both did so seemingly in a panic as if frightened by something. The author had remained hidden and motionless in a pit at the embankment edge during this time, and no other disturbances were detected on the beach. On reaching the water, both individuals quickly submerged, swam out to about 15 m, and surfaced. Although it is impossible to proove that the same turtle which dove was the one observed to surface offshore, the direction taken by the individual on entering the water, the time/distance interval between entering and surfacing, as well as their similar appearance, leads me to believe that they were one and the same. In both cases the individual returned to shore and again stranded in 5 and 7 minutes, and then scaled the embankment on their second attempt.

During stranding and embankment scaling activity, turtles are exceptionally wary and will re-enter the water at the slightest onshore disturbance.

Pre-nesting Activity

On reaching the top of the embankment, turtles begin a more or less random search for a nest-site. While doing this, they display several pre-nesting behaviors as they make their way over the sand.

Test Scratch and Sniff. Shortly after reaching seemingly suitable habitat, a turtle tests the the substrate by extending its tilted head downward, in some cases actually contacting the subsbrate, as if seeking olfactory cues. Simultaneous with this maneuver, but generally preceding it slightly in initiation, an individual makes alternating sweeping motions with its front feet, beginning at mid-center and proceeding in a backwards arc, creating depressions in the sand with its claws 1 cm deep and 5-7 cm in length (Fig. 20).

Although sand-sniffing behavior has been reported in several species of sea turtles (Hendrickson 1958, Carr and Ogren 1959, 1960, Bustard 1973, Stoneburner and Richardson 1981) few freshwater turtles have been observed demonstrating this type of behavior. Shealy (1976) reported that

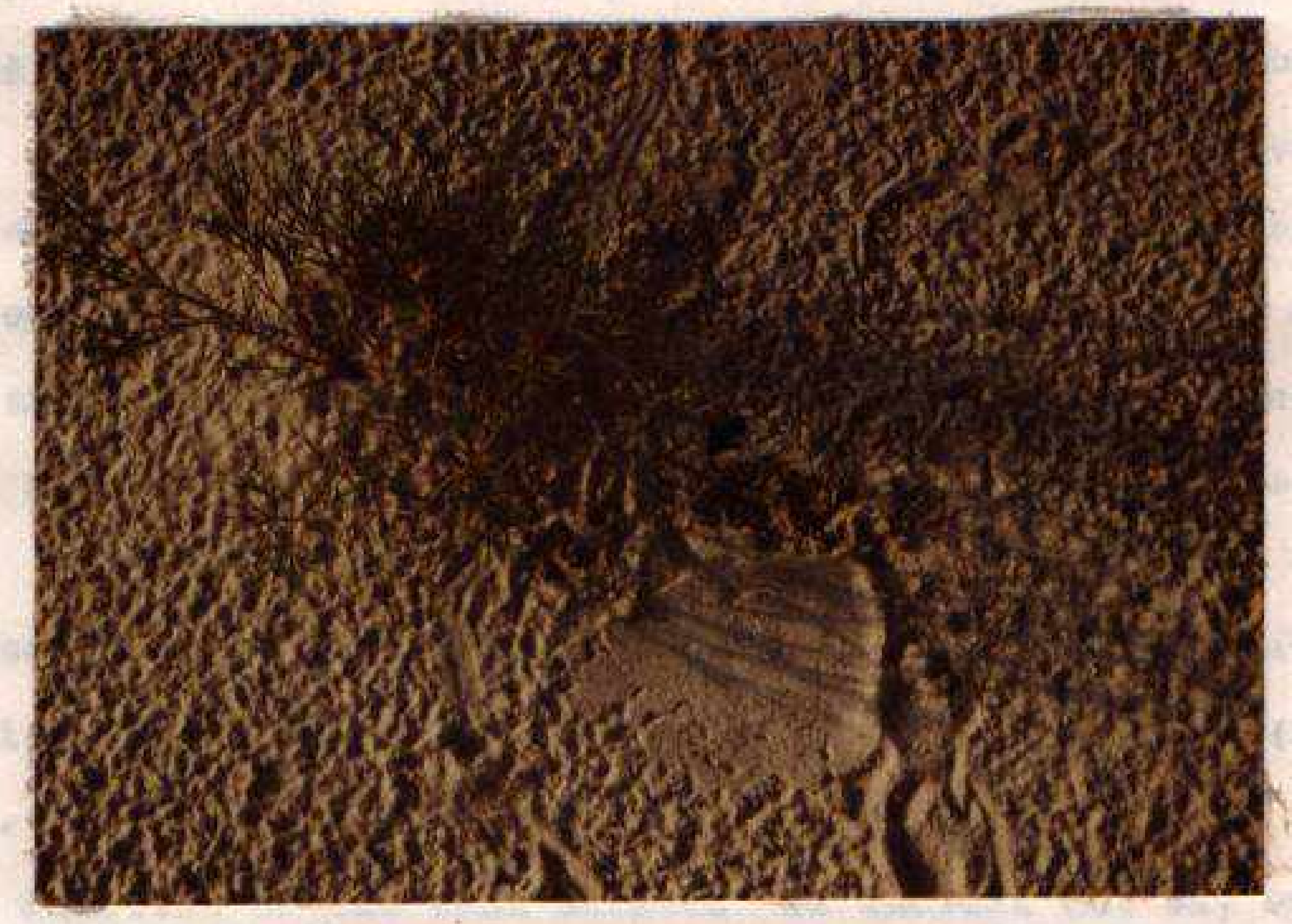


Figure 20. Test scratch (arrow) performed by <u>G. n. delticola</u> females during pre-nesting activity.

while searching for a nesting site, *G. pulchra* press their nose close to the substrate and test the sand by making sweeping motions with their front feet, cutting furrows 1-5 cm deep. Almost identical behavior was reported for *P. scripta* (Moll and Legler 1971) and *P. floridana* (Thomas 1972). Shealy (1976) and Thomas (1972), as well as the present author, observed that sand sniffing and scratching behavior was displayed only prior to nest construction, and never afterwards. Test scratch behavior was not discovered in *G. nigrinoda* until well into the nesting season (mid-July). It was, however, evident in virtually all of the subsequent nesting individuals as determined by scratch marks in the sand or sand covering a turtles carapace (see below).

The function of the test scratch is unclear but may enable the detection of specific cues required to determine the suitablility of nesting habitat, and/or as hypothesized above, functions to increase the stimulus needed to continue a feedback mechanism mediated through the endocrine system, which ultimately leads to nest construction. In any case, at least one benefit derived from test scratching behavior is certain. As turtles make sweeping motions with their front limbs, dry sand is tossed onto the carapace and in most instances, covers it completely (Fig. 21). This sand layer covering the carapace might serve to camouflage the

Figure 21. Graptemys n. delticola female in the process of nesting. Note the presence of sand on head and carapace.

turtle, allowing individuals to better escape the notice of potential predators. Black turtles moving across white sand are conspicuous even at night, whereas sand covered individuals are much less easily detected.

The number of test scratches performed by an individual varies and is generally proportional to the overall distance traveled. In addition, test scratching appeared to be performed just prior to another testing behavior, the construction of a test nest. For example, on 17 July 1980 a *G. nigrinoda* female traveled 666 m before depositing her clutch. Eight test scratches were discovered placed along the DI tract at 247.8, 330.4, 337.0, 339.9, 340.6, 352.3, 366.9, and 370.6 m, respectively. The only test nest discovered occurred at 377.9 m. Because test scratches, depending on the quality of the substrate, are sometimes difficult to detect, additional test scratches undoubtedly occurred along many of the DI tracks examined.

Test Nest. Test nests (test digs, test holes, etc.) have been reported for many emydines including *C. picta* (Cagle 1937), *T. ornata* (Legler 1960), *Clemmys guttata* (Ernst 1970), *P. scripta* (Moll and Legler 1971), *G. pulchra* (Shealy 1976), *G. pseudogeographica* and *G. o. ouachitensis* (Vogt 1980).

Test nests have been interpreted in a variety of ways, but have generally been assumed to represent a means by which turtles determine the suitability of the habitat. In some cases, when examined closely, abandoned nests have obstacles such as roots and stones at their bottoms (Cagle 1953, Moll and Legler 1971, Shealy 1976) or were constructed in unsuitable substrate (Vogt 1980). Vogt (1980) also believed that inclement weather caused female *G. pseudogeographica* and *G. o. ouachitensis* to abandon partially completed nests. More often than not, though, no habitat differences can be detected between test nest sites and those where the actual nest was constructed.

The test nest phenomenon was studied in *G. nigrinoda* to determine overall abundance, placement along the DI track, differences from the actual nest (if one was constructed) and overall physical appearance.

Of 32 DI tracks examined, 13 (40.6%) contained a total of 16 test nests. Thus, nearly half of the individuals nesting on the main beach dug test nests, and in cases where test nests were present, 14.3% dug more than one. A typical test nest along with the actual nest is illustrated in Figure 22.

The location of test nests along the DI track was analyzed in relation to their distance from the actual nest, relative to the overall DI distance. For example, if the DI track was 100 m in length, and the test nest was located 80

Figure 22. Test nest (left) and actual nest of G. n. deltịcola. Environmental conditions at each location are seemingly identical.

m from shore, its placement would be considered to be within 20% of the actual nest. This procedure was useful in determining where most test nests where constructed in relation to the site of oviposition.

Test nests may occur anywhere along the DI track but a slightly bimodal distribution is evident. Test nests were generally constructed either relatively early during an individuals wanderings (43.1% occured between 61%-80% of the nest distance) or near the actual nest (30.1% were within 20% of the nest). The remaining test nests were spread out at various distances along the DI track. It appears that G. nigrinoda females begin to test the habitat with test nests soon after they arrive at the beach and especially just prior to actually building the nest. The significance of this bimodal distribution of test nest placement is not certain, but that it may be an artifact of the limited data available cannot be ruled out.

In 87.5% of the cases, the environmental conditions at test nests appeared acceptable or virtually identical to those at the nest site. In some instances test nests were constructed in Type II substrate, whereas the eggs were deposited in Type I. However, the reverse was also observed, and both substrate types were used extensively for nesting. Likewise, some individuals abandoned potential nest-sites in Type A or B nesting situations and oviposited in types C, D, or E, and vise versa. Obstructions were found in two of the nests examined, which may have hindered construction. These include one test nest which was constructed under a canopy of river birch and contained roots, and another containing large pebbles constructed in Type III substrate.

Under certain conditions, a nesting turtle may leave a partially built nest. On 3 July 1980, for example, at 2115 h CDT an individual was found constructing a nest 25.5 m from the north shore of Gravine. I approached to within one meter, carrying a white gas lantern which illuminated the surrounding area quite well. On close approach, this female sawback ceased excavation and after a one minute pause, suddenly crawled away from the nest. Presumably, it was my presence, and/or the bright light, which frightened her into leaving. However, when she left the nest she moved off deliberately and slowly, unlike a frightened individual which generally withdraws into its shell, and then proceeded to encircle me, coming to within 12 cm. From this, it appears that this turtle was not so much disturbed by my presence as disoriented by the light. Bright lights have been observed to cause disorientation in _T. muticus_ (Anderson 1958) and _Caretta caretta_ (Mcfarlane 1962). After a moment's pause, she started crawling further inland and at 54.8 m from shore began to construct another nest, again in open sand. After a few minutes of excavation, she left this nest also and traveled another 32.9 m before constructing a complete nest and depositing her clutch. In terms of the environmental parameters considered, the two test nests were identical to the completed nest. Both the second test nest and the actual nest were excavated in my presence (though I remained about 2 m away until actual oviposition began).

When approached closely during any phase of pre-nesting activity, *G. nigrinoda* females will usually cease movement and withdraw into the shell. After a few minutes, however, normal activity resumes if a 2-3 m distance is maintained between turtle and observer. The minimum "flight" distance during pre-nesting activity appears to be approximately 1-2 m for most individuals. At 3-4 m turtles move about seemingly unafraid, though obviously aware of an observer, displaying the various pre-nesting behaviors described above.

Test Nest Appearance. Except for test nest #1 of the example provided above, test nests were shallow, generally no more than mere depressions in the sand 3-5 cm deep. While a few were obviously excavated with use of the hind limbs, most (81.0%) appeared to have been "hollowed out" by pushing the sand with the shell or by sweeping motions with the front limbs.

Time spent in pre-nesting activity (wandering, pauses, test scratch and test nest construction) is of course proportional to the distance the nest is from shore and thus may require anywhere from a few minutes to an hour or more. An individual nesting at an AD of 30 m would require approximately 15-20 minutes to reach its destination.

Nest Excavation

When a proper nest-site is located, nesting activity is initiated almost immediately, but before actual excavation can begin, an individual must achieve the correct body orientation with respect to the ground surface. This posture is one in which the anterior of the shell is tilted upwards 15-30 degrees from horizontal, and is accomplished in two very different ways. Often, some irregularity of the ground surface such as a grass clump or bump in the sand (Fig. 23) is utilized. Apparently, as indicated by a photograph, Chelydra serpentina may also utilze natural irregularities on the ground surface (Hammer 1971). But if these topographic situations are not available, proper positioning can be achieved by "bulldozing" (Fig. 24). Bulldozing behavior was first observed on 3 July 1980 and while directly observed only in a few instances, its usage can easily be inferred from the general shape and appearence of most of the test nests examined, and from the appearence of

Figure 23. Nest of G. n. delticola on the morning after construction. Note small rise in the sand utilized to achieve proper orientation for nest excavation.

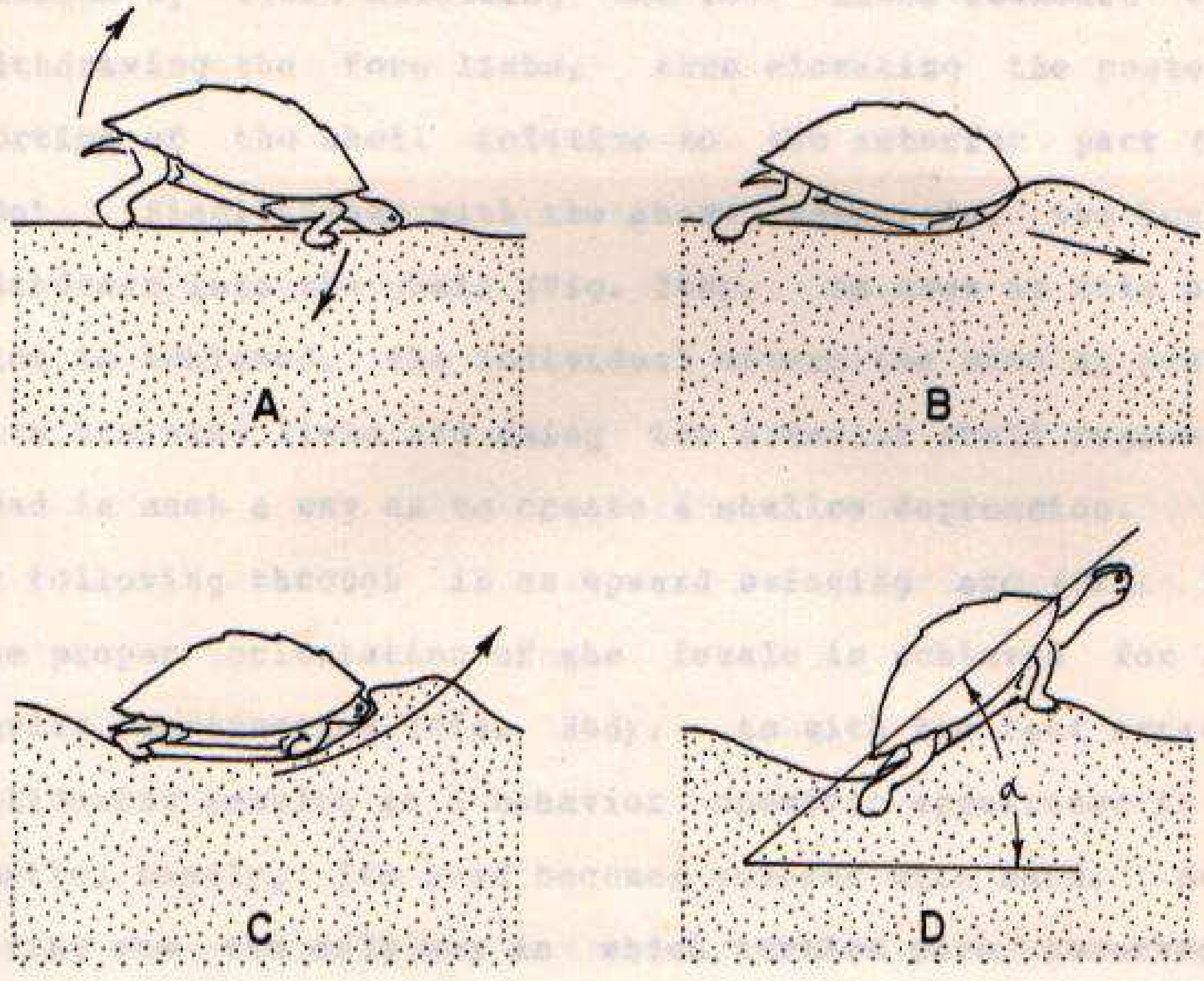


Figure 24. "Bulldozing behavior" in *G. n. delticola*. This behavior, performed during prenesting activity, results in the attainment of proper orientation for nest excavation. The sequence of events are as follows: A, rear limbs are extended, forelimbs and head are withdrawn; B, "dives" into the sand pushing with rear limbs; C, forces mound ahead and begins to arc upward until; D, proper position for nest excavation is attained. α may be from 15-30°.

the nesting turtle itself (see below). Bulldozing is accomplished by first extending the rear limbs downward while withdrawing the fore limbs, thus elevating the posterior portion of the shell relative to the anterior part (Fig. 24a). Simultaneous with the above movements, the head is withdrawn into the shell (Fig. 24b). As soon as this position is achieved, the individual enters the sand by pushing with its hind limbs and using the anterior shell region and head in such a way as to create a shallow depression. Then by following through in an upward swinging arc (Fig. 24c) the proper orientation of the female is achieved for nest cavity construction (Fig. 24d). As with the test scratch, bulldozing results in a behavior specific appearence in the turtle, namely, its head becomes covered with sand. Bulldozing was the only way in which turtles were observed to cause their heads to be covered with sand, and can easily be recognized in nesting females (Fig. 21; page 77).

Black-knobbed sawbacks were not observed to assume a specific position in relation to the water as noted in some nesting emydines (Ernst 1970, Moll and Legler 1971).

After achieving the proper nesting position, female turtles begin to excavate almost immediately. This is accomplished with alternating scrapes with the hind limbs while pivoting the body from side to side as each limb is inserted into the cavity. During all phases of nest construction, the three feet left outside the cavity are used to support the turtle as she moves the fourth. As the nest deepens, each scrape is accompanied by characteristic twisting motions of the limb which results in the production of a globular or flask-shaped cavity (Fig. 25). Additionally, as maximum depth is approached, which appears to be determined by an individual's limb length, each scoop of sand brought to the surface is accompanied by shaking or jerking movements of the limb. Resting during this phase of nesting is frequent, generally after every 2-4 "footfuls" of sand (one individual rested with every footful), and lasts about 10 seconds. When excavation is proceeding at a regular pace, a female will bring up a scoop full of sand every 4-6 seconds. Total time spent excavating the nest cavity varied from 16 to 34 minutes (X=23.0±1.94 min.) in nine instances for which the entire process was observed. Dimentions of six nests are provided in Table 5.

Oviposition. As soon as the cavity is complete, oviposition begins. Eggs are released at intervals of an egg every 1-2 minutes. Simultaneous with egg release, turtles invariably nod or draw their heads in slightly and raise their hind legs. Vogt (1980) observed this behavior in ovipositing *G. pseudogeographica* and *G. ouachitensis* females. The hind limbs remain outside the nest until an egg is released,

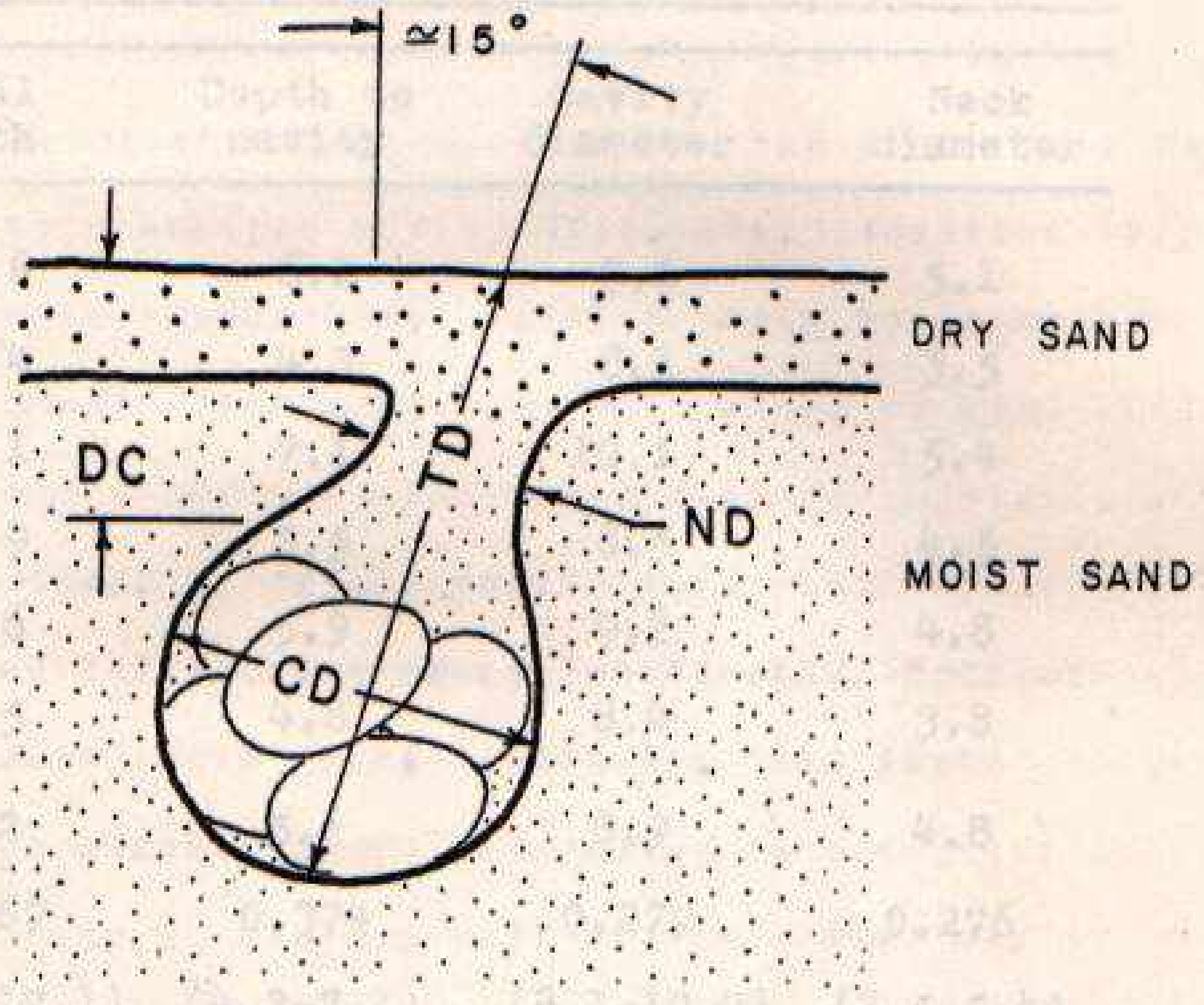


Figure 25. Nest of G. n. delticola, crossection. Nesting female would be facing to the right. Abbreviations are as follows: TD, total depth; CD, cavity diameter; DC, depth to cavity; ND, neck diameter. Nest dimensions are provided in Table 5.

Table 5. Dimensions of six *G. n. delticola* nests from Gravine Island, Tensaw River, Baldwin Co., Alabama.

No.	Total depth	Depth to cavity	Cavity diameter	Neck diameter
1.	15.8	6.2	9.6	5.1
2.	13.4	4.3	8.1	3.5
3.	17.1	7.1	10.1	5.4
4.	14.9	5.5	8.5	4.5
5.	15.6	5.9	9.2	4.8
6.	14.5	4.8	8.4	3.8
Mean	15.2	5.6	8.9	4.8
SE	0.467	0.374	0.279	0.276
Range	(13.4-17.1)	(4.3-7.1)	(8.1-10.0)	(3.5-5.4)

after which one limb (alternating with each new egg) is inserted into the nest cavity and moved about in a way that suggests egg positioning. Positioning eggs within the nest cavity by the nesting female turtles has been previously reported in _P. scripta_ (Moll and Legler 1971) and in two _Graptemys_ species (Vogt 1980) but is not considered a regular part of nesting procedure in _G. pulchra_ (Shealy 1976). The time required for oviposition is related to clutch size, but generally lasts 8-10 minutes. Anytime between the onset of oviposition and completion of the nest, turtles can be approached quite closely (to within a few centimeters) without apparent disturbance.

Burial. Burial begins soon after the last egg is deposited and arranged in the nest. Nest burial is accomplished, as was excavation, with alternating sweeps of the hind limbs, drawing sand into the nest. Initially, moist sand close to the nest is scraped in and subsequently packed down with one or both hind limbs. Unlike the nests of _Pseudemys_ and _Chrysemys_ (Cagle 1937, Carr 1952, Moll and Legler 1971, Thomas 1972), no nest plug is constructed. Rather, as a result of the packing behavior, sand fills all available space within the nest cavity, completely surrounding each egg. As the nest begins to fill, turtles reach further and further out, eventually drawing dry sand onto the nest.

Each new scoop of sand is patted, "kneaded", and otherwise compacted with the use of the only the hind limbs.

Some variation in technique was detected in the seven complete nest burials observed, but for the most part, movements were stereotyped. Four of the turtles observed remained positioned directly over the nest during the burial process. Others moved off the nest slightly, and with quick sweeping motions of the forelimbs (similar to test scratch behavior) tossed dry sand over the nest, effectively concealing it. Individuals which displayed "sand-tossing" behavior created nests that appeared to be considerably better camouflaged than nests of individuals that did not perform this behavior. Burial time ranged from 15-25 minutes (X=20.0±1.21 min.). Total nesting time averaged about an hour. Several turtle species have been observed releasing bladder contents during nest construction, including *P. scripta* (Cagle 1950, Carr 1952, Moll and Legler 1971), *G. pseudogeographica* and *G. o. ouachitensis* (Vogt 1980), *C. serpentina* (Hammer 1971), and *Gopherus agassizi* (Lee 1963, Nichols 1953, Patterson 1971). Patterson (1971) also provided evidence that in *G. agassizi*, urination on nests aids the female in excavation, repels preditors, and disguises the nest-site. Urination on nests was not observed as a regular behavior in nesting *G. nigrinoda*. On one occasion, however, drops of liquid (urine ?) were discovered along the no track in diminishing amounts as one traveled from the nest. As this situation was observed only once, it may have resulted from the accidental release of the bladder contents and probably served no useful purpose.

Post-nesting Activity

Except for one individual which was observed to circle the nest, most females return directly to the water after completing the nest. And while circling the nest after its completion has been reported in other species of _Graptemys_ (Cahn 1937), it is not believed to represent a regular part of post-nesting behavior in _G. nigrinoda_.

In most instances, nesting individuals were allowed to complete nesting and return towards shore on their own accord and were then intercepted a few meters from the water's edge. Two previously marked individuals were allowed to enter the water without being approached too closely. Both turtles appeared to realize that they were nearing the shore in that, when about 5 m from the water's edge, they quickened their pace considerably and virtually scrambled into the river. Upon entering the water, they immediately submerged and swam out of sight.

If turtles are approached closely while they are moving back to shore, they respond similarly to that of turtles well ashore and undergoing pre-nesting activity. While it is necessary for turtles which come ashore in the area of the embankment to find a cleft cut through the sand in order to gain access to the nesting area, turtles moving towards shore from the nest are not so restricted and often clamber over the steepest and highest part of the embankment.

The total time required to nest, including pre- and post-nesting activity depends on the actual distance the nest is from shore. Nesting G. nigrinoda may spend anywhere from one to three hours on shore before returning to the river.

Eggs

Eggs of G. nigrinoda were collected from freshly deposited natural nests less than 8 hrs old, and obtained from the oviducts of autopsied individuals. Freshly laid eggs are turgid, translucent pink in color, and elliptical in shape. The shell is flexible, and when indented with the fingernail, resumes its original conformity. Shell surfaces are fairly smooth due to the presence of only small sphaerulites (Young 1950). In these respects, G. nigrinoda eggs are similar to the eggs of other emydines (Legler 1960, Ernst 1970, Moll and Legler 1971, Thomas 1972, Shealy 1976, Vogt 1980). The average dimensions of 42 eggs are 37.03±0.326 mm long and 23.78±0.169 mm wide.

No correlation between clutch size and egg size, or between body size and clutch size, were evident in the sample (Table 6).

Incubation

Incubation periods and ontogenetic changes in *G. nigrinoda* eggs were determined through the observation of undisturbed natural nests, artificial nests, and one glass enclosed nest. Due to heavy predation by fish crows and human interferences only five natural nests were monitered from laying to hatching. Several late clutches were exhumed immediately upon deposition and removed to artificial nests located at the field station. Both natural and artifical nests were examined at irregular intervals during the first 50 days of incubation. After this time, nests were checked daily and all changes noted. To observe more closely changes leading up to hatching, as well as hatching and post-hatching activity, one clutch was buried in moist Type I sand in a 1 gal. aquarium and arranged so that the eggs could be viewed through the glass. This clutch of eggs was removed from a natural nest deposited on 5 August 1980 and reburied in an artificial nest. On 27 September 1980 the clutch was exhumed again and transported in sand to the laboratory at Auburn University. Upon arrival, the eggs

Table 6. Dimensions of 42 *G. n. delticola* eggs collected oviducally "*" and from fresh nests on Gravine Island, Tensaw River, Baldwin Co., Alabama.

Clutch no.	Deposition date	Clutch size	Length $\overline{X}$ ± SE (R)	Width $\overline{X}$ ± SE (R)
1.	17 June 1980	5	36.75 ± 1.090 (32.85 - 39.50)	23.74 ± 0.290 (22.81 - 24.60)
2.	18 June 1980	3	36.27 ± 0.917 (34.50 - 38.35)	23.48 ± 0.520 (22.60 - 24.70)
3.	18 June 1980	6	36.36 ± 0.639 (33.65 - 38.70)	23.57 ± 0.215 (22.70 - 24.25)
4.	20 June 1980	7*	37.52 ± 0.360 (36.10 - 38.50)	25.26 ± 0.137 (25.20 - 26.00)
5.	16 July 1980	7	38.41 ± 0.568 (35.70 - 40.35)	23.99 ± 0.300 (22.50 - 24.85)
6.	29 July 1980	5	37.90 ± 1.290 (33.75 - 41.75)	23.04 ± 0.657 (20.90 - 24.60)
7.	5 Aug. 1979	5	36.07 ± 0.992 (32.85 - 39.33)	23.47 ± 0.297 (22.59 - 24.20)
8.	5 Aug. 1980	6	36.71 ± 0.857 (33.85 - 39.97)	23.25 ± 0.280 (22.05 - 24.05)
8	Totals	42	37.03 ± 0.326 (32.85 - 41.75)	23.78 ± 0.169 (20.90 - 26.00)

were placed in the glass container. At no time were the eggs rotated or subjected to lethal temperatures or desiccating conditions. The transport of turtle eggs by this method does not appear to harm them (Ewert 1979).

In the following discussions, definitions for hatching, emergence from the egg, and emergence from the nest are those of Ewert (1979). Because eggs within a single clutch did not always hatch on the same day, a minimum and maximum period of incubation was recorded. Though the reason for nonsynchronous hatching may be intuitive, a short explanation is provided. Since soil temperature is inversely proportional to depth, those eggs nearest the surface will be subjected to more variable and higher incubation temperatures (Ewert 1979). Although Cagle (1950) and Cunningham (1939) observed no temperature-related differences in the incubation period of P. scripta and Malaclemys terrapin eggs, most workers, as summerized by Ewert (1979), have found that an increase in incubation temperature leads to a decrease in in developmental time. Because developmental rate and incubation temperature are inversly related, those eggs deposited nearest the surface will develop more quickly and consequently, will hatch before lower nestmates. Burger (1976) found this to be also true in M. terrapin.

For 9 clutches (47 eggs) the average min-max incubation periods were 62.89±0.67-64.75±1.24 (Range=60-68) days in length (Table 7). Approximately half (44.5%) hatched in two consecutive days. These incubations periods are within the range reported by Vogt (1980) for natural nests of G. o. ouachitensis and G. pseudogeographica (60-65 days), but slightly shorter than the natural incubation periods 76-82 days reported by Ewert (1979) for eggs of the latter species. Other average artificial incubation periods for Graptemys eggs provided by Ewert (1979) include G. barbouri (57.5 days), G. geographica (57.0 days), and G. oculifera (62.8 days) at 29.5-30.0°C. Shealy (1976) found that when incubated at an average temperature of 29°C, G. pulchra eggs in artificial nests hatched in 74-79 days. This incubation period is considerably longer than the 60-68 day range reported here for eggs of the black-knobbed sawback when incubated at similar average temperatures (Table 8). While mean incubation temperatures are similar, the fact that Shealy's nests were shaded half the day may account for their longer period of incubation.

To determine natural incubation temperatures, three measurements (ambient, sand surface, and nest cavity) were recorded hourly as previously described, for one 24 hour period in three different nesting situations (one each in AI, CII, and FIII; Table 8). Open areas were found to be similar to hillocks in their temperature profiles. The nest located in a dense patch of tall grass (Eragrostis sp.) was

Table 7. Incubation periods and emergence times for 51 G. n. deltícola eggs and hatchlings. "*" indicates natural nest; "**" indicates artificial nest. Nest #9 (5 Aug.) was incubated in a glass observation box at room temperature (ca. 25° C) from 27 September to emergence. All data from 1980.

No.	Deposition date	Hatching date(s) (no. hatched)	Incubation period (days)	Emergence date(s) (no. emerged)	Hatch-Emerge interval (days)	Clutch size	No. hatchlings
1.	18 June**	18 Aug.	62	26 Aug. (3) 27 Aug. (2)	8 - 9	6	5
2.	20 June*	21 Aug.	63	30 Aug. (3) 31 Aug. (1)	10 - 11	4	4
3.	3 July*	1 Sept. (4) 2 Sept. (1)	60 - 61	Removed from nest 7 Sept.	5 - 6	5	5
4.	4 July**	3 Sept.	61	12 Sept. (2) 13 Sept. (3)	9 - 10	6	5
5.	12 July*	17 Sept. (3) 18 Sept. (2)	67 - 68	Removed from nest 27 Sept.	9 - 10	5	5
6.	16 July*	18 Sept. (4) 19 Sept. (3)	64 - 65	29 Sept. (2) 30 Sept. (3) 31 Sept. (2)	11 - 13	7	7
7.	18 July*	20 Sept. (5) 21 Sept. (2)	64 - 65	Removed from nest 27 Sept.	7 - 8	7	7

Table 7. Continued.

No.	Deposition date	Hatching date(s) (no. hatched)	Incubation period (days)	Emergence date(s) (no. emerged)	Hatch-Emerge interval (days)	Clutch size	No. hatchlings
8.	29 July**	28 Sept.	61	7 Oct.(2) 8 Oct.(2)	10 - 11	5	4
9.	5 Aug.**	7 Oct.	64	19 Oct.(2) 20 Oct.(3)	12 - 13	6	5

Table 8. Temperature relations in three major nest-site situations on Gravine Island, Tensaw River, Baldwin Co., Alabama. Measurements were taken hourly for 24 hours from 13-14 August 1980.

Nest type*	Substrate** type		Temperature °C		
			Ambient	Surface	Nest
A	I	high	36.5	50.0	34.5
		low	24.2	25.0	27.0
		mean	27.9	30.6	29.5
		SE	0.95	1.78	0.53
		range	12.3	25.0	7.5
C	II	high	38.0	51.0	33.0
		low	24.0	25.0	27.0
		mean	28.5	31.5	29.2
		SE	1.01	1.88	0.39
		range	14.0	26.0	6.0
F	III	high	36.0	40.0	30.0
		low	24.0	25.0	27.0
		mean	27.5	28.7	27.9
		SE	0.91	1.13	0.18
		range	12.0	15.0	3.0

* See Table 3.
** See Table 4.

consistently cooler in all three measurements. This finding was expected because the ground surface in Type FIII situations is continually shaded. Unfortunately, only the AI nest was followed through hatching because the other two were destroyed by vandals. This clutch hatched after 64-65 days incubation. From these temperature data, it can be determined that under most nesting situations (Types A-E) accounting for 92.7% of all G. nigrinoda nests found on Gravine, the average incubation temperature in midsummer (August) is approximately 30°C.

The minimum temperatures at which normal development occurs in C. picta eggs is around 21-22°C (Ernst, 1972, Mahmoud et al. 1973). No nest temperature below 25.5°C was recorded in a G. nigrinoda nest on Gravine Island in 1980.

Critical thermal maxima have been reported for eggs of several turtle species. Moll and Legler (1971) found that neotropical P. scripta eggs would fail to develop if subjected to temperatures of 35°C early during incubation. Vogt (1980) indicated that 29% of the G. pseudogeographica and G. o. ouachitensis eggs maintained at 35°C produced hatchlings with scute anomalies. Possibly lethal temperatures were recorded in G. nigrinoda nests, but were temporary, occuring for no more than a few hours. Cunningham (1939) found that M. terrapin eggs could survive short exposures to 46°C but were killed by constant temperatures above 35°C. Brief exposures of 39.2-40.0°C did not harm *C. p. belli* eggs (Ewert 1979).

Within 24 hours after oviposition, an opaque, chalk-white spot develops on the upper most part of the egg shell (Fig. 26). This patch corresponds to and is probably associated with the attachment of the embryonic disk and adjacent vitelline membrane to the inner shell membrane as the yolk sac settles to the bottom of the egg (Ewert 1979). The embryo, now at gastrula stage, assumes an upright position atop the yolk sac. As the vitilline sac expands over the next few weeks, the opaque patch spreads laterally down over the eggshell until after one month it has extended two-thirds to three-quarters the way around (Fig. 27). Although some color change can be observed in the lower area of the shell (from pink to greyish purple), it remains translucent to within a few days of hatching. These ontogenetic changes are identical to those observed by Shealy (1976) in *G. pulchra* eggs, but are in conflict to reports by Moll and Legler (1971) and Ewert (1979). Moll and legler (1971) reported that in laboratory incubated *P. scripta* eggs, the pink area may be maintained for longer periods of time if the shell is in contact with wet substrate (in this case, cotton) but became completely chalk-white within three weeks even where moist. Ewert (1979) found that the expansion of the vitilline sac (and concomittantly, the opaque area) slows on

Figure 26. Eggs of G. n. delticola after 24 hrs natural incubation. Note opaque circular patch on eggshell.

Figure 27. Eggs of G. n. delticola after 4 wks natural incubation. Note size, shape, and color changes.

reaching the lower part of the egg, but that ultimately the entire egg may become white.

Water Relations

As the eggshell changes color, its consistancy and texture also changes. Where the shell is opaque, it feels dry and leather-like, and when indented remains so for some time afterwards. The lower, translucent area of the shell remains essentially like the original texture, moist and supple. Although it appears certain that the bicolored and bitextured phenomenon observed in incubating turtle eggs results from specific internal changes, there may also be important environmental influences selecting for these traits. It seems plausible that this peculiar shell condition represents an adaptation to incubation in a potentially desiccating environment and provides a means for water conservation.

It is well known that under normal circumstances, parchment-type eggs absorb water and enlarge considerably during incubation (Cunningham and Hurwitz 1936, Cunningham and Huene 1938, Lynn and Von Brand 1945, Cagle 1950, Legler 1960, Shealy 1976, Vogt 1980). The eggs of P. scripta (Moll and Legler 1971) did not enlarge appreciably during incubation. These workers attributed this lack of water absorption to unatural incubation conditions. The eggs of G.

nigrinoda did enlarge and became more turgid within a few weeks incubation time. A clutch of six eggs deposited 5 August 1980 averaged 36.71±0.857 mm long and 23.25±0.280 mm wide when freshly laid. Upon removal from the nest on 27 September 1980 these eggs averaged 38.83±0.650 mm long and 26.26±0.344 mm wide. This represents and increase in length of 5.5% and in width of 11.47%, compared to an increase of 11.63% for length and 11.87% for width in incubating G. pulchra eggs (Shealy 1976).

As incubation progresses, most of the eggshell becomes opaque, dry, and relatively hard, a condition which would not be conducive to the exchange of water. As such, the opaque area may serve as a "cap" on the eggs water supply, preventing the loss of water through the top of the egg as moisture is drawn up via continual evaporation at the soil surface (Fig. 28). The lower part of the egg remains soft and moist, thus allowing water to be absorbed.

A water conserving mechanism such as this would be particularly useful during drought conditions. As the dry-sand zone descends, dehydrating conditions would contact the top of the egg first, but unless it progressed lower than three-fourths the way around, the egg would maintain its moisture integrity vīa continual absorption of water through the bottom. Often, on checking eggs for signs of hatching, just this sort of situation was found. Similarly, Cagle

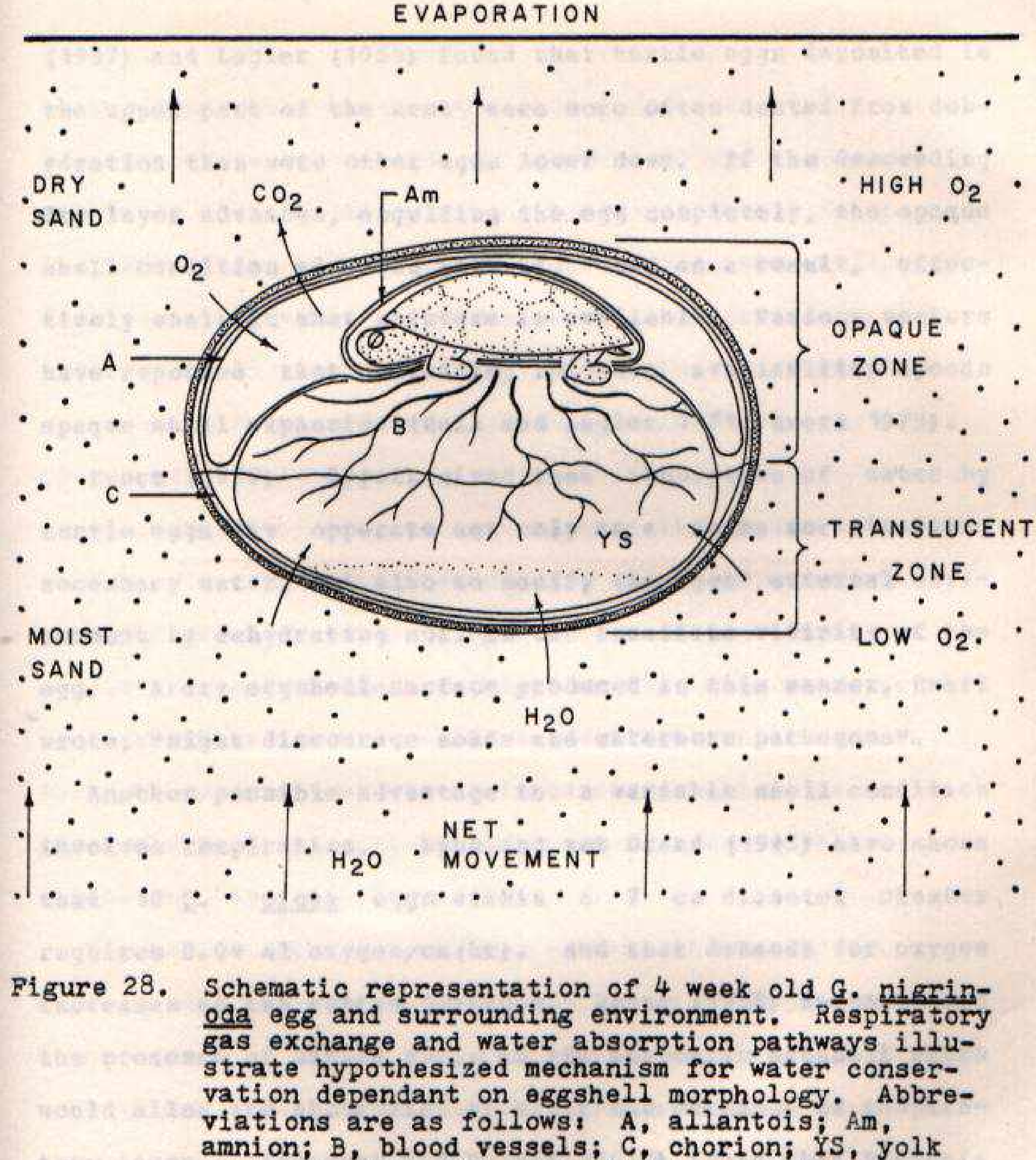


Figure 28. Schematic representation of 4 week old G. *nigrinoda* egg and surrounding environment. Respiratory gas exchange and water absorption pathways illustrate hypothesized mechanism for water conservation dependant on eggshell morphology. Abbreviations are as follows: A, allantois; Am, amnion; B, blood vessels; C, chorion; YS, yolk sac. See text for mechanism description.

(1937) and Legler (1954) found that turtle eggs deposited in the upper part of the nest were more often dented from dehydration than were other eggs lower down. If the descending dry layer advances, engulfing the egg completely, the opaque shell condition advances with it, and as a result, effectively seals in what moisture is available. Various workers have reported that decreasing moisture availability speeds opaque shell expansion (Moll and Legler 1971, Ewert 1979).

Ewert (1979) hypothesized that absorption of water by turtle eggs may opperate not only as a means for obtaining necessary water, but also to modify the eggs' external environment by dehydrating soil in the immediate vicinity of the egg. A dry eggshell surface produced in this manner, Ewert wrote, "might discourage molds and waterborn pathogens".

Another possible advantage to a variable shell condition involves respiration. Lynn and von Brand (1945) have shown that 10 C. picta eggs within a 7 cm diameter chamber requires 0.04 ml oxygen/cm(hr), and that demands for oxygen increases as the embryo develops. Young (1950) demonstrated the presence of minute pores in the chelonian eggshell which would allow the absorption of water and exchange of respiratory gases. Ackerman and Prange (1972) found that Chelonia mydas eggs were twice as permeable to oxygen as were chicken eggs, and believed that respiratory gas exchange occured through passive diffusion across shell surfaces (Prange and

Ackerman 1974). Although no direct evidence exists, it seems plausible that most of this passive diffusion of respiratory gases would occur in the dry, opaque region of the eggshell. Within this area eggshell pores would be open and thus allow for a more rapid exchange of oxygen and carbon dioxide. This notion appears even more likely in view of the fact that "most, if not all of the vascularized area lies beneath the portion of the shell that has become chalk-white" (Ewert 1979), and therefore provides the most direct avenue for rapid gas transport to and from the embryo. Early during incubation, vitelline circulation is important in gas exchange but as the embryo develops, the allanotoic circulation provides the major avenue for the exchange of respiratory gasses (Ewert 1979). During the later stages of development, when oxygen demand is highest, these blood vessels represent the only means by which oxygen reaches the embryo.

The lower, translucent area of the shell, by virtue of being continually moist, would not allow rapid gase exchange because pores in this region would be occluded with water molecules (or worse yet, by the net inward transet of water molecules). A bitextured eggshell may represent a refined system whereby both gaseous exchange and water conservation are optimized. If the entire eggshell became opaque early during incubation, respiration would be uninhibited, but there might not be enough internal water present to complete embryonic development. On the other hand, if the eggshell remained translucent, sufficient water would be absorbed but with a concomitant decrease in respiratory ability that might become limiting during late development. The turtle egg seems to have struck a fine balance, allowing both processes to occur at levels sufficient to support the embryo through all phases of development.

In association with water conservation, it seem logical that some tolerance to desiccation would also be present. Little quantitative information is available concerning the ability of turtle eggs to tolerate dehydration. Lynn and Ullrich (1950) examined the affect of dehydration as it relates to the production of morphological abnormalities in turtle embryos. Anecdotal observations on the condition of parchment-type turtle eggs in natural nests have been reported in _P. scripta_ (Cagle 1937), _C. picta_ (Legler 1954, Gemmell 1970).

The following experiment was undertaken to determine, in a general way, the ability of _G. nigrinoda_ eggs to tolerate the loss of water. A clutch of 6 eggs deposited 18 June 1980 was placed in a 1 gal. plastic container provided with moist Type I sand. The uncovered container was placed beneath the canopy of a willow tree and left alone. The only additional moisture the eggs received was in the form of occassional precipitation. Between rains the sand in the container became completely dry, as it was on 28 August 1980, when the eggs were exhumed for examination. Incubation temperatures were not recorded but were very likely close to ambient (Table 8; page 101). On inspection, the upper portion of each egg (roughly corresponding to the original opaque area) remained round and otherwise normal appearing, but the lower part (corresponding to the original translucent area but now also opaque) had collapsed inward creating a concave fold.

When first deposited these eggs weighed on the average 15.38±0.328 gm (Range=13.95-16.55). When removed from the container, their average weight had decreased to 8.32±0.086 gm (Range=8.0-8.6). One egg (not included in the above calculations) was appearently infertile, as unlike the other five, it was completely collapsed. On opening this egg, no signs of embryonic development were found. Two of the remaining five eggs were also opened. Both contained seemingly normal, live embryos approximately half way developed. These eggs then, survived an average water loss of almost half (45.9%) of their original weight. Developmental time, however, was substantially affected. As stated earlier, the natural incubation period for G. nigrinoda eggs on Gravine Island averages 62 days, yet these embryos were 72 days old. These findings are in agreement with those of Lynn and Ullrich (1950), who found that the dehydration of *C. picta* and *P. scripta* eggs caused a delay in hatching. Likewise, Muller (1921) believed that too little water retards the development of *T. muticus* embryos. The reason why embryonic development proceeds slowly in desiccated eggs may be related to protein metabolism. Whereas the yolks of avian eggs contain mostly lipid (63.5%) as a developmental energy source (Needham 1963), turtle eggs possess primarily (77%) proteins (Ewert 1979). The metabolism of lipids produce more water as by-product than does the combustion of proteins (Needham 1963). In order to make up the difference, turtle eggs must utilize external water sources. They do this, as has often been observed, by absorbing water directly from the environment. When surplus water is not available, the combustion of yolk proteins (and concomitantly, embryonic differentiation and growth) may be curtailed or even arrested (Ewert 1979). This may have been the case in the *G. nigrinoda* eggs described above.

The three remaining whole eggs (presumably also alive) were placed in an artificial nest and allowed to develop further. Whether or not these eggs would have resumed normal development and hatched is not known as they were subsequently discovered and removed by an unknown predator.

Egg Mortality

Many unrelated factors have been reported to cause mortality in turtle eggs. These include grasses or roots piercing or encasing them (Hodens and Pearson 1943, Turkowski 1972), weather related phenomena such as dehydration (Cagle 1937, Vestijens 1969, Gemmell 1970), drowning (Ragotskie 1969, Roze 1964), and low nest temperatures (Risley 1937, Breckenridge 1960). Although the greatest cause of egg mortality is obviously predation (see page 231), many eggs fail to develop or die at some stage of development. Of 51 eggs incubated, 47 (92.15%) hatched. Of the 4 which did not hatch, 2 did not develop and 2 died during development. Similar success rates were found in *G. pseudogeographica* and *G. o. ouachitensis* in which 95% of the eggs in 285 natural nests hatched succesfully (Vogt 1980). Of the 64 *G. pulchra* eggs incubated by Shealy (1976) in artificial nests, 55 (85.9%) hatched. It must be noted though that in this case, 8 of the 9 eggs which failed to develop represented a single clutch.

Graptemys nigrinoda was never observed to deposit eggs at or below the high tide water level. Therefore no data on the affect of nest inundation was secured. Egg survial following temporary inundation has been reported in *G. pulchra*: one week (Shealy 1976), *P. scripta*: 60 minutes (Moll and Legler 1971).

Several authors reported fungi associated with dead or infertile eggs (Legler 1954, Good and Russell 1968, Moll and Legler 1971, Shealy 1976). It was observed during the course of the present study that within the same clutch, dead eggs may be covered with mold while viable eggs remain unaffected. There are, however, a few reports of infertile or inviable eggs remaining in the nest appearently unmolested by decomposers for long periods of time, up to 75 and 100 days in *C. picta* and *C. serpentina*, respectively, (Ewert 1979). Perhaps some kind of antimicrobial substance similar to that found in *Testudo horsfieldi* eggs (Movchan 1964, 1966) was operating.

The affect of rotating turtle eggs on development of the embryo was not formally studied here, but generally has been considered detrimental. Ewert (1979) found that when 2-4 day old turtle eggs representing several species were gently turned, many survived, but some did not, presumably due to rotation. In two instances involving 11 eggs, previously undisturbed natural *G. nigrinoda* nests (one 2 days old and the other 15 days old) were dug up by unknown persons who, after inspection, returned the eggs to the nest. None of the eggs hatched in either nest, probably due to rotating.

Hatching

The process of hatching in turtles has been recorded in many species and the information available was summerized by Ewert (1979). However, with the exception of <u>Caretta caretta</u> (Caldwell et al. 1959), all observations were made in the lab while the egg rested on top of some medium.

The following description of the changes in the egg leading up to hatching, and of the hatching process, result from observations on the glass enclosed nest, and on artificial nests.

Several days prior to pipping, a sequence of predictable changes occur in the egg. The remaining translucent area of the shell becomes like the upper part, opaque and dry. Three to four days prior to hatching small droplets of water appear on the outer shell surface. Vogt (1980), observed the latter in <u>G. pseudogeographica</u> and <u>G. o. ouachitensis</u> and believed that these droplets result from condensation but offered no clue as to the mechanism involved. Ewert (1979) also reported that "beads of water appear on the shell" in both chelydrid and emydid eggs, and likewise, offers no explanation. It is the author's suggestion that the droplets of liquid represents fluid escaping from the egg in the following manner. The extra-embryonic membranes are torn (amnion) or parted and pushed posteriorly (allantois) prior to hatching (Agassiz 1857). Parting of the allantois occurs about two days prior to pipping in emydids (Ewert 1979) and therefore coincides with the occurrence of the droplets on the shell. In view of this it seems likely, as first hypothesized by Mount (1963) in _Eumeces egregius_ eggs, that extra-embryotic fluid escapes from the egg under pressure through the pores in the shell subsequent to rupture of the membranes.

Two lines of evidence support this conclusion. First, as Ewert (1979) also pointed out, the droplets of liquid are concentrated nearest the head and fore limbs of the embryo. This is as to be expected since the caruncle (Fig. 30) and claws of the forefeet are used for escape from the shell (Cahn 1937, Booth 1958, Caldwell et al. 1959, Legler 1960, Thomas 1972, Shealy 1976, Vogt 1980). Moll and Legler (1971) suggested that the primary function of the caruncle is not escape from the egg, but rather, to rupture extra-embryonic membranes. Both Thomas (1972) and Ewert (1979) noticed numerous scrapes on the inner shell surface, indicating that hatchlings make lacerations in these membranes before hatching succeeds. Additional lesions such as these would promote the loss of internal fluids. The second line of evidence stems ffom the observation that shortly following the occurrence of the external droplets, (1-2 days prior to hatching), the egg becomes somewhat flaccid, indicating loss of internal fluid.

Hatching begins with pipping of the shell. Pipping is usually accomplished with the aid of the caruncle and results in a small, jagged, longitudinal tear in the eggshell 2-3 mm long, and located just above the level of the hatchlings head (Fig. 29). Occasionally, a forelimb claw will be first to rupture the eggshell, creating a ragged tear 5-20 mm long and running ventro-laterally. Within a few hours additional tears are made by the head, or one or both front limbs. The original holes are enlarged with further struggling movements of the protruding head and limbs until they merge together, forming a single large opening, extremely ragged in appearence (Fig. 29).

If the egg is not buried, but rather rests on top of the incubation medium, the hatchling emerges from the shell almost as soon as the exit hole will accommodate it. If in the nest cavity, however, hatchlings remain within the eggshell fragments until the external yolk sac is retracted. Vogt (1980) reported that *G. pseudogeographica* and *G. o. ouachitensis* hatchlings remain in the shell from 3-6 days after hatching, the time required for yolk sac retraction. Time required for retraction of the yolk sack in *G. nigrinoda* is similarly variable and appears to be dependent on relative yolk sac' size at the time of hatching. Moll and Legler (1971) found this also to be the case in *P. scripta*. Moll and Legler (1971) beleived that unfolding of the

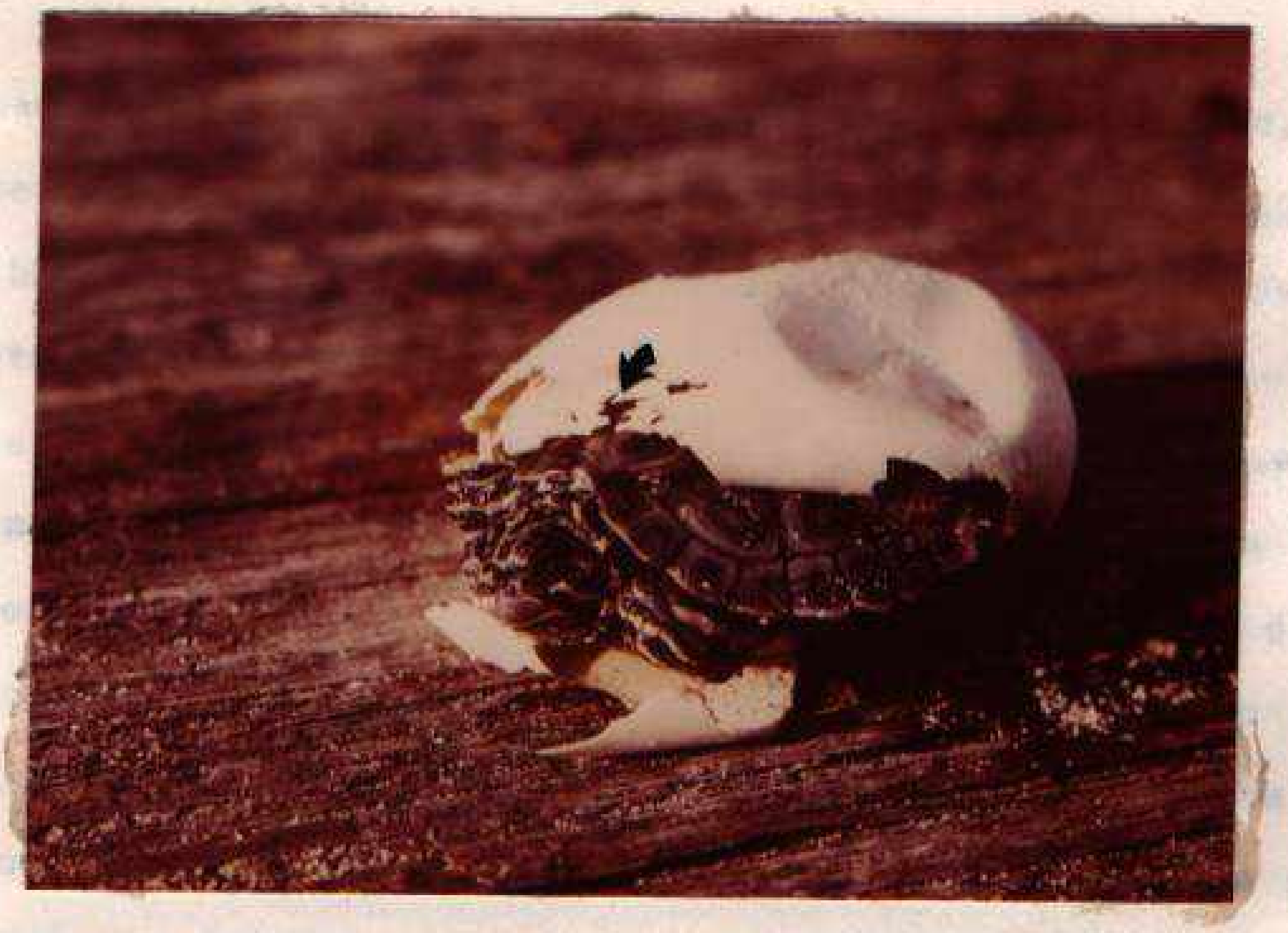


Figure 29. Hatching process in G. n. delticola. Arrow indicates point of initial rupture produced with the caruncle.

Figure 30. Hatchling G. n. delticola at 1 hr after emergence from the egg. Note external yolk sac and caruncle (arrow).

carapace after hatching aids retraction of the yolk sac, or the reverse. This might explain why an aberrant G. nigrinoda hatchling possessing gross skeletal deformities failed to retract its yolk sac after more than four weeks.

The yolk sacs of G. nigrinoda are yellow and are provided with numerous small blood vessels. In 25 hatchlings less than one hour old, yolk sacs measured from 15-21 mm in diameter ($\bar{X}=17.0\pm0.359$) and were generally retracted in 2-5 days. In no instance was a hatchling observed to leave the nest cavity (or eggshell for that matter) before the yolk sac was completely retracted. Umbilical scars measured approximately 3 mm in length.

The caruncle (Fig. 30), is retained after hatching from a few days to two months: 90% of 47 hatchlings lost it within 30 days. Vogt (1980) reported that G. pseudogeographica and G. o. ouachitensis lose their caruncles within three weeks. Shealy (1976) found that most G. pulchra hatchlings lost their caruncles within two weeks after hatching. Approximately 69% of the P. scripta hatchlings studied by Moll and Legler (1971) lost caruncles within 60 days. Under natural conditions, loss of the caruncle probably occurs much more quickly than in the lab since brushing against various objects within the environment (limbs, vegetation, etc.) would facilitate its removal.

The earliest date of hatching on Gravine Island in 1980 as predicted from emergence dates, was approximately 17 August in 1980. The final clutch of the 1980 season, deposited 5 August, began to hatch 7 October 1980. Since warm weather persists until at least the end of October, it seems unlikely that G. n. deltitcola hatchlings overwinter in the nest with any regularity, as reported to occur in P. scripta (Cagle 1944), C. picta (Hartweg 1946, Sexton 1957, Ernst 1971b), and Graptemys species (Newman 1906).

As mentioned previously, not all the eggs within a single clutch hatched on the same day. Consequently, within the same nest cavity one may find, around hatching time, a continuum within which all stages of hatching from unpipped eggs to individuals showing total yolk retraction.

Why hatching precedes yolk retraction is not specifically known. Lynn and Von Brand (1945) have shown that near-term embryos require as much oxygen as hatchlings. Thus, as Shealy (1976) suggested, "rupture of the shell and pulmonary respiration before yolk absorption is perhaps made necessary by a decreased allantoic capacity for adequate gas exchange." It may also be that hatchlings require a stored food supply to help them suvive the first few months of life and perhaps the first winter. As pointed out earlier, unfolding of the carapace is correlated and perhaps intimately associated with yolk sac retraction. The size restraints of egg dimensions would not allow unfolding of the carapace within the shell. Therefore, hatching probably precedes yolk sac retraction simply because there is not enough room within the egg for marginal scute unfolding.

Emergence from Nest

After yolk sac retraction, hatchling *G. nigrinoda* may spend a considerable time within the nest before they emerge. Emergence from the nest is not simultaneous but extends over two or three consecutive days (Table 7; page 99). From the time of hatching, turtles remain in the ground from 8-13 days (X=10.0±0.53-11.16±0.59, n=47). As a result, hatchlings of a single clutch may be found at various levels between the nest cavity and the surface. For example, on 3 September 1980, a nest deposited 3 July 1980 was examined and found to contain four hatchlings. One individual was still within the eggshell fragments while the other three were lying loose in the sand at various distances above the nest cavity. Yolk sacs were completely retracted and caruncles were present in all.

At about 0900 h on the same day a nest was discovered by back tracking one individual which had emerged. Three hatchlings were still within the nest cavity free of their eggshells and another was found 5 cm below the surface. All yolk sacs were completely retracted, but only two individuals possessed a caruncle. Delays of 7-8 weeks between hatching and emergence from the nest have been reported in hatchling _P. scripta_ (Moll and Legler 1971).

Timing and Stimulus for Emergence

With the exception of sea turtles, little information is available on the time, mode, or stimulus for emergence in most turtles. That temperature might be important as a stimulus for emergence in sea turtle hatchlings was first suggested by Hendrickson (1958) and later elaborated on by Bustard (1967) and Mrosovsky (1968). The latter workers demonstrated that the upward movement of _C. mydas_ and _Eretmochelys imbricata_ hatchlings was arrested when they encountered sand temperatures in excess of 30°C, 2.5-5.0 cm below the surface. As sand temperatures cooled at night, hatchling activity was resumed and continued until they emerged from the sand.

Nocturnal emergence, as Moll and Legler (1971) pointed out, appears to be selected for in species that nest on open sand bars or beaches. Evidence supporting this contention stems from the observation that hatchlings of species nesting in heavily vegetated areas may emerge at any time (_P. scripta_; Moll and Legler 1971), whereas those that nest on open sand emerge primarily or exclusively at night (sea turtles; Carr and Ogren 1959, Carr 1967, *T. muticus*, *G. pulchra*, *G. oculifera*; Anderson 1958, *Podocnemis expansa*; Roze 1964). Major environmental factors thought to contribute to nocturnal emergence in the hatchlings of open beach nesters are extremely high diurnal sand temperatures and exposure to diurnal predators (Bustard 1967, Hendrickson 1958, Mrovosky 1968, Moll and Legler 1971).

Except for *P. scripta* (Cagle 1950, Moll and Legler 1971) and *C. serpentina* (Hammer 1971), no studies, of which I am aware, of the timing mechanism or stimulus for emergence in freshwater turtles have been made. The above authors believed that rain, rather than temperature, was the major environmental stimulus causing emergence. Moll and Legler (1971) found that *P. scripta* hatchlings began to emerge within 24 hours following brief heavy rains. Additionally, water poured on an artificial nest caused hatchlings to emerge. However, because the soil in which these *P. scripta* hatchlings were buried was hard (Moll and Legler 1971), hatchlings were probably unable to dig out unless the soil was softened by rain. Conversely, sand is most friable when dry. Hendrickson (1958) believed that heavy rains packing the upper layers of beach sand was the major factor prolonging emergence in *C. mydas* hatchlings. At no time were *G. nigrinoda* hatchlings observed to emerge during or within 14 hours of a heavy thundershower.

It was realized early during the study of emergence in *G. nigrinoda* that hatchlings possess specific behavior patterns that somehow allows for nocturnal emergence. It was further observed that these post-emergence behaviors would, after emergence, become progressively less pronounced until after four or five days they dissappear entirely. Consequently, 1-3 day post-emerged hatchlings were considered to be the same as pre-emerged hatchlings in terms of their emergence behavior. Other authors (Moll and Legler 1971, Morovosky 1968, and Anderson 1958) have also employed recently emerged hatchlings to study emergent and early post-emergent behavior.

One such behavior identified in *G. nigrinoda* occurs in response to light. If post-retractive hatchlings are removed from the nest and placed on the ground in daylight, many rebury themselves. Fourteen hatchlings, representing three clutches, were removed from artificial nests and placed in a container provided with sand. Of these, 8 (57%) reburied themselves within three hours, two more did so after 6 hours, and 4 did not rebury after 24 hrs. This same behavior has been reported for *T. muticus* hatchlings by Anderson (1958), who observed that individuals placed in in a 5 gal. bucket Supplied with sand, were active at the surface at night and burrowed underground during the day. Vogt (1980), who observed hatchling behavior in the laboratory, reports that often after emergence from the egg, *G. geographica*, *G. pseudogeographica* and *G. ouachitensis* "bury themselves in the substrate." Likewise, Thomas (1972) reports that invariably self burial occurs in newly hatched *P. f. floridana*. Thomas also observed that "these hatchlings remained buried from 3-5 days, after which they emerged and began to bask and eat small mealworms." Similarly, Moll and Legler (1971) discovered than when newly hatched *P. scripta* were placed in a experimental enclosure designed for orientation studies, they secreted themselves beneath the ground cover for 1-36 days.

In view of the preceeding observations and discussion, it seems that there must be some internal time clock mechanism programming pre-emergence behavior which, when "switched on" at the time of hatching, persists only for a prescribed length of time once emergence is accomplished. Possible stimuli which initiate the decline of pre-emergent behavior may include the act of burrowing from the nest, exposure to light, locomotor activity, or a combination of these.

An experimental enclosure (Fig. 31) was designed to determine if temperature functions as a stimulus for nighttime emergence in *G. nigrinoda* hatchlings.

At 1000 h CDT on 7 September 1980, 16 pre-emerged and less than day-4 post-emerged hatchlings were buried in the enclosure as described in Materials and Methods. Of the 3

Figure 31. Enclosure used to study nest emergence and orientation in hatchling G. n. delticola; level surface, Type AI nest. One of several drift fences occurs in right background.

groups of hatchlings buried (not representing natural clutches), (A) and (B) each contained 5 hatchlings and (C) contained 6. Turtles were allowed to dig out at will.

The enclosure was examined hourly throughout the night, and by daybreak no hatchlings had emerged. At 1300 h, 8 September, the positions of the hatchlings in nests (A) and (B) were checked. All 10 individuals had moved up to within 8 cm of the surface. After noting their positions, hatchlings were reburied without removal. Clutch (C) was not disturbed. By 0800 h the following morning (9 Sept.) no hatchlings had emerged. Hatchlings in (A) and (B) were examined again. Three individuals in (A) had moved up to within 5 cm of the surface. Similarly, four hatchlings in (B) were also within 4-5 cm of the surface. The hatchlings were covered as before. Turtles began to emerge the following night. As in the previous nights, the arena was checked hourly thoughout the night and the time of emergence was recorded as well as the corresponding ambient, sand surface and nest cavity temperatures. In addition, because it was observed that turtles burrow to within 4 or 5 cm of the surface, temperatures at this depth were also occasionally recorded. As Figure 32 indicates, emergence began between 2000-2100 h, approximately one hour after dark. More hatchlings (6, 40%) emerged at this time than at any other hour. Numbers of emerging hatchlings diminished as the

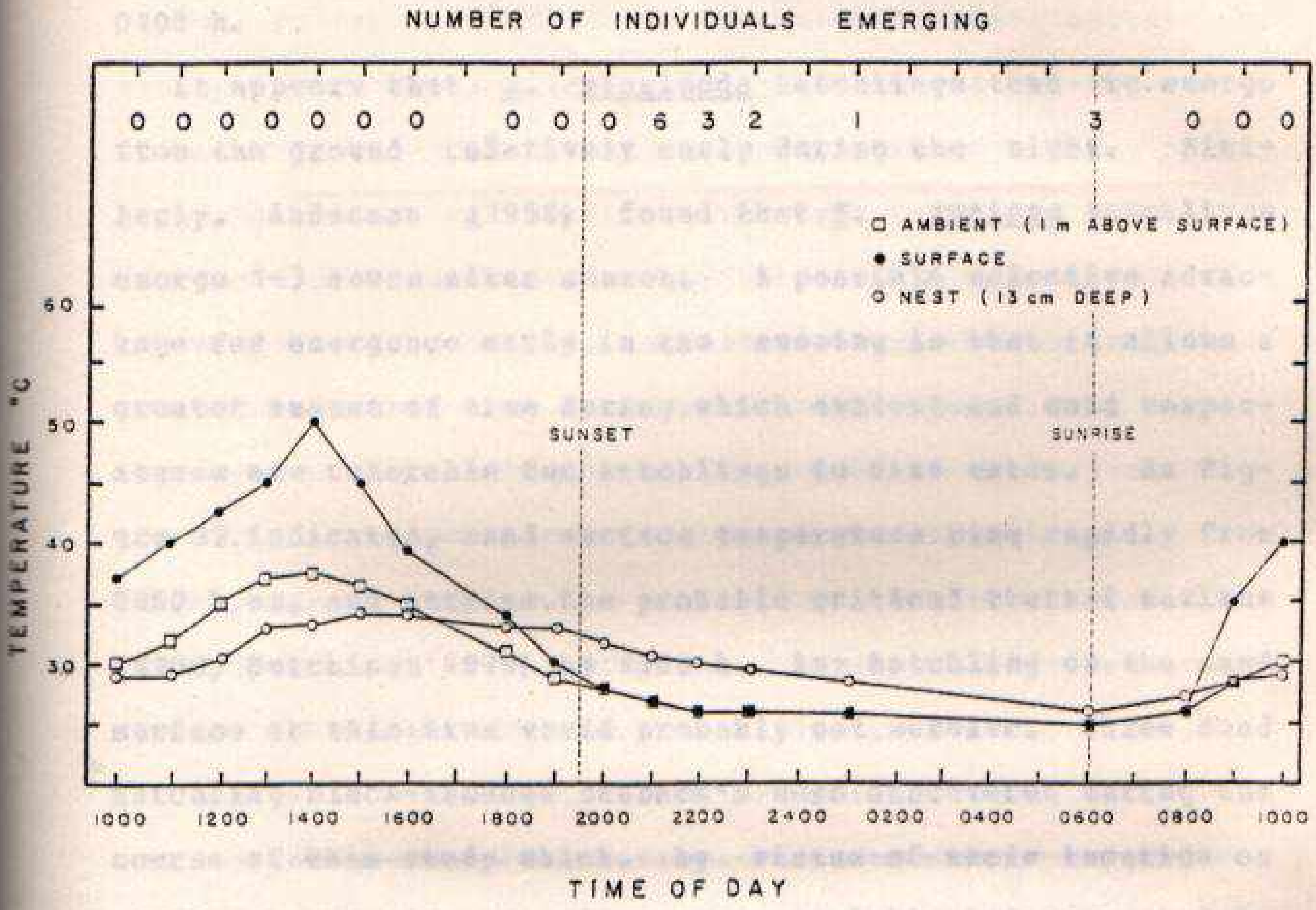


Figure 32. Nest emergence in G. n. delticola hatchlings as correlated with temperature and time of day. Graph drawn from data collected during one 24 hr period extending from 9-10 September 1980.

night progressed, with 12 individuals (80%) above ground by 0100 h.

It appears that *G. nigrinoda* hatchlings tend to emerge from the ground relatively early during the night. Similarly, Anderson (1958) found that *T. muticus* hatchlings emerge 1-3 hours after sunset. A possible selective advantage for emergence early in the evening is that it allows a greater amount of time during which ambient and sand temperatures are tolerable for hatchlings to find water. As Figure 32 indicates, sand surface temperature rise rapidly from 0800 h on, and attains the probable critical thermal maximum (41°C, Hutchison 1979) by 1000 h. Any hatchling on the sand surface at this time would probably not survive. Three dead hatchling black-knobbed sawback's were discovered during the course of this study which, by virtue of their location on the beach and time of discovery, probably had succumbed to extreme temperatures and desiccation.

Sand temperatures begin to drop at about 1400 h and steadily decrease until approximately 0600 h the following day (Fig. 32). Turtles began to emerge when the sand temperature surrounding them (at 5 cm deep) was 27.5°C and dropping. The nest cavity at this time was 31.0°C, while the ambient and sand surface temperatures were both 27.0°C.

Burrowing activity occurred at all hours in the glass fronted nest observed in the lab (see next section) which was maintained at 25-26°C. It can be assumed then that burrowing activity could occur in natural nests anytime at these temperatures, night or day. In view of the preceding, it seems likely that upward burrowing activity in _G. nigrinoda_ hatchlings is inhibited by temperatures above 30°C. Once sand (and so, body) temperatures drop below this critical activity temperature, burrowing resumes until hatchlings escape. Because the arena was examined only once hourly, the exact time of hatchling emergence, and corresponding temperature, is not known. Therefore, if hatchlings at 5 cm deep resume burrowing when sand temperatures reach 27-29°C, (1900-2000 h), it would allow them anywhere from a few minutes to an hour to make their final assualt.

While not conclusive, these results and discussion suggests strongly that the timing of emergence in the black-knobbed sawback is tied to a decrease in substrate temperature. It could be argued that if emergence were temperature dependent, a cool summer shower reducing sand temperatures should stimulate diurnal emergence. As mentioned previously, rain compacts the sand and probably inhibits or prevents the emergence of hatchlings at this time.

Method of Escape

Due to the difficulty of observation, the method by which emydine hatchlings make their way to the surface has received little attention. Muller (1921) found that *T. muticus* hatchlings burrow straight upwards from the nest. Hatchlings of neotropical *P. scripta* escape from the nest singly by either burrowing around or through the nest plug, or by floating out of the nest chamber when it becomes inundated by heavy rains (Moll and Legler 1971). Moll and Legler also found that when recently emerged hatchlings from a single clutch were placed in a tin can about the size of the nest chamber, some individuals spent proportionally more time on top of the pile than did others. This, Moll and Legler reasoned, suggests that some social facilitation may be involved in escape from the nest in this species. Social facilitation was first alluded to by Hendrickson (1958) and later described in detail by Carr and Hirth (1961) for sea turtles. From direct observation of a glass fronted nest, Carr and Hirth discovered that a crude division of labor existed among the hatchlings. Those individuals in the upper layers scrape sand away from the ceiling and sides of the nest chamber, and the sand which filters down to the bottom is subsequently packed by those individuals at the lowest level. This results in the entire group of hatchlings moving upward until they reach the surface simultaneously.

Observations on the method of burrowing by black-knobbed sawback hatchlings were made primarily from the five individuals in the glass fronted nest, but were augmented with field observations.

Unlike the nest chamber of some Pseudemys (Moll and Legler 1971, Thomas 1972) which are hollow, allowing hatchlings unrestricted movements of limbs, G. nigrinoda eggs become completely surounded with sand. This condition, as well as the difference in substrate texture, results in an entirely different mode of escape in black-knobbed sawback hatchlings.

Turtles under direct observation exited out the side, front, or top of the eggshell by scraping with limbs and by squirming. The eggshell fragments remain in the nest cavity. A sequence of specific behaviors involving the use of limbs and carapace allow hatchlings to burrow most of the way to the surface. First, the turtle applies pressure to the sand directly above by pushing straight upwards, and thereby creating a space beneath itself. Simultaneously, the carapace is rotated slightly, about 4-5 degrees each way from center. Sand loosened from immediately above and to the side is subsequently shifted under the shell with movements of the limbs, and the process is repeated. In this manner, hatchlings twist and scrape their way, individually, to the surface while maintaining an upright position.

During the earlier period of upward movement, resting is frequent, often lasting an hour or more after only a few minutes of activity. When dry, loose sand is encountered (at about 3-7 cm below the surface, depending on the amount of recent precipitation), the rate of burrowing increases. Shell movements now become more of a shuffle, lifting first one side and swiveling, and then the other. In the lab, hatchlings maintained under constant room temperature, were not observed to cease burrowing activity just below the surface, but continued until they emerged.

The actual emergence at the surface was observed only a few times, and then only in artificial nests, emergence arena, and glass enclosed nest. The head, which was kept retracted with eyes closed during the ascent, is protruded through the sand first. After a brief pause, the hatchling pulled itself from the sand and immediately crawled off, leaving behind a small circular depression in the sand (Fig. 33).

Those hatchlings that emerged first remained in the ground after hatching for a total of 59 hours. However, since most of these individuals were within 5 cm of the surface by 0800 h on the same day, and presumably only required an hour or less to dig the rest of the way out, an adjusted period of 47 total hours in the ground is probably more accurate. Therefore, the average rate of ascent was roughly 7.5 cm per day, or 3.19 mm per hour. The rate of burrowing is probably inversely proportional to depth. The

Figure 33. Cone-shaped depression formed by the emergence of hatchling _G. n. delticola_ from the nest.

individuals observed in the glass enclosed nest required from 30-40 hours to reach the surface, once burrowing began.

Hatchling Orientation

The orienting ability of hatchling turtles towards water has received a considerable amount of attention. Various factor claimed, suggested, or indicated to affect orientation in hatchling turtles included positive or negative phototropism (Parker 1922, Noble and Breslau 1938, Daniel and Smith 1947, Anderson 1958, Carr and Ogren 1959, 1960, McFarlane 1963), geotropism (Parker 1922, Noble and Breslau 1938, Burger, 1976), humidity gradients (Noble and Breslau 1938) and vegetation (Burger 1976). Ehrenfeld (1979) believed that vision is probably most important for orientation in hatchling freshwater turtles.

Orientation in G. *nigrinoda* hatchlings was studied with the use of the orientation arena described in Materials and Methods, and through the analysis of emergence patterns from undisturbed natural nests. Both arenas (Moll and Legler 1971) and natural emergence patterns (Anderson 1958, Burger 1976) have been used previously to study orientation in hatchling freshwater turtles.

Natural Emergence Patterns

The directions taken by hatchling G. nigrinoda from natural nests appear to be chosen at random, and seems to depend on the direction a hatchling happens to be facing at emergence. In ten nests located on level ground and representing 25 individuals, 4 went north towards the nearest water, 6 traveled east, 8 west, and 7 crawled due south, directly away from the water. Four representative natural emergence patterns are provided in Figure 34 (see also Fig. 33). That some individuals manage to move more or less directly towards water seems to result from chance alone. Hatchlings are just as likely to travel directly away from water as towards it. The following examples provided illustrate some individuals inability to find water:

> 27 August 1980. Nest located on the east side of Quadrat I, 18 m from and 2.5 m above the north shore. One hatchling left the nest and traveled west, paralleling the embankment (and shoreline) for 102 m until eventually veering north to the river.
>
> 9 September 1980. Nest located on the west side of Quadrat I, 4.5 m from and 3 m above the north shore and 10 cm from the embankment scarp. An individual emerged and headed due south. After 5 m it veered slightly to the east and continued inland, away from shore. This

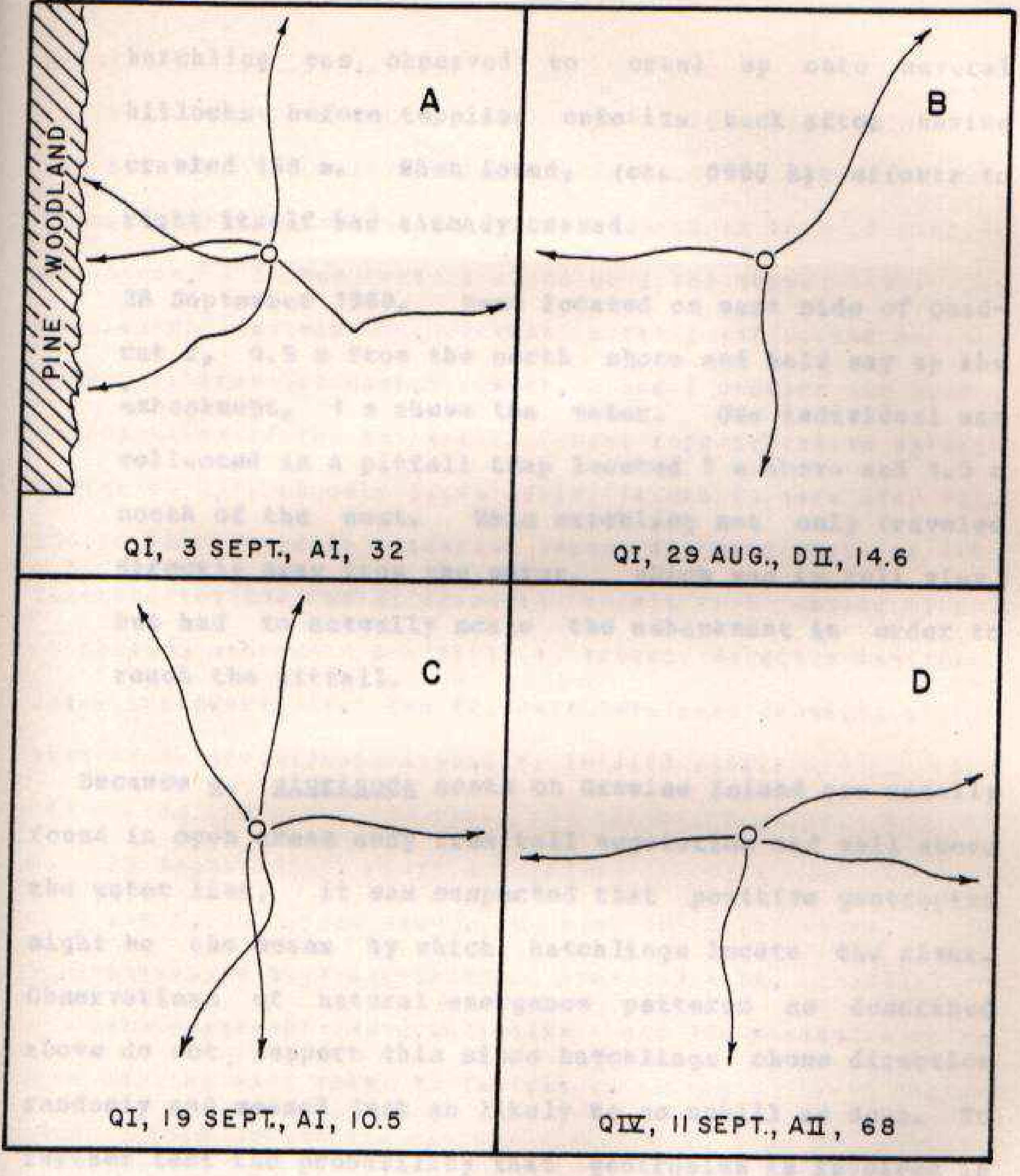


Figure 34. Natural emergence patterns of G. n. deltlcola hatchlings (4 nests). Information provided beneath each pattern include: quadrat, date of emergence (all 1980), nest and substrate type, and distance in meters to nearest water. All patterns are oriented with nearest water and north at top. Scale: 1 cm = 1 m.

hatchling was observed to crawl up onto several hillocks before toppling onto its back after having crawled 158 m. When found, (ca. 0900 h) efforts to right itself had already ceased.

28 September 1980. Nest located on east side of Quadrat I, 4.5 m from the north shore and half way up the embankment, 1 m above the water. One individual was collected in a pitfall trap located 1 m above and 1.5 m south of the nest. This hatchling not only traveled directly away from the water, which was in full view, but had to actually scale the embankment in order to reach the pitfall.

Because G. nigrinoda nests on Gravine Island are usually found in open areas away from tall vegetation and well above the water line, it was suspected that positive geotropism might be the means by which hatchlings locate the river. Observations of natural emergence patterns as described above do not support this since hatchlings chose direction randomly and seemed just as likely to go uphill as down. To further test the probability that geotropism is involved in orientation, hatchlings were tested within the orientation arena on both level and sloped surfaces.

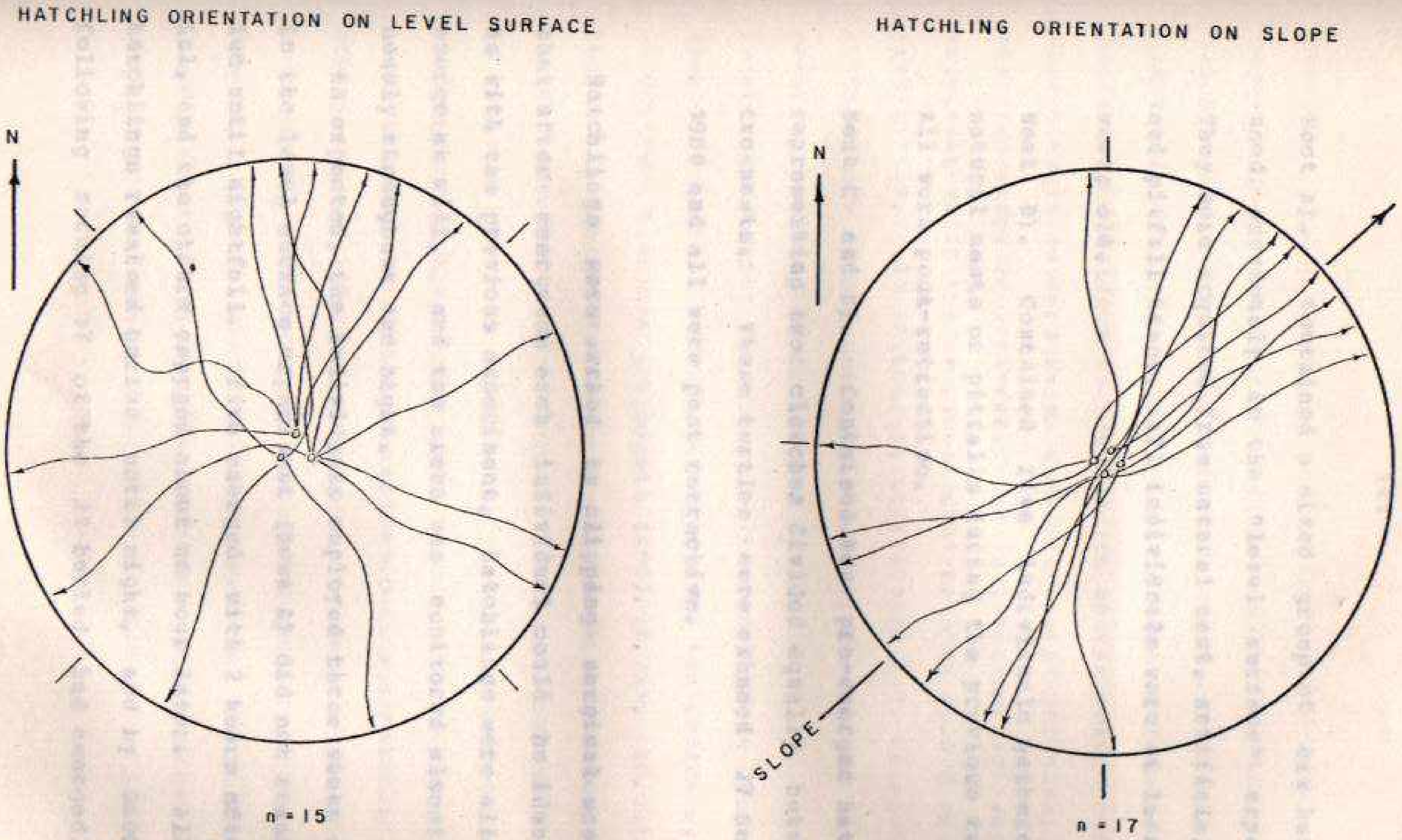
Orientation on Level Surface

The enclosure used to study orientation on level surface was the same one as used for the study of emergence. This arena (Fig. 31; page 126) was located in Type AI nesting situation, 3 m above and 24 m south of the north shore. The same hatchlings were also used (in fact, it could be said that the study of orientation on a level surface was just a continuation of the emergence study). By 0600 h on 10 September 1980, 15 of the 16 individuals had emerged. The routes taken by each hatchling was duplicated on paper with reference to compass direction.

Although there was a slight tendency to go north (Fig. 35), the overall pattern of emergence was random with respect to the four compass points ($X^2=3.93$, NS, $P>0.05$). The sky during the night was clear and temperatures were typical for the season.

Orientation on Sloped Surface

On 28 September the orientation arena was relocated to an area on the east side of Quadrat I having a 10-15 degree slope facing northeast. It was situated in Type BII nesting situation, 3.5 m above and 26 m south of the north shore. At 1400 h 21 *G. nigrinoda* hatchlings were placed in four (A-D) artificial nests 5 cm deep and arranged as a square in the center of the arena. The hatchlings used were characterized as follows:



HATCHLING ORIENTATION ON LEVEL SURFACE

HATCHLING ORIENTATION ON SLOPE

Figure 35. Orientation in hatchling G. n. deltícola as determined from emergence patterns. Flat surface: Directions chosen are random with respect to the four compass points ($X^2 = 3.93$, DF = 3, $P_{.025} = 9.348$). Sloped surface: Directions chosen varied significantly from random with respect to slope ($X^2 = 10.04$, DF = 3, $P_{.025} = 9.348$).

Nest A). Contained a mixed group of six hatchlings used previously in the "level surface" experiment. They were acquired from natural nest, artificial nests, and pitfall traps. All individuals were at least three weeks old.

Nest B). Contained five individuals gathered from natural nests or pitfalls during the previous two days. All were post-retractive.

Nest C and D). Contained ten pre-emerged hatchlings representing two clutches divided equally between the two nests. These turtles were exhumed 27 September 1980 and all were post retractive.

Hatchlings were marked by clipping marginal scutes so that after emergence each individual could be identified. As with the previous experiment, hatchlings were allowed to emerge at will, and the arena was monitored almost continously throughout the night.

As expected, the individuals employed three weeks earlier in the level surface experiment (Nest A) did not remain buried until nightfall. Five emerged with 2 hours after burial, and the others emerged about an hour later. All other hatchlings remained buried until night, and by 0600 h the following morning 17 of the 21 buried had emerged. As before, routes taken by each turtle were duplicated on paper. As Figure 35 illustrates, direction chosen by the hatchlings on emergence varied significantly from random ($X^2=10.04^*$, $P<0.05$). Turtles crawled either downhill or up, but not laterally with respect to the direction of slope. Hence, there was a marked tendency to show positive or negetive geotropism. Except for the timing of emergence, orienting ability of post-emergent hatchlings did not differ from pre-emergent individuals.

The above experiments and observations suggest that under both natural and experimental conditions, *G. nigrinoda* hatchlings display no innate ability to orient towards the nearest water. As with *G. nigrinoda* hatchlings, Burger (1976) found that *M. terrapin* hatchlings moved in all directions from nests located on level ground, but moved predominantly downhill or occassionally up when nests were located on a slope. Additionally, as with black-knobbed sawback, hatchlings terrapins were never observed to move across the angle of slope. Unlike the present study, however, Burger (1976) discovered that geotropic tendency could be negated if hatchlings were offered a choice between vegetation and slope. Hatchlings invariably selected the vegetation regardless of its direction relative to the direction of slope.

Noble and Breslau (1938) noted that under experimental conditions, *C. serpentina*, *C. picta*, and *S. odoratus* hatchlings crawled up hill. The negative geotropic tendency demonstrated in these three species increased directly with slope. Burger (1976) believed that negetive geotropism as exhibited in newly hatched turtles reflects nest escape behavior carried over to post-emergence. After observing directly the process by which *G. nigrinoda* hatchlings make their way to the surface from the nest cavity, I find it difficult to believe the two phenomena are related. The method of emergence in black-knobbed sawback hatchlings in no way resembles walking up hill.

Anderson (1958) observed that when nests were located near the center of a sandbar, emerging *T. muticus* hatchlings moved away in a random pattern. He believed this was caused by the absence of specific cues by which these hatchlings orient. Anderson concluded that *T. muticus*, and two other species studied, *G. pulchra*, and *G. oculifera*, locate water not by moving towards an area of large or intense illumination as reported for sea turtles, but rather, by moving away from large dark masses such as the forest. As Figure 34a (page 137) illustrates, some *G. nigrinoda* hatchlings actually moved towards and into such dark masses. Appearently, black-knobbed sawback hatchlings do not utilize this method of orientation.

Although G. nigrinoda hatchlings do not always travel to water via the most direct route, most individuals appear to reach it by the end of the first night they emerge. In regards to activity during the post-emergent terrestrial period, black-knobbed sawbacks appear to lie between those species which move immediately and directly towards water (T. muticus, G. oculifera, G. pulchra, Anderson 1958) and those which require longer periods of time; about a day in M. terrapin (Burger 1976) and up to one month for neotropical P. scripta (Moll and Legler 1971).

Arrival at Water

hatchlings entering the water were made. On separate occasions, 5 hatchlings were released at night a few meters from shore and observed from approximately 3 m away. After a period of 2-5 minutes and a brief "look around", these individuals crawled towards shore in a quick but unhurried pace. On entering the water, all the hatchlings immediatly submerged and swam out of sight.

In summary, G. nigrinoda hatchlings appear to locate water not by orienting towards it, but simply by continuing in one general direction until water is encountered. This orthotactic behavior appears to work well in an island situation, but how hatchlings from mainland nest locate water is unclear. They appear to move about until, virtually by accident, they encounter the river or some other water source by which they ultimately make their way to the river. In view of the fact that G. nigrinoda remain restricted to one river system, it seems unlikely that hatchlings, like adults, have the ability to disperse very far overland.

Growth

Growth in turtles has usually been expressed in terms of ontogenetic increase in shell size or as allometric changes is shell shape. Apparently growth of the soft parts has been largely ignored. Cagle (1946) believes that weight is a poor choice as an indicator of growth because of the variability created through the retention of cloacal water, feces, and oviducal eggs. Graham (1971), however, found a good relationship between weight and carapace length in Pseudemys rubriventris. In the present study, only lineal measurements were use in the analysis of growth.

The mechanisms of shell growth in emydids are discussed in detail by Legler (1960) and Moll and Legler (1971). Growth rings (annuli), the basis for aging and determining growth in hard-shelled turtles, form when lamellar deposition of keratinized material slows or ceases during periods of inactivity. Other direct methods for aging, such as the counting of annular rings in bones, has met with limited success (Mattox 1935, Dobie 1971). New plastral growth in *G. nigrinoda* appears shiny and light in color, ranging from translucent pale yellow to various flesh tones.

Two types of growth rings are produced: minor (accessory) rings and major (primary) rings. Sexton (1959) thought that accessory annuli were formed at the time of ecdysis, but more recently Moll and Legler (1971) clearly demonstrated that both types of rings arise in essentially the same manner. Minor rings are relatively shallow, never being more than one lamellar layer deep and as such, are less distinct than major rings. Minor rings are formed during the season of active growth and result from inactivity due to temporary changes in environmental conditions such as food availability or inclement weather. Moll and Legler (1971) reported that minor growth rings can form in as little as two days in food deprived *P. scripta*, and may be loss during ecdysis. Major growth rings are considerably deeper, transecting several lamella layers, and only result from the cessation of growth during brumation, at least in the United States. Neotropical *P. scripta*, have been reported to form major rings at any time of year, and purportedly do so from as little as five days quiescence (Moll and Legler 1971).

Not all workers agree on the validity of growth rings as useful indicators of age in turtles. Woodbury and Hardy

(1948), and Miller (1955) were unable to demonstrate a correlation between the number of annuli and age. These conclusions may have resulted from their inability to distinguish between major and minor annuli, or because complete sets of growth rings were not always present on the animals they examined. In any case, more recent investigations have shown a good correlation between major growth rings and age in at least young, rapidly growing individuals (Sexton 1959, Legler 1960, Patterson 1972, Patterson and Brattstrom 1972).

There are three ways to analyze ontogenetic shell growth in turtles; through mark-recapture data, by scute summation, and by various estimation methods. The latter method is apparently most popular probably because of the ease that it can be applied. Many workers have utilized, either in its original or modified form, a formula employed by Sergeev (1937) to estimate growth in turtles (Cagle 1946, 1954b, Moll and Legler 1971, Ernst et al. 1972, Ernst 1975, Vogt 1980). Similar growth estimation methods have been used by Jackson (1970), Dobie (1971), and Wilbur (1975).

In the present study, seasonal and ontogenetic growth in *G. nigrinoda* was estimated using Sergeev's growth formula:

$$\mathrm{PLi} = \frac{\mathrm{PL\ X\ ALi}}{\mathrm{PS}}$$

Where PLi is the predicted plastron length at age i, PL is the plastron length at the time measurements are taken, ALi is the length of the annulus at age i, and PS is the pectoral scute length at the time measurements are taken.

To use growth annuli as a means of estimating growth, four basic assumptions must be made: 1) A discernable growth ring is laid down every year, 2) only one major annulus is formed per year, 3) no annuli are lost, and 4) length of the medial border of the plastral scute selected for growth analysis does not change after formation. The validity of these assumptions are discussed throughly by Moll (1979).

One additional assumption must be made in connection with the use of Sergeev's and other estimation methods utilizing annuli from only one representitive scute. To predict the plastron length based on the annulus length at any given age, it must be assumed that no allometric change in scute length relative the plastron length, has occurred. Moll and Legler (1971) found that the relative length of the abdominal scute in P. scripta increased slightly with age. Consequently, the authors used a modified version of the Sergeev formula to account for this allometric change. Mosimann (1956) noticed that in Kinosternon integrum, the abdominal scute increased and that the humeral scute decreased with age relative to plastron length, but that no other plastral scute showed allometric change. Ernst et al. (1972), however, found that relative abdominal scute length in K. *subrubrum* remains approximately the same throughout life.

Seasonal Growth

Cagle (1946) suggested that normal turtle activity occurs within a temperature range of 10-37°C. Waters (1974) found that *G. nigrinoda* from the Cahaba River of Alabama became inactive (did not bask) when water temperatures fell below 10°C. Water temperiatures of 10°C or less were recorded in the lower Tensaw and Mobile rivers in early December and in March. At no time did water temperature become warmer than 35°C even during the warmest months. Although the rate would vary considerably, growth would theoretically be possible anytime turtles are active and feeding. Adults and juvenile black-knobbed sawbacks were active and fed in all months from April to November, inclusive. The theoretical growing season for *G. nigrinoda* in the delta region extends from early April to late November, eight months or approximately 250 days.

Seasonal growth was analyzed by first determining, from ontogenetic growth data, the average or normal amount of growth an individual would be expected to achieve during each year of life, and then comparing this age-specific expected value with the amount of growth actually obtained in each individual by a known time into the growing season. Age-specific expected values were calculated in terms of plastron length for each sex. Hypothetically, the expected growth values for juveniles of unknown sex were determined by averaging male and female values for the age in question. The percentage of the age-specific expected yearly growth was calculated for each individual and grouped according to the month in which the increment was measured. A synopsis of these, and other growth data are provided in Table 9.

A total of 37 turtles (20 males, 17 females) displaying recent growth were used in seasonal growth analysis. Only three individuals were examined from April, and none showed signs of recent growth. Judging from their large size, and the fact that no annuli were distinguishable, these individuals were beyond the age of rapid growth. It seems more likely, therefore, that the lack of growth observed in the individuals from April is due to their advanced age rather than resulting from the absence of growth during this month. As in _G. pulchra_ (Shealy 1976), growth was first observed in _G. nigrinoda_ collected in May. By this time, ten individuals examined showed an average growth of 38.9% of their age-specific values (Fig. 36). In view of this rather significant amount, it seems likely that growth begins as early as April. Growth increases steadily at about 15.0% per

Table 9. Ontogenetic growth in *G. n. delticola* as expressed in yearly average increase in plastron length. All values are in mm.

Age	Male			Female		
	Plastron length X̄ ± SE; n (R)	Mean increase	Growth* rate	Plastron length X̄ ± SE; n (R)	Mean increase	Growth* rate
H	34.63 ± 0.79; 13 (30.77 - 40.77)	--	--	32.19 ± 1.08; 17 (28.27 - 40.19)	--	--
1	50.98 ± 2.21; 13 (36.60 - 67.20)	16.35	0.096	57.51 ± 2.67; 17 (43.71 - 77.62)	25.32	0.149
2	66.01 ± 2.84; 13 (49.38 - 82.23)	15.03	0.088	77.30 ± 3.64; 17 (50.13 - 105.6)	19.79	0.116
3	73.36 ± 3.16; 12 (59.50 - 89.70)	7.35	0.043	101.49 ± 5.32; 13 (67.03 - 123.2)	24.19	0.142
4	81.00 ± 4.20; 7 (65.15 - 99.90)	7.64	0.045	116.30 ± 5.91; 12 (78.59 - 143.0)	14.81	0.087
5	84.08 ± 5.26; 3 (71.30 - 91.80)	3.08	0.018	130.49 ± 5.39; 11 (92.00 - 154.2)	14.19	0.083
6				141.32 ± 5.97; 9 (101.0 - 161.0)	10.83	0.064
7				158.49 ± 3.63; 5 (143.6 - 168.0)	17.17	0.099

Table 9. Continued.

Age	Male			Female		
	Plastron length $\bar{X}$ ± SE; n (R)	Mean increase	Growth* rate	Plastron length $\bar{X}$ ± SE; n (R)	Mean increase	Growth* rate
8				165.17 ± 7.53; 3 (150.5 - 182.2)	6.68	0.039
9				178.50 ± 7.42; 2 (168.0 - 189.0)	13.33	0.078
Beyond aging	93.74 ± 2.20; 17 (74.85 - 108.8)	9.66	--	184.00 ± 5.05; 5 (167.0 - 198.0)	5.50	--

* Values calculated based on a growing season of 170 days.

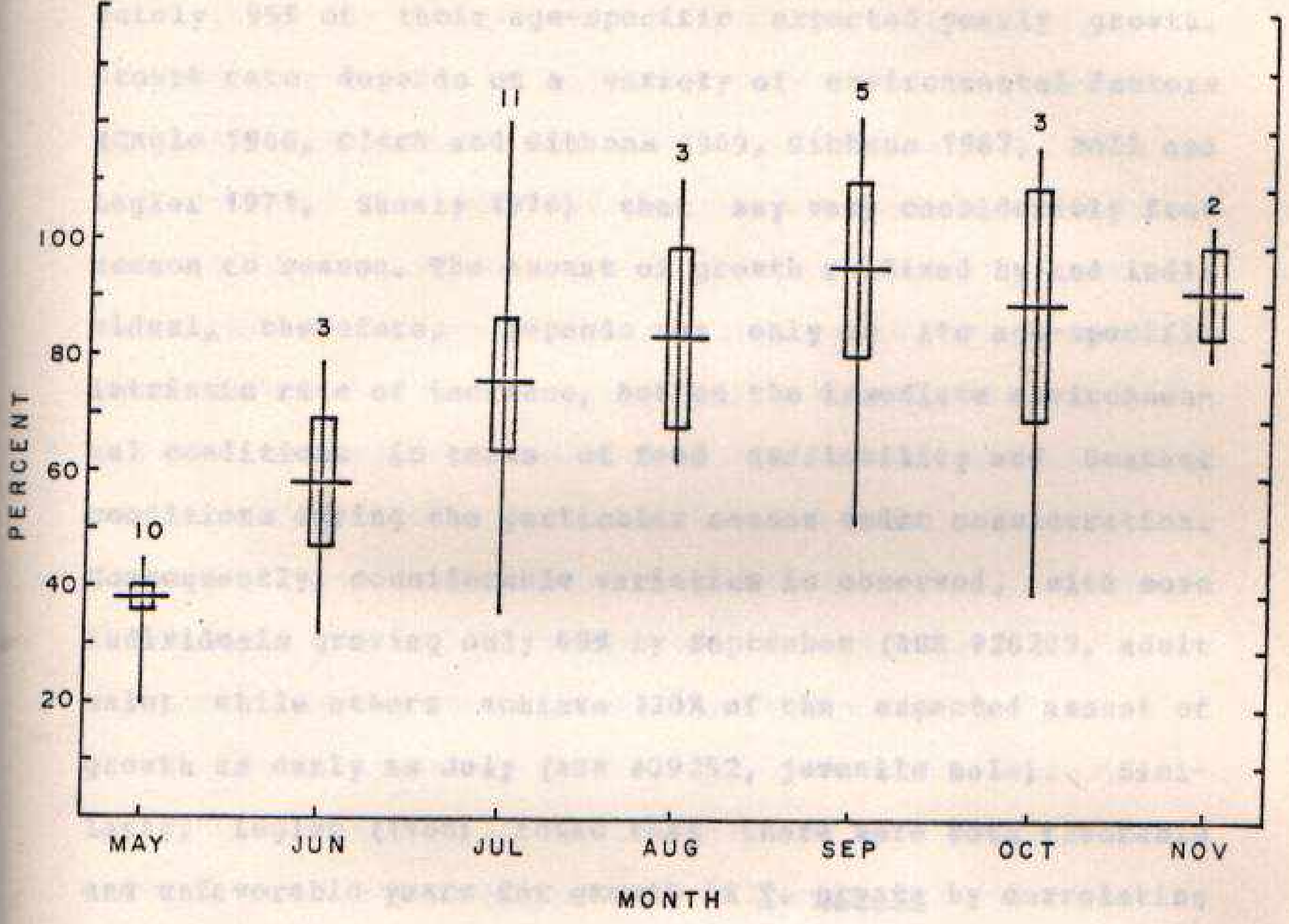


Figure 36. Seasonal growth in G. n. delticola as determined by the amount of normal growth attained by each month of the growing season. Horizontal line represents the mean; vertical line, the range; box, two standard errors; number, sample size.

month until September when turtles have accumlated approximately 95% of their age-specific expected yearly growth. Growth rate depends on a variety of environmental factors (Cagle 1946, Clark and Gibbons 1969, Gibbons 1967, Moll and Legler 1971, Shealy 1976) that may vary considerably from season to season. The amount of growth realized by and individual, therefore, depends not only on its age-specific intrinsic rate of increase, but on the immediate environmental conditions in terms of food availability and weather conditions during the particular season under consideration. Consequently, considerable variation is observed, with some individuals growing only 40% by September (AUM #28209, adult male) while others achieve 120% of the expected amount of growth as early as July (AUM #09252, juvenile male). Similarly, Legler (1960) found that there were both favorable and unfavorable years for growth in _T. ornata_ by correlating the amount of growth an individual achieved with the season in which the individual achieved it.

The results obtained in seasonal growth analysis suggests that while the theoretical or possible growing season spans 250 days, the realized period of growth is only 170-180 days in length.

Virtually all growth is achieved by September, yet almost two months of favorable weather remain. Sexton (1965) believed that this slowing of growth in late summer results from a redirection of food energy towards fat storage in preparation for brumation. Though not quantified, relatively large amounts of body fat were found in autopsied G. nigrinoda from October and November, whereas almost no fat was detected in specimens collected from April through through August. Shealy (1976) suggested that rather than being used in fat deposition, energy is used for follicular development in female G. pulchra, but offered no explanation for male turtles. It seems most likely that food energy is converted into body fat reserves and used in follicular development. Follicular proliferation and subsequent enlargement in female black-knobbed sawbacks takes place primarily during the winter and early spring. Because females probably do not feed during much of this time, fat deposits accumulated in late summer and fall would provide most of the energy required for follicular enlargement. In both sexes, fat undoubtedly serves to maintain life during the winter.

Ontogenetic Growth

Of the 86 adult and juvenile G. nigrinoda collected from the lower delta region, only 42 (47.5%) possesed any plastral annuli. A total of 52 animals (including 10 AUM specimens collected from the study area) were used in the present growth study. Of these, only 30 possessed clearly defined complete sets of growth rings considered reliable enough to represent growth. The remaining 22 individuals were grouped together according to sex, and represent maximum growth. Because they consistantly showed less wear, only the annuli present on pectoral scutes were used in the analysis.

To test if change occurred in relative pectoral scute length, 81 hatchlings, juveniles, and adults were measured for pectoral scute length and plotted relative to plastron length, against plastron length (Fig. 37). Because the slope of the regression line ($Y=17.66-0.003X$) is not significantly different from zero ($t=0.98$, $P>0.05$), no allometric change is indicated. Therefore, the representation of growth as derived from the Sergeev estimation method is considered herein valid and accurate.

Because *G. nigrinoda* displays considerable sexual dimorphism with respect to size, growth in males and females was analyzed separately. Sex was determined either by dissection or by overall size and the presence of pronounced secondary sexual characteristics.

Plastral growth in black-knobbed sawbacks was variable, but more so in females than males, especially at greater ages (Fig. 38). Similarly, Jolicoeur and Mosimman (1960) found that *C. picta* females vary more than males in size and shape.

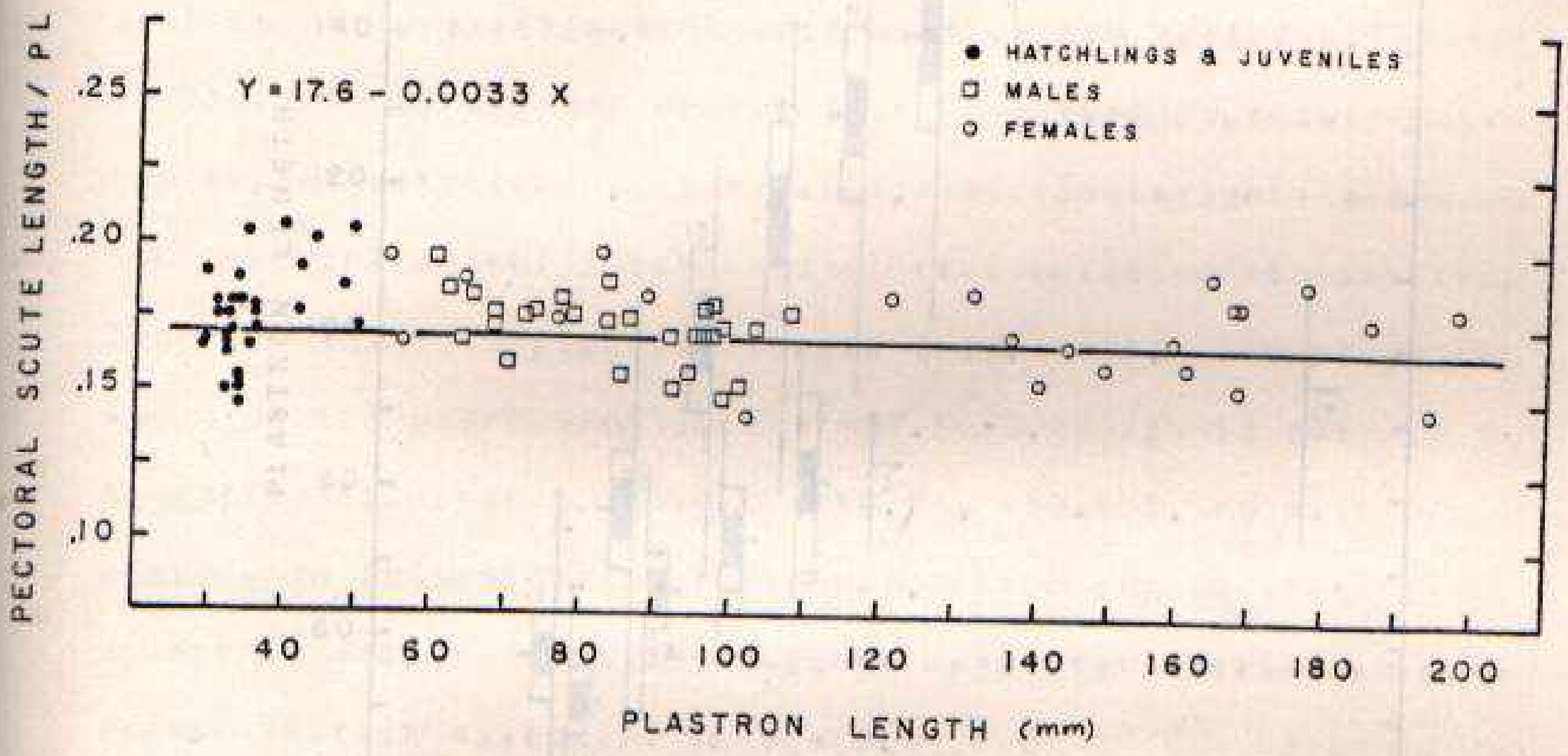


Figure 37. Ontogenetic change in relative pectoral scute length in _G. n. delticola_. Regression line drawn by method of least squares. Slope of the line is not significantly different from zero ($t = 0.98$, $n = 81$, $P > 0.05$).

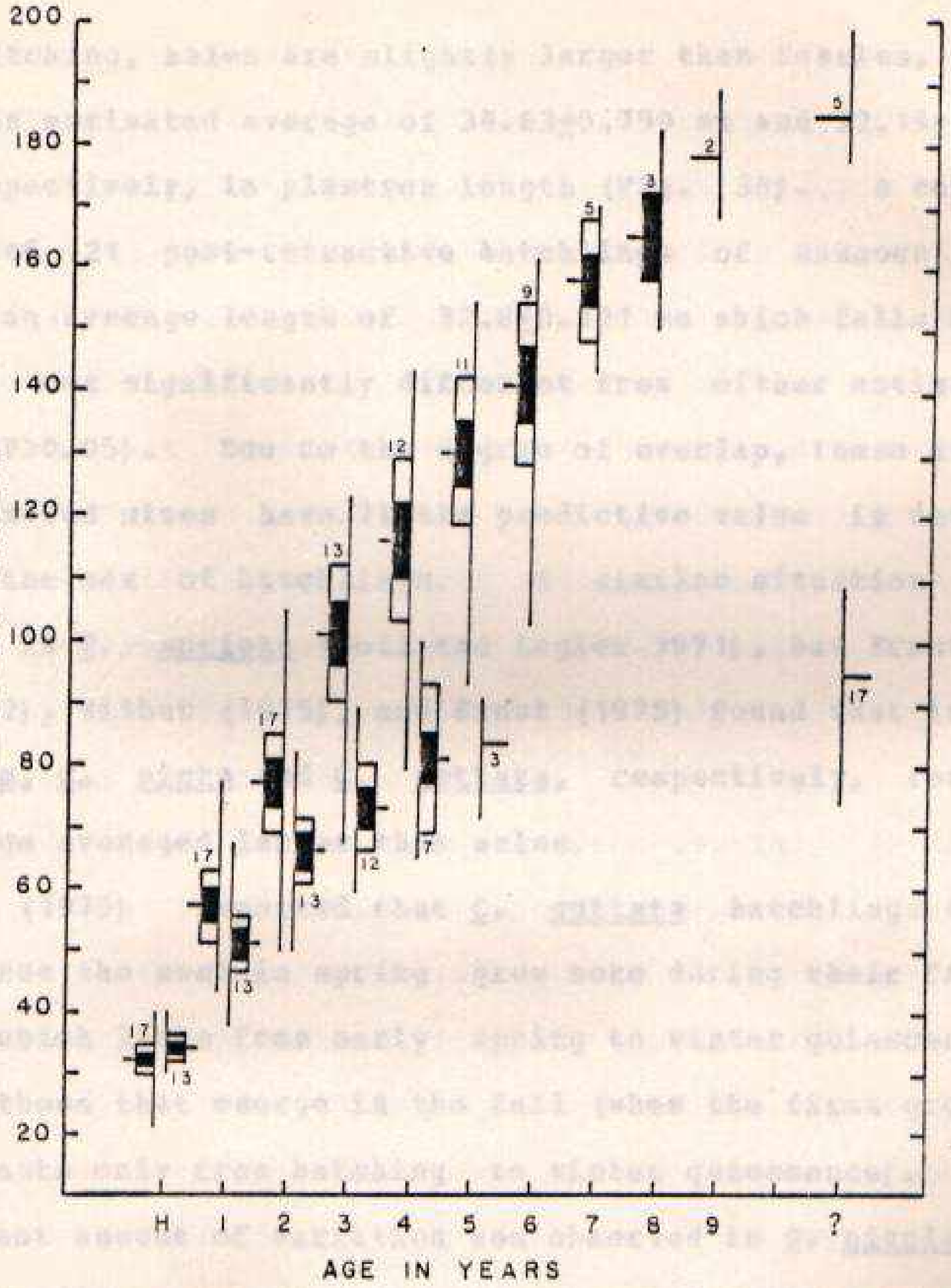


Figure 38. Growth curves of G. n. delticola from the Tensaw River, Baldwin Co., Alabama. Upper curve, female; lower curve, male. Horizontal line represents the mean; vertical line, the range; solid box, two standard errors; open box, 95% confidence limits. Numbers represent sample sizes.

At hatching, males are slightly larger than females, measuring an estimated average of 34.63±0.799 mm and 32.19±1.08 mm, respectively, in plastron length (Fig. 38). A random sample of 21 post-retractive hatchlings of unknown sex yielded an average length of 32.8±0.331 mm which falls between and not significantly different from either estimated values ($P>0.05$). Due to the degree of overlap, these average estimated sizes have little predictive value in determining the sex of hatchlings. A similar situation was observed in *P. scripta* (Moll and Legler 1971), but Ernst et al. (1972), Wilbur (1975), and Ernst (1975) found that in *K. subrubrum*, *C. picta* and *C. guttata*, respectively, female hatchlings averaged larger than males.

Ernst (1975) reported that *C. guttata* hatchlings that emerge from the nest in spring grow more during their first season (which lasts from early spring to winter quiescence) than do those that emerge in the fall (when the first growth season lasts only from hatching to winter quiescence). No significant amount of variation was observed in *G. nigrinoda* during the first year of growth to warrant a similar conclusion. This, when taken together with the known incubation period in relation to oviposition date, suggests that unlike spotted turtles, black-knobbed sawback hatchlings do not regularly overwinter in the nest.

No demonstrable growth occurred as a result of yolk absorption in lab reared hatchlings. Similarly, Legler (1960) found that hatchling *T. ornata* did not grow unless fed. Hatchling *G. nigrinoda* refused to feed for several weeks after yolk sac retraction even under presumably optimal light and temperature conditions. In view of these observations, it seems probable that hatchlings emerge in September or October and do not feed significantly prior to or during brumation, but subsists until spring on the energy provided through yolk catabolism. This situation was also suggested by the observations of Cagle (1944) in overwintering *P. scripta* hatchlings.

Male and female *G. nigrinoda* differ markedly in their rate of growth as determined through regression analysis (Fig. 39). Females grew significantly more rapidly than males ($t=365.8^*$, $P<0.05$). Plastral length increases by 44.88%, 25.6%, 23.84%, 12.74%, and 10.88% during the first five years of growth in females, whereas males increased only 32.0%, 22.77%, 10.02%, 9.43%, and 3.66% for the same period of time. Faster growth rates have also been reported in female *P. concinna* (Jackson 1970). Why *G. nigrinoda* females grow more rapidly is problematical. Diet and temperature, as previously mentioned, are thought to affect rate of growth in turtles most substantially, with higher percentages of animal food coupled with optimal temperatures

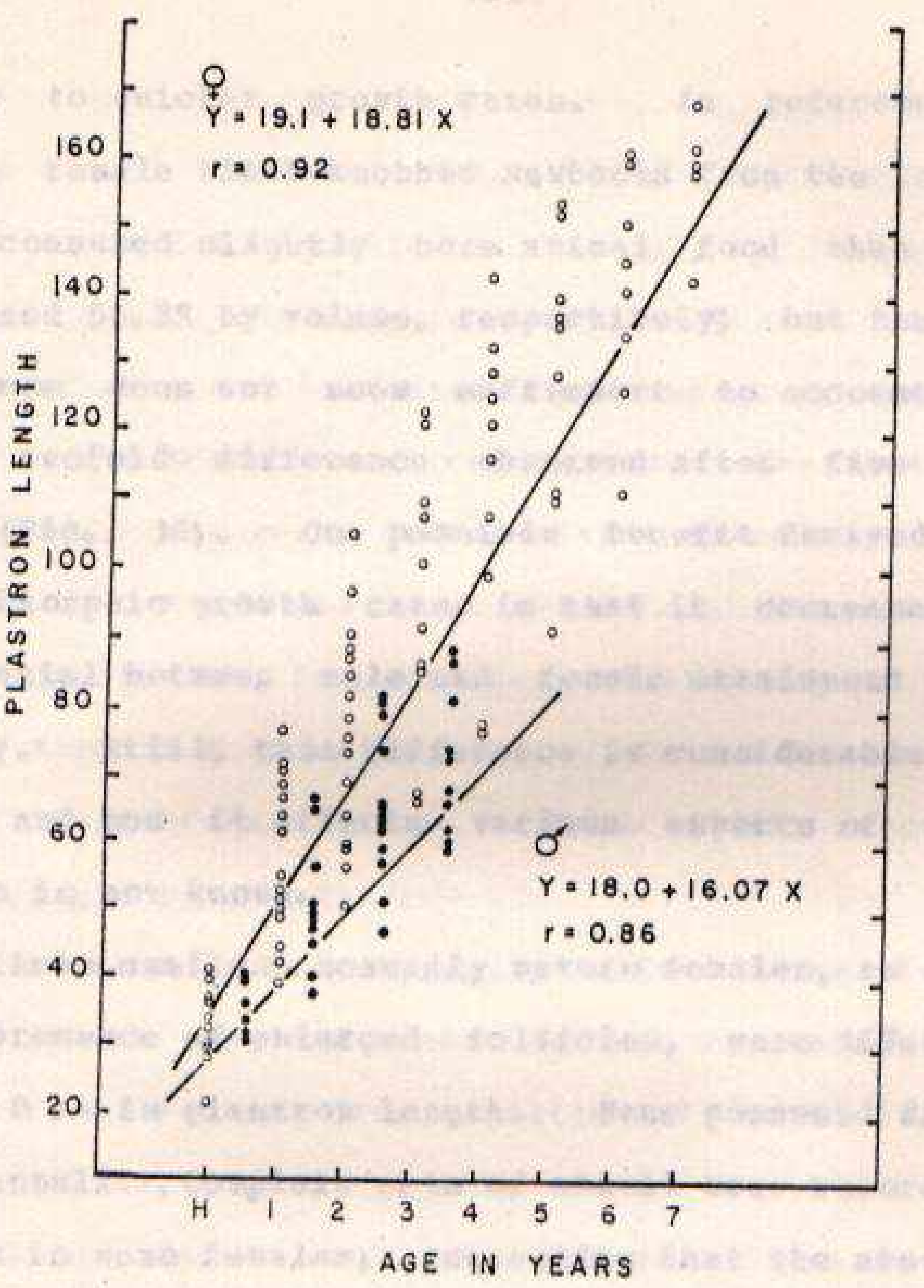


Figure 39. Rate of ontogenetic growth in G. n. delticola from the Tensaw River, Baldwin Co., Alabama, as demonstrated by linear regression. Regression lines drawn by method of least squares. Slopes are different (t = 365.8*, P<0.05).

leading to quicker growth rates. In reference to food habits, female black-knobbed sawbacks from the lower Tensaw River consumed slightly more animal food than did males (69.2% and 58.3% by volume, respectively) but the degree of difference does not seem sufficient to account for the nearly twofold difference observed after five years of growth (Fig. 38). One possible benefit derived from sexually dimorphic growth rates is that it decreases the time differential between male and female attainment of sexual maturity. Still, this difference is considerable (ca. 4-5 yrs), and how it affects various aspects of population dynamics is not known.

The three smallest sexually mature females, as determined by the presence of enlarged follicles, were 167.0, 168.0, and 177.0 mm in plastron length. None possesed discernable growth annuli. Complete sets of annuli were recorded for up to 9 yrs in some females, suggesting that the above individuals were probably at least this age. The five largest females examined which were not sexually mature were 168.0 (7), 164.0 (8), 161.0 (6), 161.0 (6), and 159.0 (7) mm in plastron length and (age). The attainment of sexual maturity in turtles appears to be more dependent on size than age (Cagle 1950, Ernst 1971a, Gibbons 1968, Legler 1960). Most female _G._ _nigrinoda_ probably mature at a plastron length of around 170 mm, while in their 8th through 9th year of growth. Shealy (1976) found that *G. pulchra* matured at a carapace length of 220 mm after 14 years of growth. The smallest sexually mature female *G. o. ouachitensis* and *G. pseudogeographica* examined by Vogt (1980) were both in their 8th year of growth (152-162 mm PL), and *G. geographica* was immature after 10-12 years. The smallest sexually mature *G. barbouri* and *G. pulchra* females had plastron lengths of 176 mm and 170 mm, respectively (Cagle 1952). The smallest sexually mature female *G. oculifera* examined by Cagle (1953) was 128 mm PL, and *G. flavimaulata* females were mature at a PL of 133.0 mm (Cagle 1954a). Shoop (1967) found that two female *G. n. nigrinoda* from the Tombigbee River of Mississippi were sexually mature at 135 mm and 142 mm PL each.

The smallest sexually mature male, as evidenced by the presence of sperm in the epididymides, was 71.3 mm PL and was in its fifth year of growth. No males smaller than this were examined histologically, but sexually dimorphic characteristics are evident by the end of the third growing season. Average plastron length at age three is 73.36 mm. Cagle (1953) reported that motile sperm were present in the testes of the smallest *G. oculifera* male examined and that sexual features were not yet pronounced. Moll and Legler (1971), on the other hand, found good agreement between the first appearence of sexually dimorphic characters and spermatogenesis in *P. scripta*. The data available suggests that male G. nigrinoda become sexually mature by the end of their third year of growth or by the beginning of their fourth year. Shoop (1967) found that G. n. nigrinoda males mature at 68.0 mm PL. Graptemys flavimaculata and G. oculifera males mature at 67.0 mm and 64.0 mm respectively (Cagle 1953, 1954a).

The ability to produce mature sperm does not necessarily mean that an individual is sexually active. Zovickian (1973), for example, reported that male Geochelone radiata attempt to mate at about 30 cm CL but were rarely successful until they were at least 33 cm CL. Graptemys nigrinoda males may require one or two additional years of growth from the time spermatogenesis begins, before mating occurs.

In both sexes G. nigrinoda, growth rates declined sharply after reaching sexual maturity. Decreased growth rates corresponding to the attainment of sexual maturity is common to most turtle families including the Emydidae (Cagle 1946, Legler 1960, Webb 1961, Gibbons 1969, Moll and Legler 1971, Shealy 1976, Vogt 1980), Chelydridae (Dobie 1971), Trionychidae (Breckenridge 1955), Testudinidae (Patterson and Brattstrom 1972). Because food habits do not change drastically after maturity in the black-knobbed sawback, it must be assumed that this decrease results from inherent genetic factors. Moll (1979) discussed the evolutionary implications regarding the cesation of growth with the attainment of sexual maturity in turtles.

Assuming that there are 6 months or approximately 170 days for growth, average absolute rates of plastral increase were calculated individually for males and females, and the results are provided in Table 9; page 151. Figure 40 graphically illustrates the yearly percent increase in plastron length for both males and females.

The actual absolute rate of plastron length increase as exhibited in males is probably higher than that actually realized in nature because of their small size. It is common knowledge that seasonal activity in terrestrial ectotherms is size related. By virtue of their smaller size, young reptiles of any given species are able to reach their thermal optimum more quickly than do larger members of the same species and can remain active on days too cool or short for larger individuals. Consequently, small male and juvenile _G. nigrinoda_ are active at ambient temperatures too low for adult females and are thereby active more days per year. An example of this situation was observed 1 December 1979 when two small sawbacks were observed basking in the vicinity of Gravine Island at about 1300 CST. The weather was clear but cold and with a moderate southerly breeze. Air and water temperatures were 7.2°C and 10.0-12.0°C, respectively. During approximately 10 hours on the river, these two small turtles were the only _G. nigrinoda_ observed.

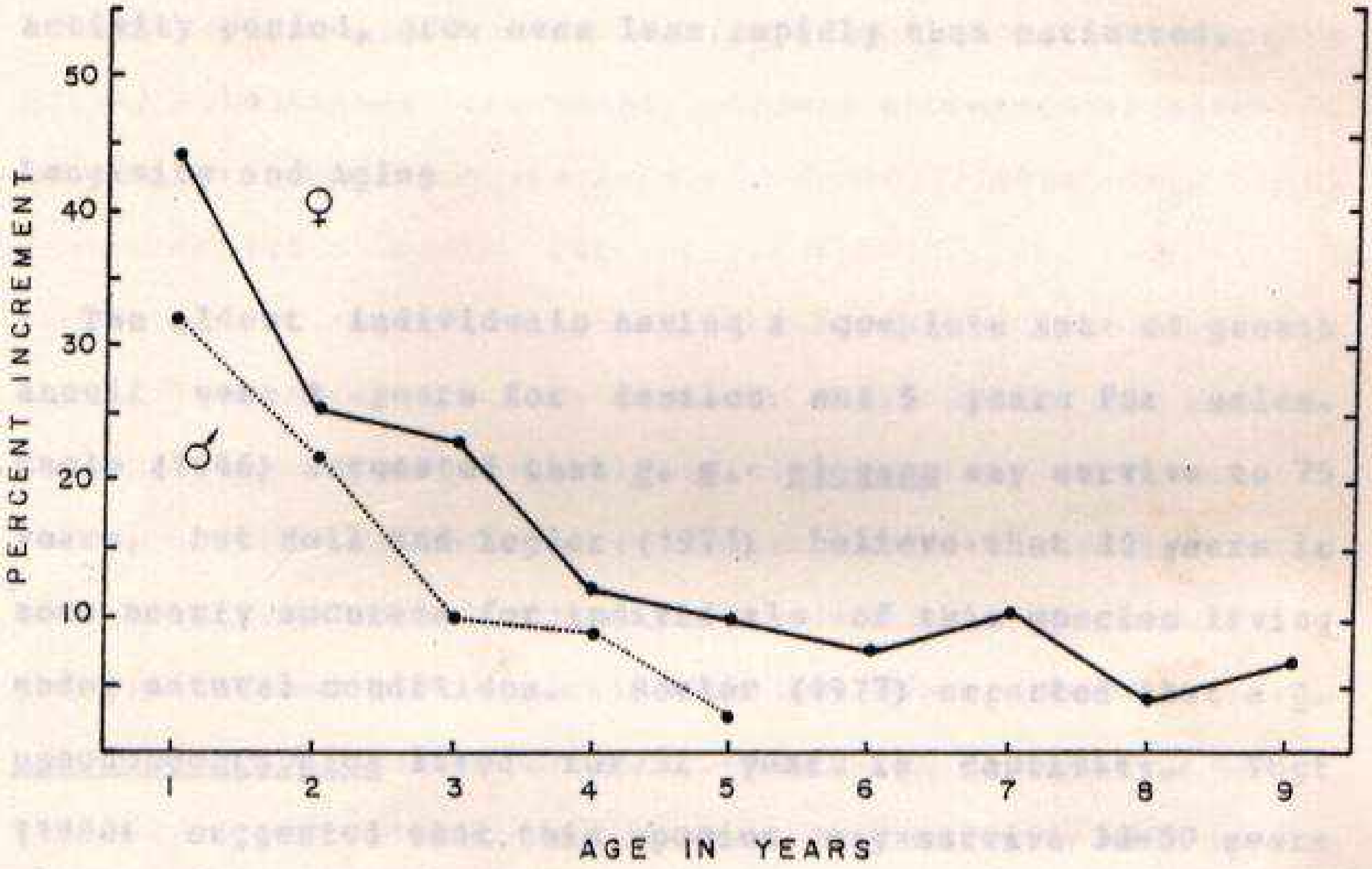


Figure 40. Average percent increase in plastron length in 30 G. n. delticola from the Tensaw River, Baldwin Co., Alabama.

While it is unlikely that growth was occurring on this day, it does illustrate size related activity levels and therefore suggests that males, because of their longer activity period, grow even less rapidly than estimated.

Longivity and Aging

The oldest individuals having a complete set of growth annuli were 9 years for females and 5 years for males. Cagle (1946) suggested that *P. s. elegans* may survive to 75 years, but Moll and Legler (1971) believe that 30 years is more nearly accurate for individuals of this species living under natural conditions. Bowler (1977) reported that a *G. pseudogeographica* lived for 32 years in captivity. Vogt (1980) suggested that this species may survive 30-50 years in the wild. Shealy (1976) felt that 50 years is probably the age reached in *G. pulchra*. Likewise, while unsupported by direct evidence, I feel that natural longevity in *G. nigrinoda*, might approximate 50 years, at least in females.

As *G. nigrinoda* approaches advanced age, they become somewhat melanistic as described in *G. barbouri* (Cagle 1952) and *P. scripta* (Mount 1975, Conant 1976), primarily through the loss of light carapacial and softpart colors. Shealy (1976) lists wandering of plastral seams, change in the relative size of plastral scutes, loss of light head pigmentation, and greater increases in tail length (males) and head width (females) in older _G. pulchra_. Other indicators of advanced age in _G. nigrinoda_ include sunken eyes, smooth shells, thinner scutes, and jagged jaws. No examples of senile black-knobbed sawbacks were discovered during the course of this study, and it is doubtful that many reach advanced ages.

Sexual Dimorphism

Few studies exist which focus primarily on either allometric growth or sexual dimorphism in turtles, and most of the present information is purely qualitative. Among the sexually dimorphic differences found in _C. serpentina_ by Mosimman and Bider (1960) were in posterior lobe and bridge length and pre-anal tail length. They found no differences in shell dimensions. McRae et al. (1981) found that male _Gopherus polyphemus_ have longer gular projections and concave plastrons. A general overview of sexual dimorphism in turtles which includes specific examples is provided by Graham (1979).

More conspicuous sexually dimorphic features expressed in turtles appears 'to include size, tail length (especially pre-anal length), and plastron shape. In addition, males in many families show peculiar sexual dimorphisms such as enlongated foreclaws (Emydidae), elongated fontenelle (Testudindae), enlarged scales on the rear legs (Kinosternidae), and enlarged spines on the forelimbs (Cheloniidae and Testudinidae) as summerized by Graham (1979).

Sexual dimorphism with respect to size is particularly pronounced in the genus Graptemys where females may become twice the size of males in carapace length, and many times their bulk (Cagle 1952, 1953, 1954, Shealy 1976, Graham 1979, Vogt 1980).

Because sexual dimorphism results as a function of differential allomentric growth, both aspects were studied more or less simultaneously from the same specimens. A total of 21 hatchlings and 50 juveniles and adults (28 males, 22 females) received ten lineal measurements each. The morhometric features considered herein include carapace length (CL), carapace width (CW), shell height (SH), total shell height (TH), plastron length (PL), plastron width (PW), tail length (TL), post-anal length (PaL), head width (HW), and foreclaw length (ClL). All measurements were taken as illustrated in Figure 3 (page 15) and analyzed both directly and as a function of carapace length.

Characters were considered to be sexually dimorphic when the slopes of the regression lines drawn from raw data (employed only in the analysis of TL and ClL) or the means derived as percentages of carapace length (to remove size related differences) were significantly different between the two sexes. Results of these analyses appear in Table 10. Of the nine relative morphometric features examined, four were intersexually different, and are discussed below. Relative PL, PW, CW, TH, and HW were similar in both sexes.

The most conspicuous sexually dimorphic character in *G. nigrinoda* is absolute size. Mount (1975) reported that the black-knobbed sawback attains a maximum carapace length of at least 155.0 mm in females and 115.0 mm in males. Folkerts and Mount (1969) reported that the largest female they examined, which constituted the known size record, was 204.0 mm CL. The largest female (AUM #28208) and male (AUM #28683) *G. n. delticola* collected during the present study were 221.0 mm and 122.0 mm respectively, and appear in Figure 41. The seven largest females obtained in the vicinity of Gravine Island averaged 200.6±5.58 mm CL, whereas the seven largest males averaged only 113.0±1.91 mm. These females are significantly larger than males ($t=13.61$*, $P<0.05$).

Females have relatively higher shells than males. The selective advantage for deeper shells in female turtles appears to be associated with her reproductive function, i.e., that of developing and carrying eggs. Due to relatively longer vertebral spines in males, total shell height appeared to be similar in both sexes. Vertebral spines

Table 10. Sexual dimorphism in G. n. delticola as represented by 9 relative morphometric features. Standard statistic values represent percentages of carapace length. Features considered are carapace length (CL), plastron length (PL), carapace width (CW), plastron width (PW), shell height (SH), total height (TH), tail length (TL), post-anal length (PaL), head width (HW), and fore-claw length (ClL). All probabilities are 0.05.

Feature	Male $\overline{X} \pm$ SE (n) (R)	Female $\overline{X} \pm$ SE (n) (R)	Test statistic	Calculated t value	
CL*	113.9 ± 1.908 (7) (109.0 - 122.9)	200.6 ± 5.580 (7) (183.0 - 221.0)	H_o: $u_1 = u_2$	13.61	**
PL	88.9 ± 0.508 (28) (84.2 - 97.6)	90.2 ± 0.328 (22) (87.9 - 93.0))	H_o: $u_1 = u_2$	1.930	NS
CW	87.4 ± 0.682 (28) (81.6 - 93.9)	84.9 ± 0.987 (22) (79.6 - 98.0)	H_o: $u_1 = u_2$	0.715	NS
PL	45.9 ± 0.304 (28) (43.3 - 49.4)	45.1 ± 1.920 (22) (42.1 - 50.7)	H_o: $u_1 = u_2$	0.296	NS
SH	37.5 ± 0.277 (28) (33.0 - 40.0)	42.9 ± 0.453 (22) (39.3 - 48.2)	H_o: $u_1 = u_2$	10.79	**

Table 10. Continued.

Feature	Male $\overline{X} \pm$ SE (n) (R)	Female $\overline{X} \pm$ SE (n) (R)	Test statistic	Calculated t value	
TH	42.8 ± 0.349 (28) (36.3 - 47.3)	45.58 ± 0.433 (22) (41.5 - 50.7)	H_o: $u_1 = u_2$	0.732	NS
TL	46.0 ± 0.827 (28) (33.5 - 53.5)	28.1 ± 0.502 (22) (24.4 - 35.7)	H_o: $B_1 = B_2$	ee 3.668	**
PaL	22.2 ± 0.473 (28) (18.0 - 27.2)	19.9 ± 0.350 (22) (17.8 - 24.9)	H_o: $u_1 = u_2$	3.447	*
HW	15.6 ± 0.252 (28) (13.7 - 18.1)	15.2 ± 0.517 (21) (13.3 - 24.0)	H_o: $u_1 = u_2$	0.626	NS
ClL	7.64 ± 0.246 (27) (5.8 - 10.6)	5.34 ± 0.077 (21) (4.7 - 5.9)	H_o: $B_1 = B_2$	7.663	**

* Absolute values for the largest individuals of each sex.

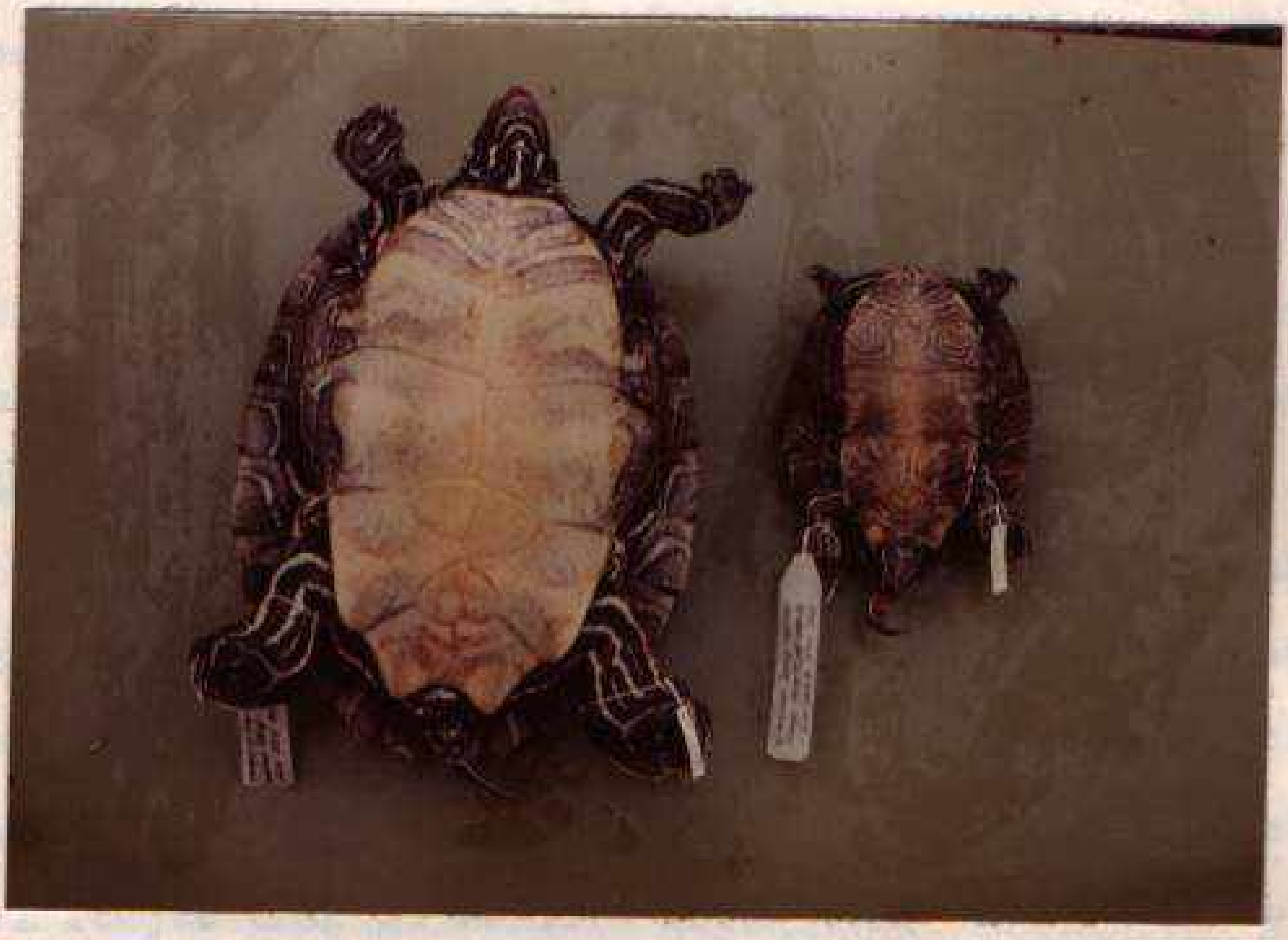


Figure 41. Ventral view of largest female (AUM #28208; 221 mm CL) and largest male (AUM #28683; 122 mm CL) <u>G. n. delticola</u> collected near Gravine Island, Tensaw River, Baldwin Co., Alabama. Note supernumery scutes present in female.

averaged 5.39% of Cl in males, but averaged only 2.65% in females. This 2.74% difference in relative vertebral spine length apparently compensates just enough for total shell height so that both sexes appeared statistically similar. By inspection, however, total relative shell height is clearly greater in females than in males. Total shell volume, not considered quantitatively in the present study, is considerably greater in females and may be a particularly useful size related parameter for future studies where animals will be sacrificed.

Adult male turtles of many species possess considerably longer tails than do females (Carr 1952, Ernst and Barbour 1972, Mount 1976, Conant 1976, Pritchard 1979). Similarly, black-knobbed sawback males have significantly greater relative tail length than do females (Fig. 42). Longer tails in male *C. serpentina* (Mosimman and Bider 1960) and *M. temmincki* (Dobie 1971), result as a function of pre-anal length. Additionally, these workers found that post-anal length was statistically similar in both sexes. While pre-anal length was not measured directly in the present study, it can be easily derived from the data at hand. In male *G. nigrinoda*, pre-anal length averaged 13.82% CL, whereas in females it averaged only 10.11%, a difference of 3.71%. Unlike members of the Chelydridae, post-anal length is different between male and female black-knobbed sawbacks. Male

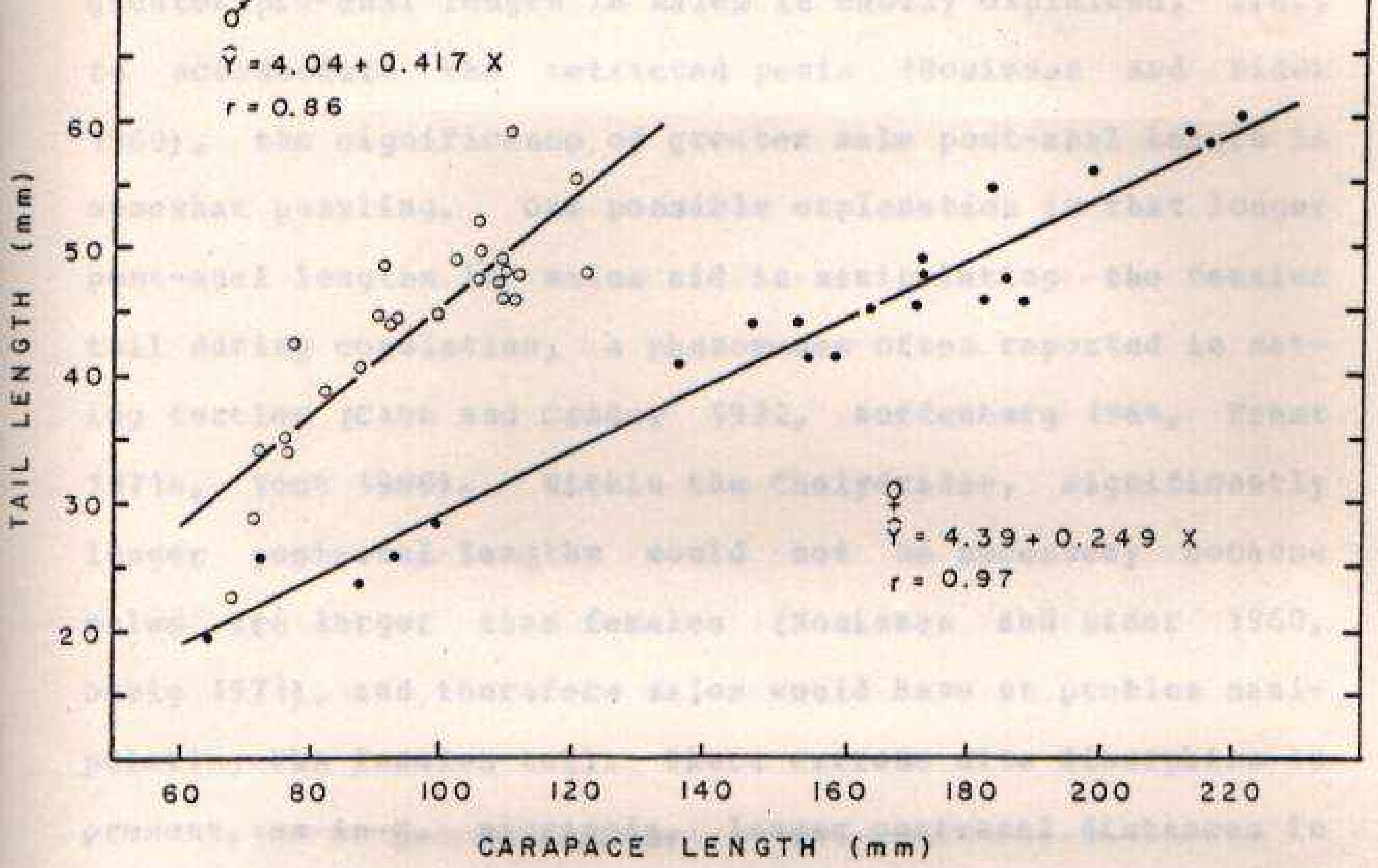


Figure 42. Relative tail length in 28 male and 22 female *G. n. delticola*. Regression lines drawn by method of least squares. Slopes are different ($t = 3.668^*$, $P < 0.05$).

post-anal length (22.2±0.47%) averaged significantly longer than female post-anal length (19.94±0.35%). Although greater pre-anal length in males is easily explained, i.e., to accommodate the retracted penis (Mosimman and Bider 1960), the significance of greater male post-anal length is somewhat puzzling. One possible explanation is that longer post-anal lengths in males aid in manipulating the females tail during copulation, a phenomenon often reported in mating turtles (Cahn and Condor 1932, Auffenburg 1964, Ernst 1971a, Vogt 1980). Within the Chelydridae, significantly longer post-anal lengths would not be necessary because males are larger than females (Mosimman and Bider 1960, Dobie 1971), and therefore males would have no problem manipulating the females tail. Where extreme size dimorphism is present, as in _G._ _nigrinoda_, longer post-anal distances in the much smaller male may be crucial to mating success.

Graptemys _nigrinoda_ males have significantly longer foreclaws than do females (Fig. 43). Other male emydines, particularly members of the genus _Pseudemys_, display this sexually dimorphic character (Cagle 1948, 1954b), which has generally been associated with a claw titillation-type courtship pattern. Similarly, _G._ _pseudogeographica_ (Vogt 1980) and _G._ _p._ _ouachitensis_ (Webb 1961, Vogt 1980) males have elongated foreclaws and display a courting behavior which involves claw titillation. The presence of elongated

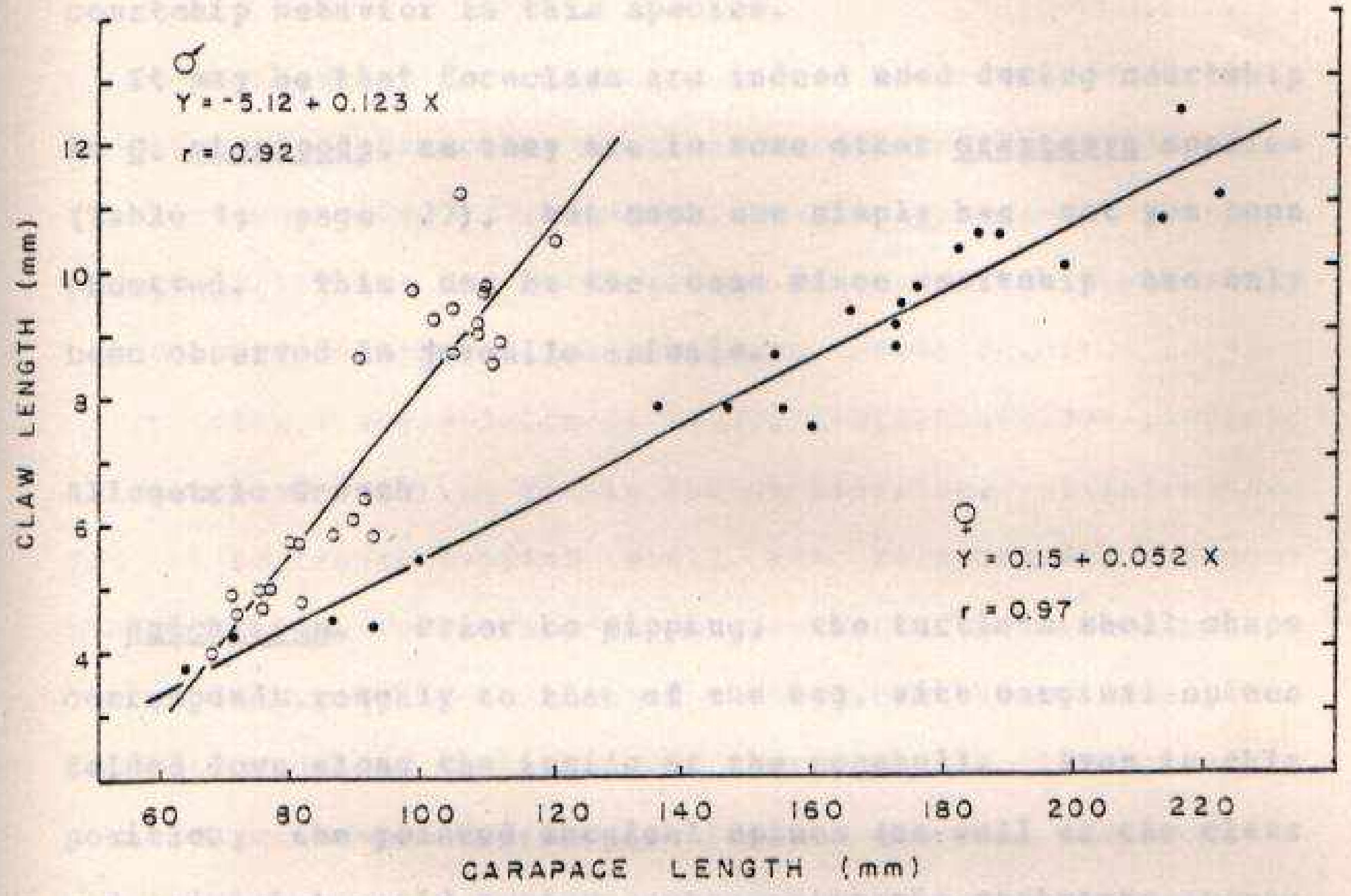


Figure 43. Relative fore-claw length in 27 male and 21 female G. n. delticola. Regression lines drawn by method of least squares. Slopes are different ($t = 7.663^*$, $P < 0.05$).

foreclaws in G. nigrinoda males is, therefore, puzzling because claw titillation was not observed as a part of courtship behavior in this species.

It may be that foreclaws are indeed used during courtship in G. nigrinoda, as they are in some other Graptemys species (Table 1; page 27), but such use simply has not yet been observed. This may be the case since courtship has only been observed in juvenile animals.

Allometric Growth

Hatchlings. Prior to pipping, the turtle's shell shape corresponds roughly to that of the egg, with marginal spines folded down along the inside of the eggshell. Even in this position, the pointed marginal spines (as well as the claws and caruncle) could rupture extra-embryonic membranes prematurely. Consequently, as in G. barbouri and G. oculifera (Ewert 1979), all sharp spines in G. nigrinoda are coated with gelatinous sheaths which disappear just prior to hatching.

Concurrent with and slightly preceeding retraction of the yolk sac, the carapacial margins unfold. The unfolding process is completed in a day or two, while the hatchling remains within the fragmented eggshell. Because carapace width is greater than the maximum eggsell diameter, the sharp marginal spines tear and split the eggshell even further. This probably aids the hatchling's escape from the egg.

Hatchlings of G. nigrinoda have not been described. Agassiz (1857) depicted a hatchling of this species in plate II, Figures 10, 11, 12, and 12a, as G. lesueuri (G. pseudogeographica), but did not describe them. Folkerts and Mount (1969) provided photograghs of young juveniles.

In color, newly-hatched southern black-knobbed sawbacks are quite similar to adults except that contrasting shades and colors are more pronounced. The carapace has a greenish-grey ground color and possesses one to several thin yellow-green concentric rings on each of the major scutes and similarly colored lines or circular figures on the marginals. The vertebral knobs are black. The plastron is pale yellow with a grey to black irregular pattern that roughly corresponds to plastral seams and covering at least 60% of the surface area in this subspecies (Folkerts and Mount 1969). With the exception of changes associated with old age, no ontogenetic color changes are evident.

The shape of the hatchling varies considerably from the adult (Table 11). Unlike adults, hatchlings are sightly wider than long, and marginal indentations are more pronounced. Probably the most dramatic difference between hatchlings and adults is the shape and position of the

Table 11. Ten morphometric features measured in hatchling *G. n. delticola* (post-retractive, pre-absorptive) from Gravine Island, Tensaw River, Baldwin Co., Alabama. Features considered are carapace length (CL), carapace width (CW), shell height (SH), total height (TH), plastron length (PL), plastron width (PW), tail length (TL), post-anal length (PaL), head width (HW), and fore-claw length (ClL).

Feature	n	$\bar{X}$ ± SE (mm)	Range (mm)	% CL
CL	21	36.5 ± 0.331	32.35 - 38.60	100.0
CW	21	36.7 ± 0.328	33.10 - 40.35	100.6
SH	20	14.6 ± 0.189	12.85 - 16.35	39.89
TH	21	18.8 ± 0.257	17.30 - 20.05	51.56
PL	21	32.8 ± 0.331	29.23 - 34.75	89.89
PW	21	17.7 ± 0.193	16.35 - 19.30	48.41
TL	20	14.8 ± 0.215	12.90 - 16.70	40.52
PaL	19	10.9 ± 0.173	10.30 - 12.30	29.92
HW	20	9.35 ± 0.033	9.00 - 9.55	25.61
ClL	20	2.55 ± 0.050	2.20 - 2.90	6.98

vertebral spines. Unlike the rounded vertebral spines of the adults (between the 60-120 mm CL range), which are well separated along the mid-dorsum, hatchlings possess knobs that are somewhat compressed laterally and abut against each other at their bases to form a prominent and continuous keel. Relative vertebral spine length is much greater in hatchlings, (11.67% CL). This is more than twice the value determined for adult males and greater than four times the relative length in adult females. In addition to those features already discussed, hatchlings have relatively greater plastron and head widths than do adults, as well as a longer post-anal length. As expected, those morphological characters which are significantly different in the adults, were intermediate in hatchlings, including PA, TL, and ClL.

Allometric Changes. In the analysis of allometric growth, all relative values for nine morphometric features examined were plotted in the form of scatter grams as percent carapace length against actual carapace length. Linear regression lines were drawn by the method of least squares and their slopes tested for significant deviation from zero. Allometric growth, or change, is indicated when the slope of the regression line is significantly different ($P<0.05$) from horizontal. Those morphological features that do not change as the individual grows will display regression line slopes approaching zero. When analyzing relative data in this manner, it is important to note that an increase in character variation decreases the probability of significance. Two sets of data may have identical slopes, yet one set may be significant and the other not. As such, some features are herein judged from a qualitative viewpoint as well as in a statistical sense. A synopsis of the results derived from the regression analysis of allometric growth in *G. nigrinoda* appears in Table 12. Each morphometric feature considered is discussed separately.

Plastron length (PL, Fig. 44). This feature shows little change in either males or females, but the slope of the regression line in females is significant, indicating a slight gradual relative increase with age. Males display a large amount of variation with respect to relative plastron length, whereas females show little. The importance of this difference, if any, is unknown.

Plastron Width (PW, Fig. 45). The variation displayed in this character is considerable in both sexes, but more so in females than males. Allometric change is in opposite directions in each sex; increasing in females and decreasing in males. Only the slope of the regression line in males was statistically significant. For what reason this feature

Table 12. Allometric growth in *G. n. delticola* as determined by change in 9 relative morphometric features. Features considered are plastron length (PL), plastron width (PW), carapace width (CW), shell height (SH), total height (TH), tail length (TL), post-anal length (PaL), head width (HW), and fore-claw length (ClL). All probabilities are 0.05.

Feature	Sex	n	Test Statistic	Calculated t value	
PL	♂	28	$H_o: B_1 = 0$	0.052	NS
	♀	22	$H_o: B_2 = 0$	2.857	*
		50	$H_o: B_1 = B_2$	2.757	*
PW	♂	28	$H_o: B_1 = 0$	3.450	*
	♀	22	$H_o: B_2 = 0$	1.190	NS
		50	$H_o: B_1 = B_2$	13.26	**
CW	♂	28	$H_o: B_1 = 0$	6.327	**
	♀	22	$H_o: B_2 = 0$	4.372	**
		50	$H_o: B_1 = B_2$	2.733	*
SH	♂	28	$H_o: B_1 = 0$	1.826	NS
	♀	22	$H_o: B_2 = 0$	0.087	NS
		50	$H_o: B_1 = B_2$	7.097	**
TH	♂	28	$H_o: B_1 = 0$	1.645	NS
	♀	22	$H_o: B_2 = 0$	3.722	**
		50	$H_o: B_1 = B_2$	0.000	NS
TL	♂	28	$H_o: B_1 = 0$	1.486	NS
	♀	22	$H_o: B_2 = 0$	2.959	*
		50	$H_o: B_1 = B_2$	0.218	NS

Table 12. Continued.

Feature	Sex	n	Test Statistic	Calculated t value	
PaL	♂	28	H_o: $B_1 = 0$	3.722	**
	♀	22	H_o: $B_2 = 0$	1.645	NS
		50	H_o: $B_1 = B_2$	15.77	**
HW	♂	28	H_o: $B_1 = 0$	11.67	**
	♀	21	H_o: $B_2 = 0$	5.012	**
		49	H_o: $B_1 = B_2$	1.930	NS
ClL	♂	27	H_o: $B_1 = 0$	3.725	**
	♀	21	H_o: $B_2 = 0$	0.623	NS
		48	H_o: $B_1 = B_2$	3.526	**

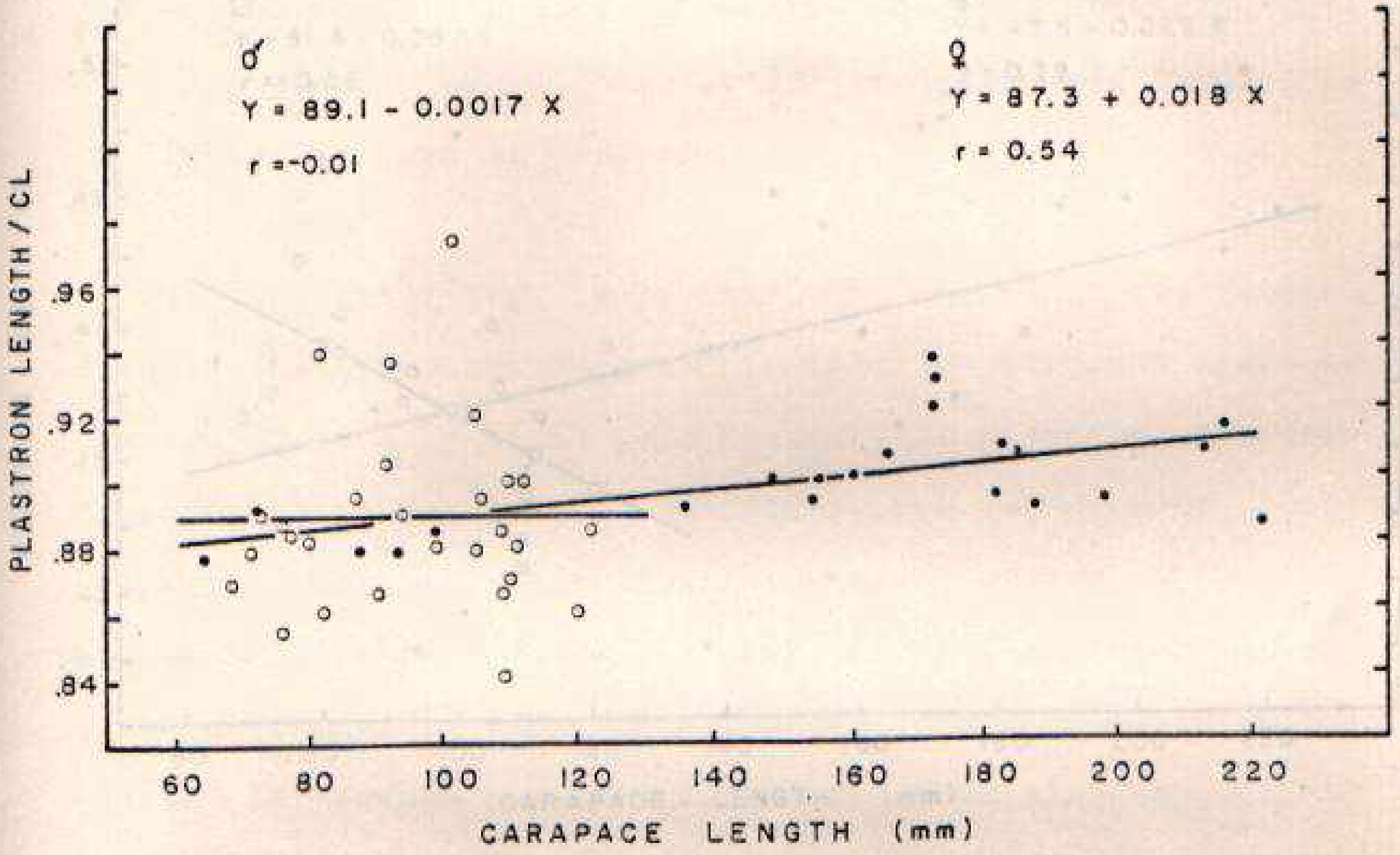


Figure 44. Allometry in plastron length (PL) in male (circles) and female (dots) *G. n. delticola*. Regression lines drawn by method of least squares. Male slope is similar to 0 ($t = 0.052$ NS, $P > 0.05$). Female slope is different from 0 ($t = 2.857^*$, $P < 0.05$). Slopes are different ($t = 2.757^*$, $P < 0.05$).

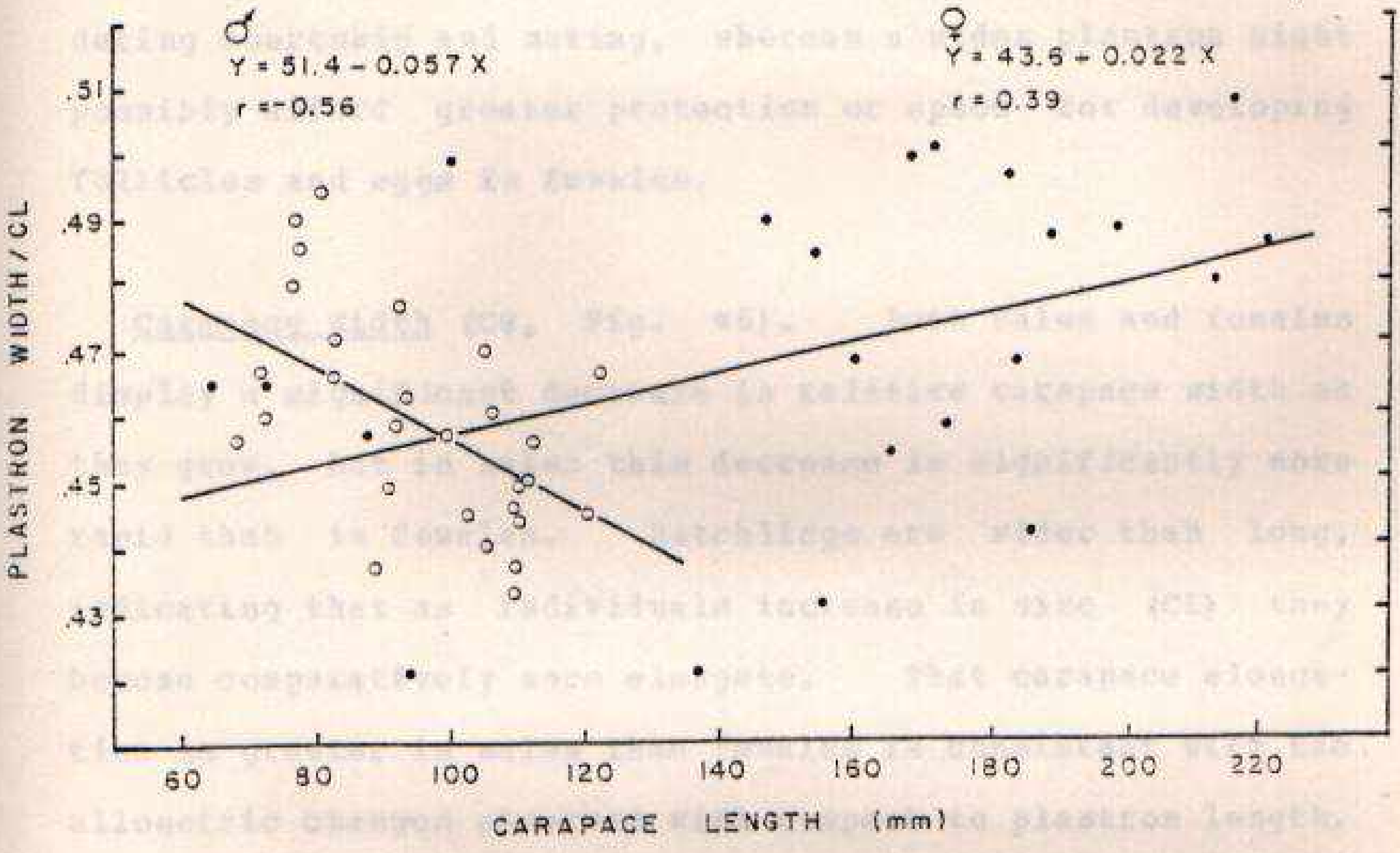


Figure 45. Allometry in plastron width (PW) in male (circles) and female (dots) G. n. delticola. Regression lines drawn by method of least squares. Male slope is different from 0 ($t = 3.450^*$, $P < 0.05$). Female slope is similar to 0 ($t = 1.190$ NS, $P > 0.05$). Slopes are different ($t = 13.26^*$, $P < 0.05$).

displays allometric change in opposite directions in males and females is not known for certain, but a decrease in plastron width as seen in males may allow them more agility during courtship and mating, whereas a wider plastron might possibly afford greater protection or space for developing follicles and eggs in females.

Carapace Width (CW, Fig. 46). Both males and females display a significant decrease in relative carapace width as they grow, but in males this decrease is significantly more rapid than in females. Hatchlings are wider than long, indicating that as individuals increase in size (CL) they become comparatively more elongate. That carapace elongation is greater in males than females is consistant with the allometric changes observed with respect to plastron length.

Shell Height (SH, Fig. 47). In neither males or females were allometric changes associated with shell height significant, though a slight increase is indicated in males. These results were unexpected as it appeared, through inspection, that relative shell height was greater in females than males. It may be, as discussed also in relation to tail length in males, that most if not all of the allometric increase in shell height occurs early during growth, increasing proportionally afterwards. That juvenile

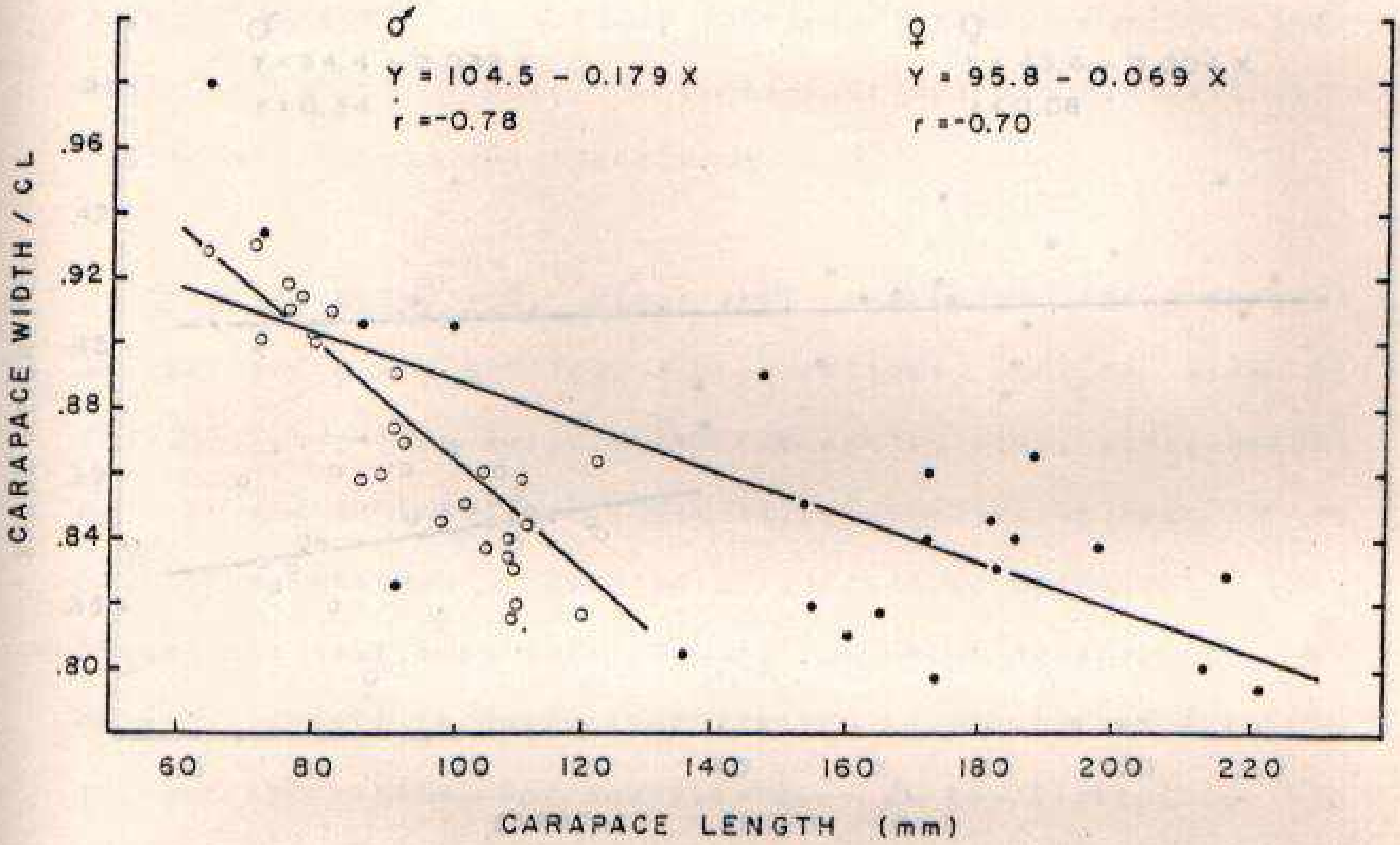


Figure 46. Allometry in carapace width (CW) in male (circles) and female (dots) *G. n. delticola*. Regression lines drawn by method of least squares. Both male and female slopes are different from 0 ($t = 6.237^*$, $P < 0.05$ and $t = 4.372^*$, $P < 0.05$). Slopes are different ($t = 2.733^*$, $P < 0.05$).

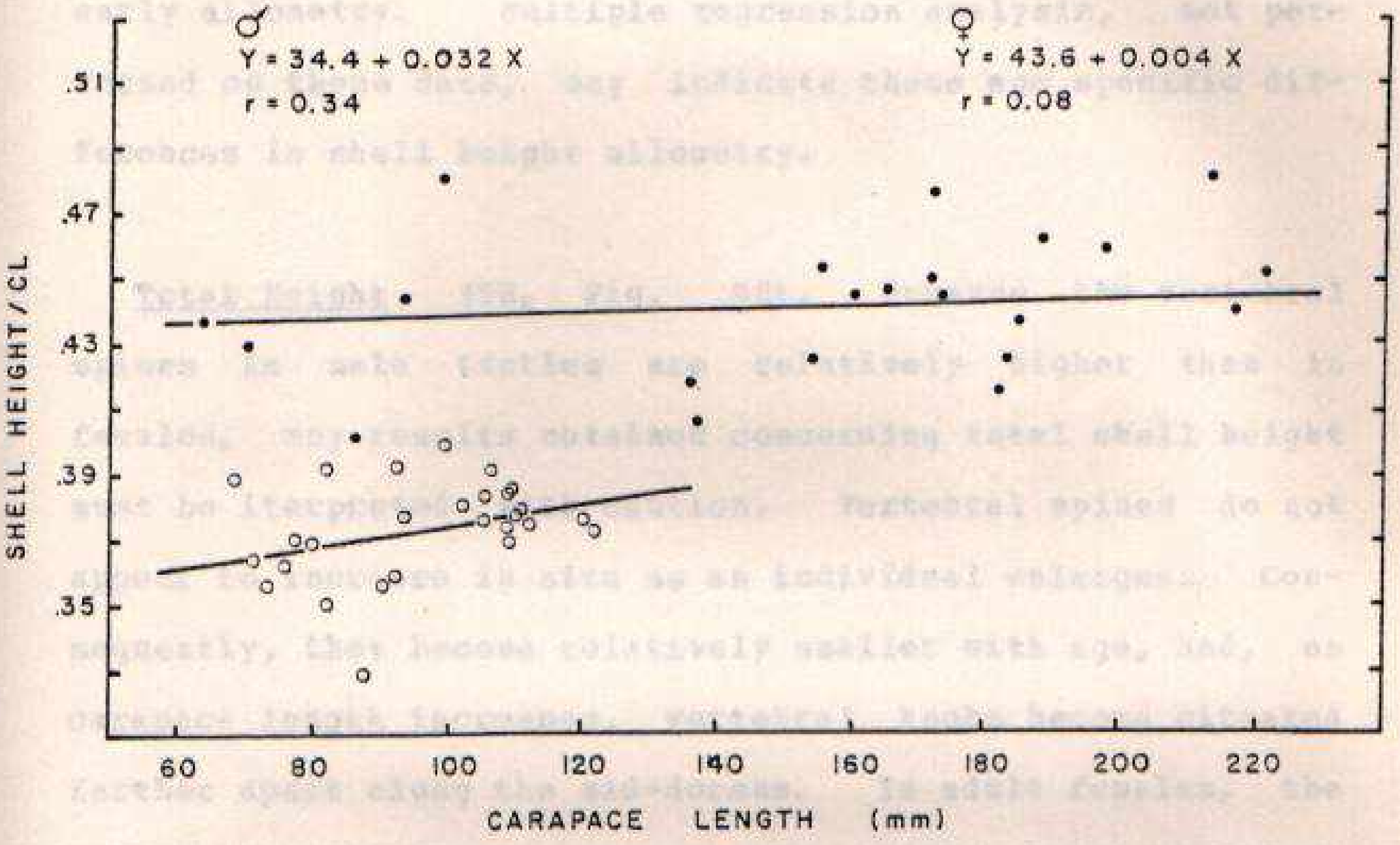


Figure 47. Allometry in shell height (SH) in male (circles) and female (dots) *G. n. delticola*. Regression lines drawn by method of least squares. Both male and female slopes are similar to 0 ($t = 1.826$ NS, $P > 0.05$ and $t = 0.087$ NS, $P > 0.05$). Slopes are different ($t = 7.097^*$, $P < 0.05$).

females can be sexed by shell height as early as age three years, well before the appearance of other sexually dimorphic characters, lends substance to the hypothesis of early allometry. Multiple regression analysis, not performed on these data, may indicate these age specific differences in shell height allometry.

Total Height (TH, Fig. 48). Because the vertebral spines in male turtles are relatively higher than in females, any results obtained concerning total shell height must be iterpreted with caution. Vertebral spines do not appear to increase in size as an individual enlarges. Consequently, they become relatively smaller with age, and, as carapace length increases, vertebral knobs become situated farther apart along the mid-dorsum. In adult females, the vertebral knobs become no more than slight bumps or ridges (Mount 1975, Figs. 306 and 308; Folkerts and Mount 1969, Fig. 4). Thus, the difference between the average relative means for total height, was not significant, and allometry, as indicated by identical slopes, was also similar. However, due to a greater amount of variation observed in males (perhaps a result of differential wear to the spines), only the slope fitted to female data demonstrated a significant deviation from zero. Moreover, that total height decreases allometrically in both sexes is expected in view of the

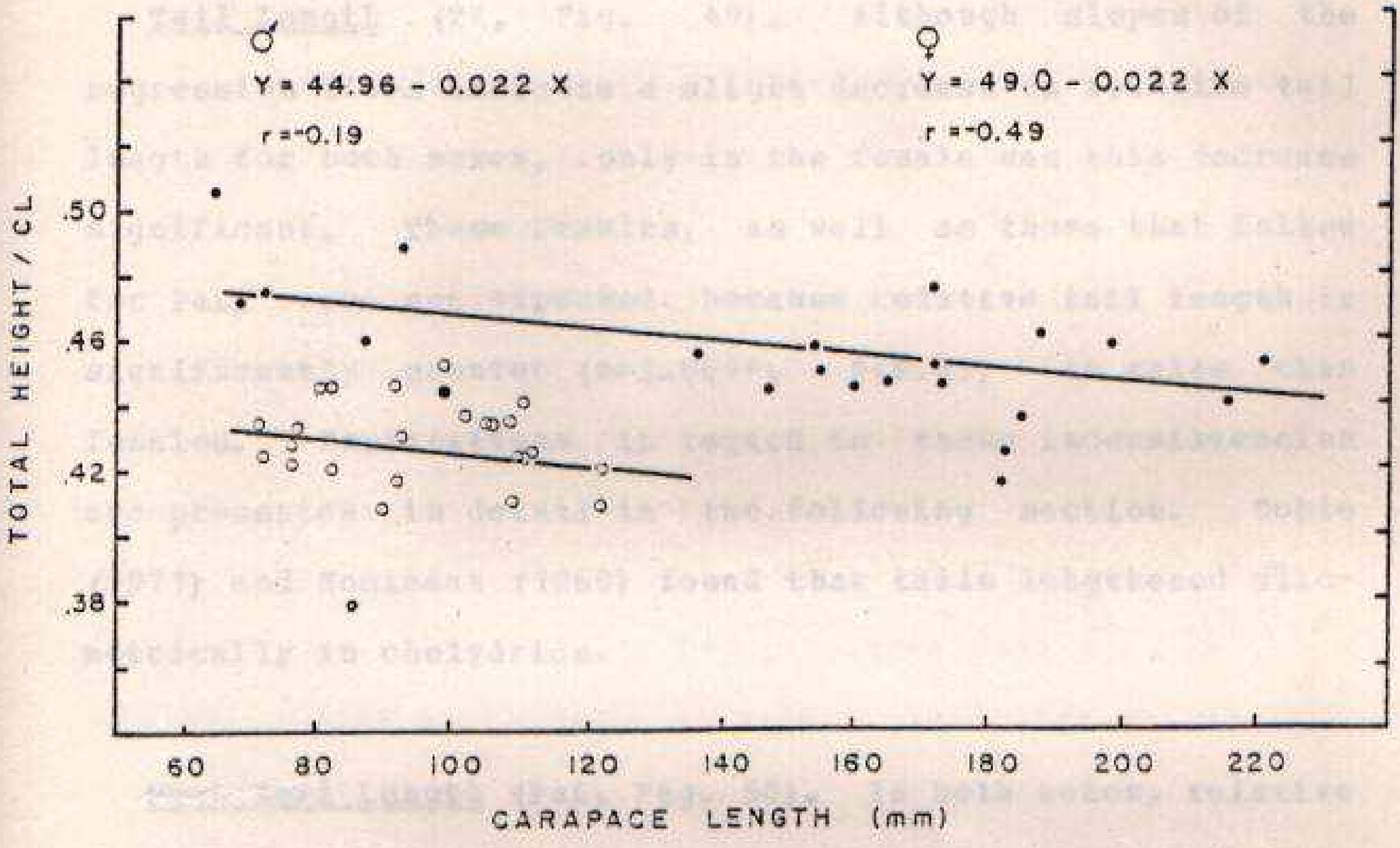


Figure 48. Allometry in total shell height (TH) in male (circles) and female (dots) *G. n. delticola*. Regression lines drawn by method of least squares. Male slope is different from 0 ($t = 3.722^*$, $P < 0.05$). Female slope is similar to 0 ($t = 1.646$ NS, $P > 0.05$). Slopes are similar ($t = 0.00$ NS, $P > 0.05$).

differences observed between relative TH in hatchlings (51.56%) and adults (45.58%).

<u>Tail Length</u> (TL, Fig. 49). Although slopes of the regression lines indicate a slight decrease in relative tail length for both sexes, only in the female was this decrease significant. These results, as well as those that follow for PaL, were not expected because relative tail length is significantly greater (t=3.669*, P<0.05) in males than females. Explanations in regard to these inconsistencies are presented in detail in the following section. Dobie (1971) and Mosimman (1960) found that tails lengthened allometrically in chelydrids.

<u>Post-Anal Length</u> (PaL, Fig. 50). In both sexes, relative post-anal length varies inversely with carapace length, but only signifantly so in males. In males, there is a strong allometric decrease in relative post-anal length which, as was the case in TH and TL, seems incongruous with the conclusion, based on average relative means, that post-anal length is significantly greater in males than females. The seeming paradox results from the fact that males become reproductively mature much earlier (4-5 years) and at a much smaller size (mature at ca. 60% ultimate CL) than do females (mature in 8-10 years at ca. 90% ultimate CL). Males with a

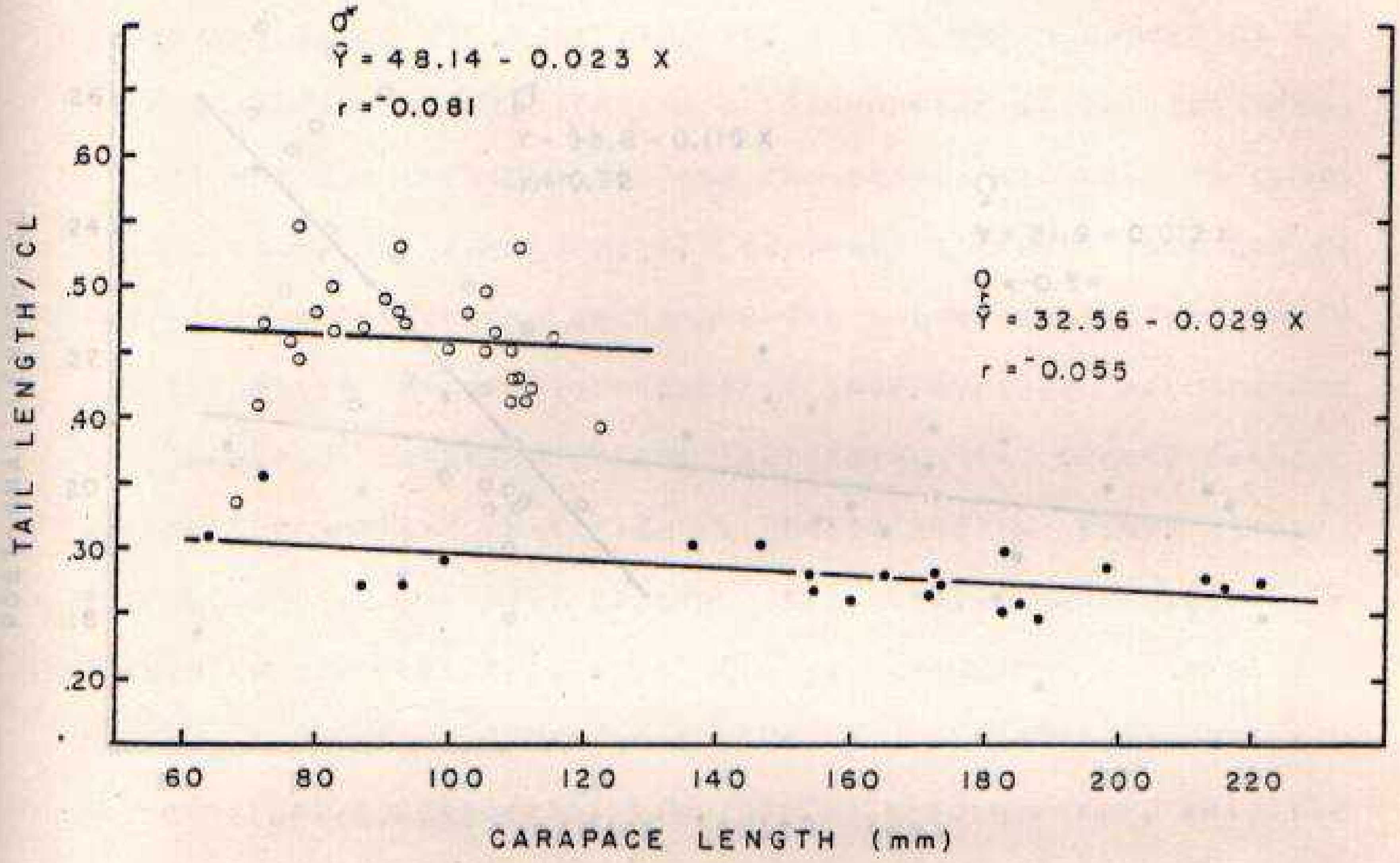


Figure 49. Allometry in tail length (TL) in male (circles) and female (dots) *G. n. delticola*. Regression lines drawn by method of least squares. Male slope is similar to 0 ($t = 1.486$ NS, $P > 0.05$). Female slope is different from 0 ($t = 2.959^*$, $P < 0.05$). Slopes are similar ($t = 0.218$ NS, $P > 0.05$).

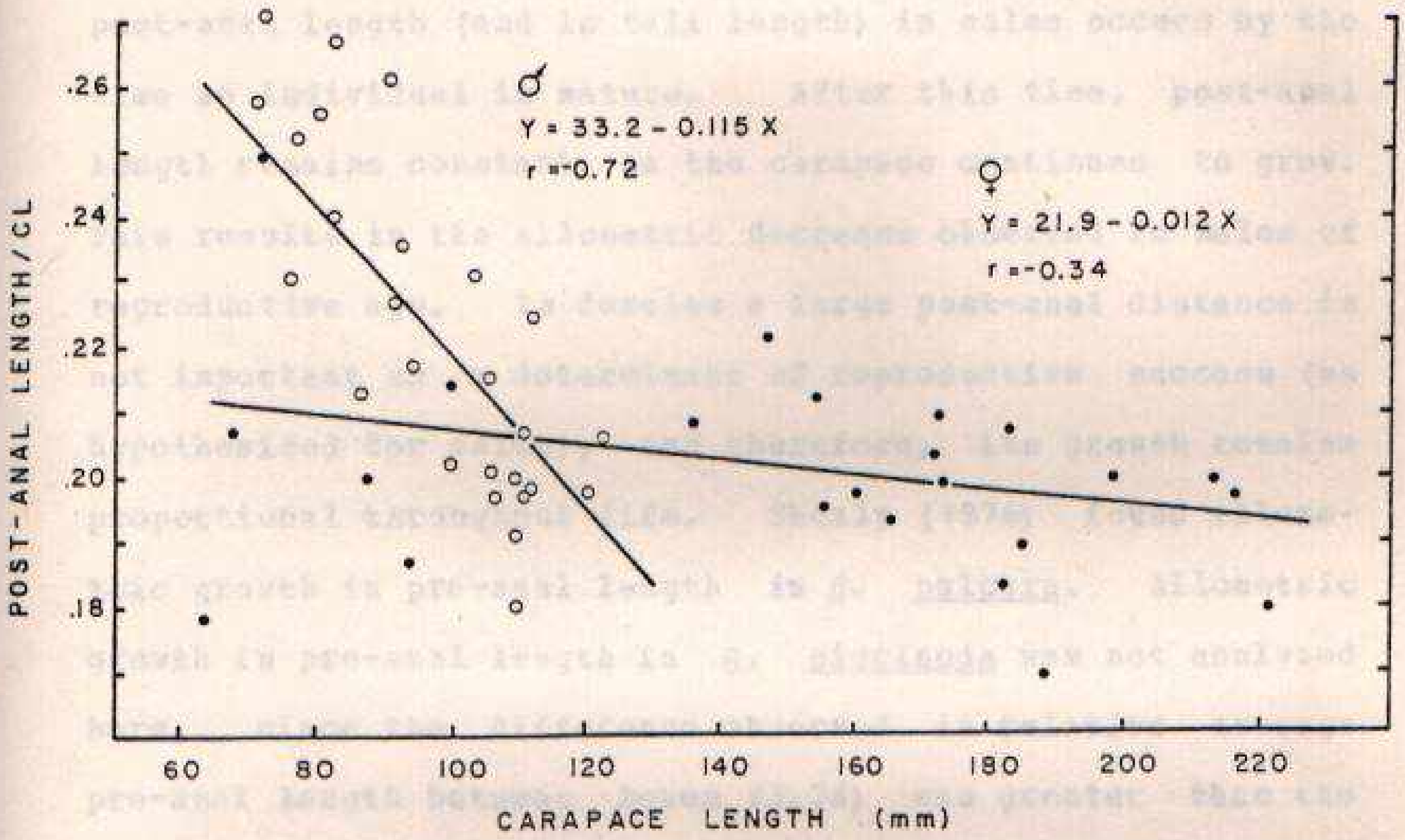


Figure 50. Allometry in post-anal length (PaL) in male (circles) and females (dots) G. n. delticola. Regression lines drawn by method of least squares. Male slope is different from 0 ($t = 3.722^{**}$, $P < 0.05$). Female slope is similar to 0 ($t = 1.645$ NS, $P > 0.05$). Slopes are different ($t = 15.77^{**}$, $P < 0.05$).

CL of 80 mm are sexually mature. Approximately 90% of those males used in this study were larger than 80 mm. Thus, it appears that most, if not all of the allometric increase in post-anal length (and in tail length) in males occurs by the time an individual is mature. After this time, post-anal length remains constant as the carapace continues to grow. This results in the allometric decrease observed in males of reproductive age. In females a large post-anal distance is not important as a determinant of reproductive success (as hypothesized for males), and therefore, its growth remains proportional throughout life. Shealy (1976) found allometric growth in pre-anal length in *G. pulchra*. Allometric growth in pre-anal length in *G. nigrinoda* was not analyzed here, since the difference observed in relative average pre-anal length between sexes (3.7%) was greater than the average post-anal difference (2.3%), one can predict that pre-anal length in males will prove to show allometric increase.

Head Width (HW, Fig. 51). Relative head size in both male and female *G. nigrinoda* decrease with age to about the same degree. Shealy (1976) found that in female *G. pulchra*, the head shows allometric increase relative to carapace length. The heads of female *G. barbouri* and *G. geographica* become similarly enlarged (Cagle 1952, Vogt 1980). Females

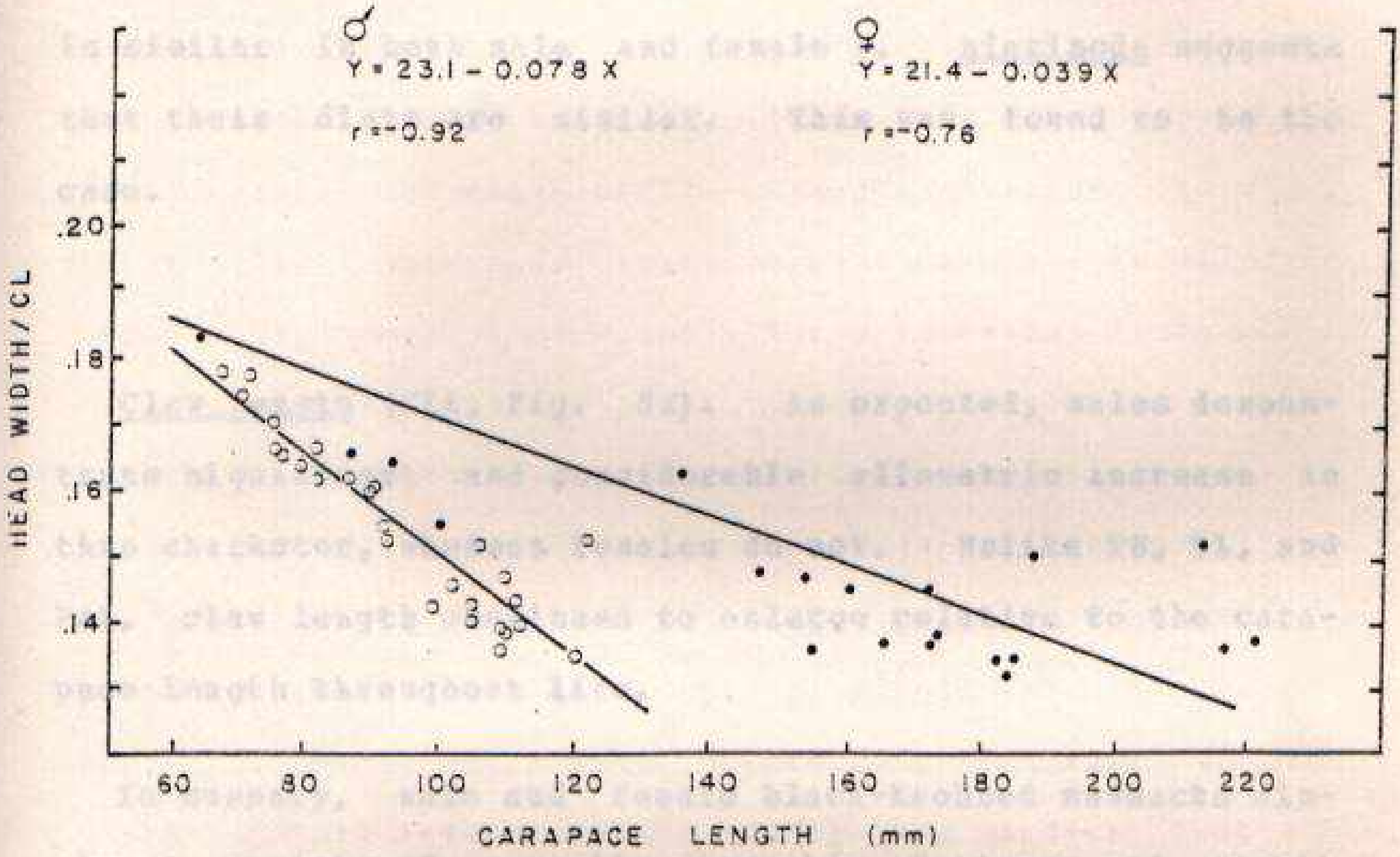


Figure 51. Allometry in head width (HW) in male (circles) and emale (dots) *G. n. delticola*. Regression lines drawn by method of least squares. Both male and female slopes are different from 0 ($t = 11.67^{**}$, $P < 0.05$ and $t = 5.021^{**}$, $P < 0.05$). Slopes are similar ($t = 1.930$ NS, $P > 0.05$).

of these three species are primarily mollusk feeders, whereas the males, which have relatively narrow heads, feed on a greater variety of foods. The fact that relative head size is similar in both male and female G. nigrinoda suggests that their diets are similar. This was found to be the case.

Claw Length (ClL, Fig. 52). As expected, males demonstrate significant and considerable allometric increase in this character, whereas females do not. Unlike TH, TL, and PaL, claw length continues to enlarge relative to the carapace length throughout life.

In summary, male and female black-knobbed sawbacks display a variety of sexually dimorphic features and growth patterns. An overview of how sexual dimorphism and allometric growth are related is provided in the form of size specific polygrams drawn by grouping the 10 morphometric features examined into 10 mm intervals and plotting each mean the appropriate distance from the origin (O) along an axis. Overall size, relative widths, lengths and shapes of the polygram indicate the extent of sexually dimorphic differences. Parallel lines and nonparallel lines represent the absence and presence of allometry, respectively.

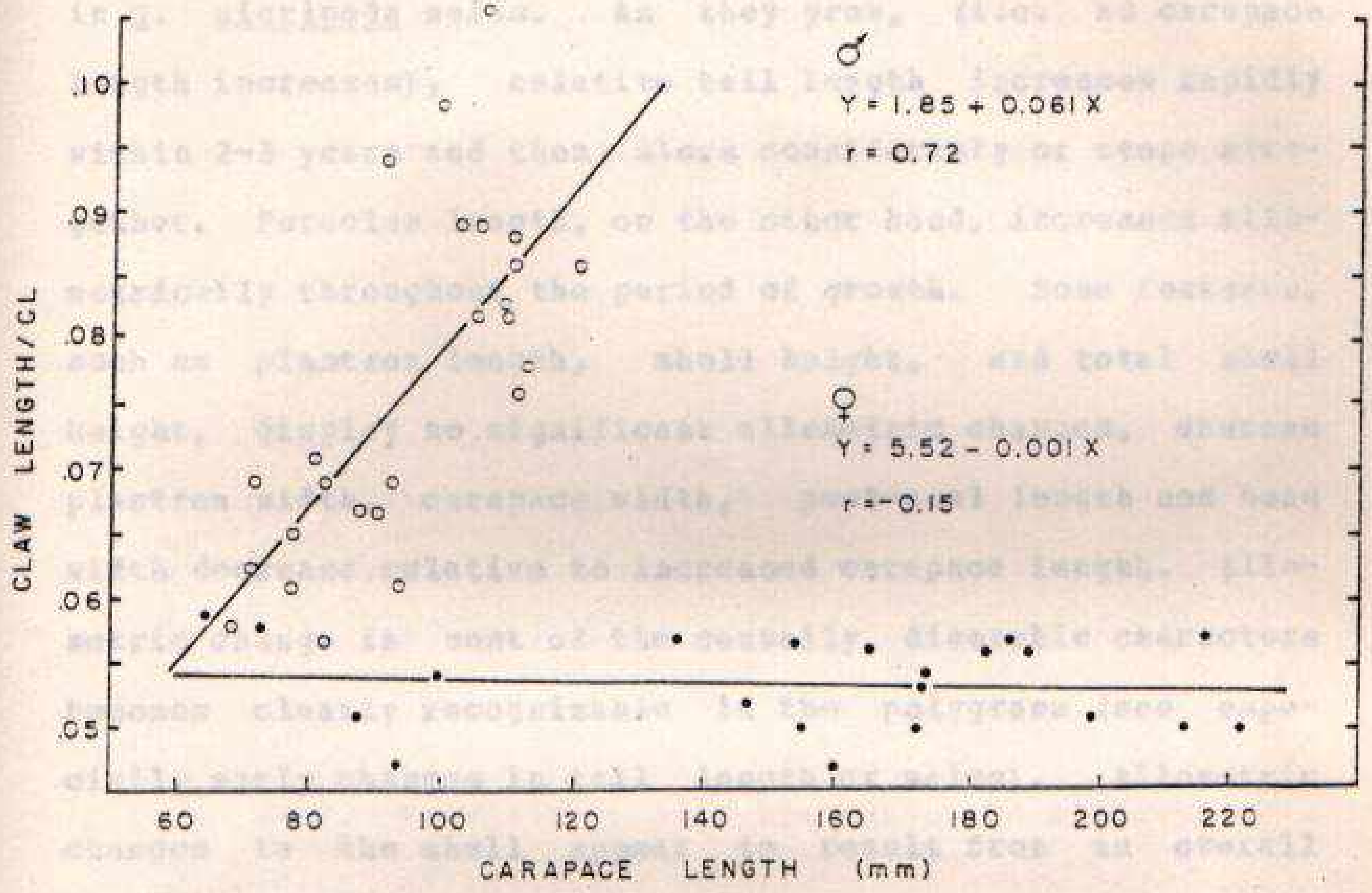


Figure 52. Allometry in fore claw length (ClL) in male (circles) and female (dots) *G. n. delticola* Regression lines drawn by method of least squares. Male slope is different from 0 ($t = 3.725^{**}$, $P < 0.05$). Female slope is similar to 0 ($t = 0.623$ NS, $P > 0.05$). Slopes are different ($t = 3.526^{**}$, $P < 0.05$).

Males (Fig. 53). Many of the previously recognized sexually dimorphic characters of turtles, are also present in *G. nigrinoda* males. As they grow, (i.e. as carapace length increases), relative tail length increases rapidly within 2-3 years and then slows considerably or stops altogether. Foreclaw length, on the other hand, increases allometrically throughout the period of growth. Some features, such as plastron length, shell height, and total shell height, display no significant allometric changes, whereas plastron width, carapace width, post-anal length and head width decrease relative to increased carapace length. Allometric change in most of the sexually dimorphic characters becomes clearly recognizable in the polygrams (see especially early changes in tail length of males). Allometric changes to the shell appear to result from an overall lengthening of the carapace.

Females (Fig. 53). As carapace length in female *G. nigrinoda* increases, relative plastron length increases and relative carapace width, total height, tail length, and head width, decreases. Relative plastron width, shell height, post-anal length, and foreclaw length show no allometric change.

Males and females appear to differ considerably with respect to growth patterns. However, some allometric changes

Figure 53. Composite polygrams illustrating sexual dimorphism and allometry in 28 male and 22 female G. n. delticola. Graph was drawn from ten morphological features measured in each sex as illustrated in Figure 3. Raw data were divided into 10 mm CL intervals and resulting means were plotted along axes the appropriate distance from the origin (O). Concentric lines connect means of corresponding size intervals. In males, intervals are from 60-120 mm. Female intervals are from 60-200 mm but with no individuals represented in the 100-120 mm size range. Feature abbreviations are carapace length (CL), shell height (SH), total height (TH), plastron width (PW), carapace width (CW), plastron length (PL), tail length (TL), post-anal length (PaL), fore-claw length (ClL), and head width (HW). Both graphs drawn to same scale: 1 cm = 20 mm.

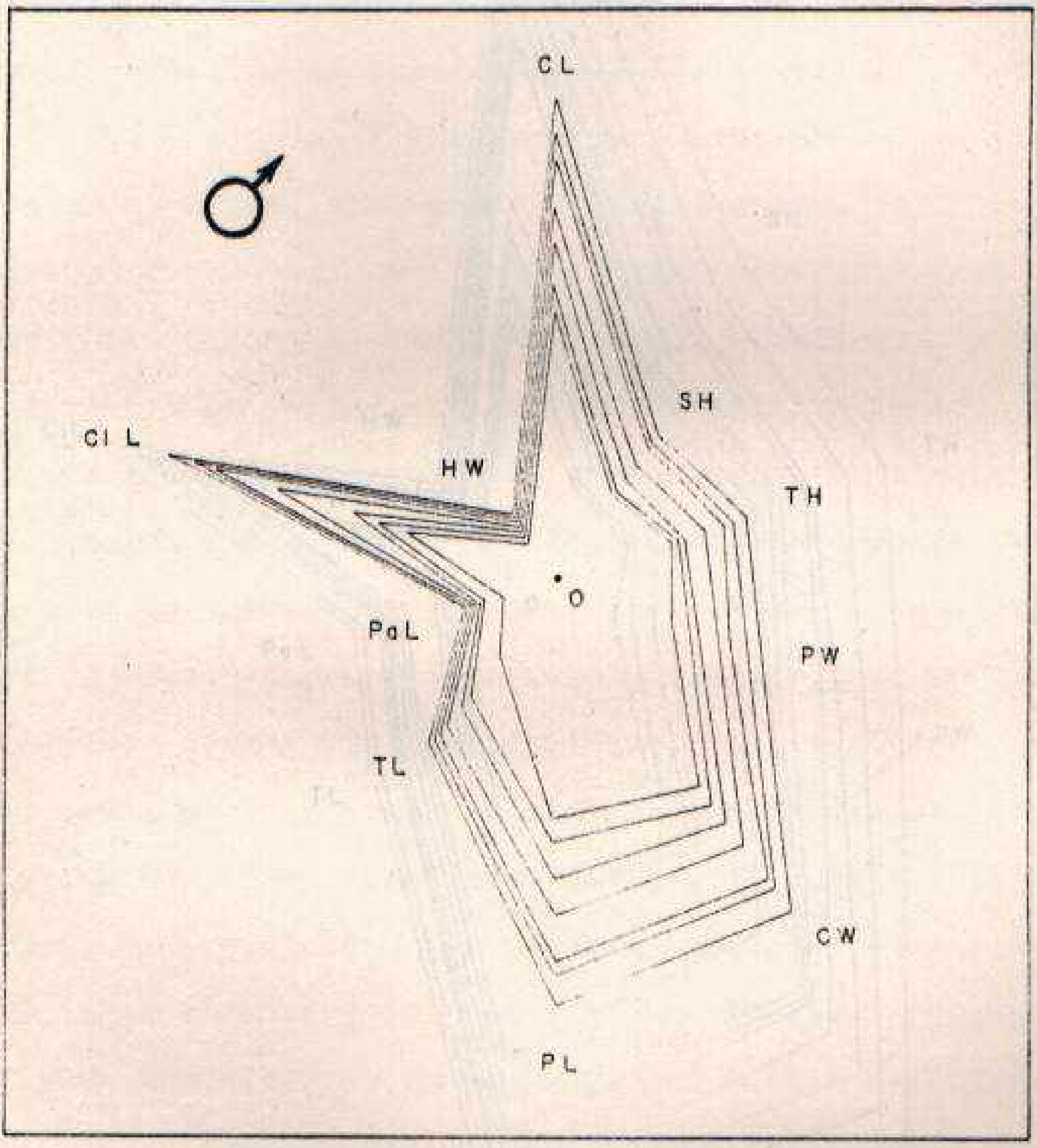


Figure 53. Male.

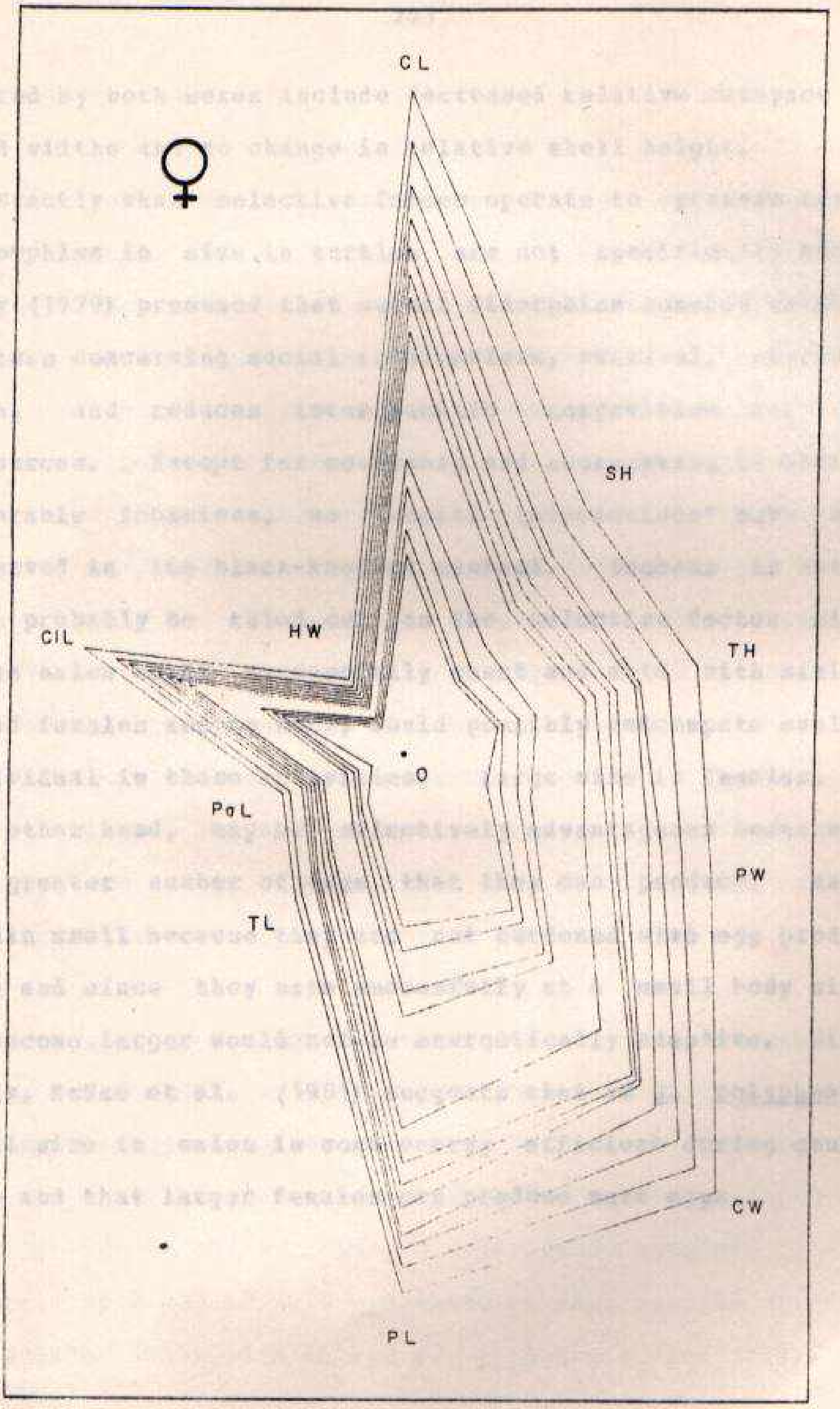


Figure 53. Female.

shared by both sexes include decreased relative carapace and head widths and no change in relative shell height.

Exactly what selective forces operate to promote sexual dimorphism in size in turtles are not specifically known. Bury (1979) presumed that sexual dimorphism somehow reflects factors concerning social interactions, survival, reproduction, and reduces interspecific competition for food resources. Except for courtship and aggregating to bask at favorable locations, no "social interactions" have been observed in the black-knobbed sawback. Success in mating can probably be ruled out as the selective factor since large males could successfully court and mate with similar sized females and in fact, could possibly outcompete smaller individual in these activities. Large size in females, on the other hand, may be selectively advantageous because of the greater number of eggs that they can produce. Males remain small because they are not burdened with egg production and since they mate succesfully at a small body size, to become larger would not be energetically adaptive. Similarly, McRae et al. (1981) suggests that in *G. polyphemus*, small size in males is more energy efficient during courtship and that larger females can produce more eggs.

Morphological Abnormalities

There have been few studies on the type or frequency of morphological anomalies in natural turtle populations. Ewert (1970) provided an overview of present knowledge concerning teratological conditions in turtles.

A total of 95 *G. nigrinoda* collected from the lower delta region on the Mobile Bay drainage in Baldwin and Mobile counties, were examined for external morphological abnormalities. Of these, 21 were hatchlings obtained from Gravine Island during the 1980 season, 14 were juveniles of unknown sex, 38 were males, and 22 were females. Each specimen was examined for the presence of nine abnormalities, including supernumerary carapacial and plastral scutes, asymmetrical carapacial and plastral scutes, carapacial and plastral injuries and pits, and head or limb injuries and terata. Results of this examination appear in Table 13.

Supernumerary Scutes. Supernumery carapacial and plastral scutes (Fig. 41), which result either through the addition of a new lamellar element, or by splitting an existing one, were the most common morphological terata encountered and were present in 40% of all the individuals examined. This compares with 43% of 2220 specimens of many species (Zangerl and Johnson 1957), 21% in 243 *M. terrapin* (Coker 1910), and

Table 13. Morphological abnormalities in 95 *G. n. delticola* (21 hatchlings, 14 juveniles, 38 males, 22 females) from the Tensaw River, Baldwin Co., Alabama. Values are percents of sample.

Terata	Hatchling	Juvenile	Male	Female	Sample
Carapace scute addition	33.0	14.3	10.5	40.9	23.2
Carapace injury	0.0	0.0	10.5	0.5	4.2
Carapace scute asymmetry	0.0	0.0	2.6	9.0	4.4
Plastron scute addition	9.5	21.4	10.5	36.4	16.8
Plastron injury	0.0	0.0	5.2	0.0	2.1
Plastron scute asymmetry	0.0	14.3	2.6	18.2	7.4
Head or limb deformity	0.0	0.0	2.6	0.0	1.0
Head or limb injury	0.0	0.0	13.2	4.5	6.3
Shell pits	0.0	0.0	13.1	18.2	9.5

10% in 476 G. geographica (Webb 1961). The number of hatchlings possessing supernumerary scutes fell between values for males and females. This is to be expected if such anomalies persist in the individual throughout life.

Ewert (1979) claimed that supernumerary scutes are not as common in adult turtles as they are in hatchlings. In the present study, 6 out of 7 (85.57%) sexually mature females and 5 out of 20 (25.0%) sexually mature males possessed supernumerary scutes. Collectively, 40.74% of the mature adult black-knobbed sawbacks had this type of anomaly compared to 42.8% in hatchlings. This 2.06% difference between adults and hatchlings is not significant ($X^2=0.250$ NS, $P>0.05$; 2x2 contingency table). Supernumerary scutes in G. nigrinoda appear to be as common in adults as they are in hatchlings and probably do not reduce an individual's survival ability.

The reason(s) for the vast differences between sexes (male, 21.09%; female, 77.27%) is not definitely known, but it may be associated with environmentally induced sex determination as reported in Testudo gracea and Emys orbicula (Pieau 1971), C. serpentina (Yntema 1976), and Graptemys sp. (Bull and Vogt 1979, Vogt 1980). Bull and Vogt (1979) and Vogt (1980) reported that high incubation temperatures (35°C) produced scute abnormalities in 29% of 41 individuals, where as at 25°C, only 5% of 60 had them. At 25°C, only males were produced while at 35°C, only females (Vogt 1980). Ynetema (1976) reported similar but varying conclusions. Thus, it seems likely that in G. nigrinoda, the abundance of supernumerary scutes is correlated with sex (females) because both phenomena are temperature dependent. As such, the sex of hatchlings might be cautiously predicted by the presence or absence of supernumerary scutes.

In addition to high incubation temperatures, other teratological agents include exposure to cold temperatures (Yntema 1960), dehydration (Lynn and Ullrich 1950), and possibly oxygen deprivation (Grabowsky 1970).

Occasionally, a greater percentage of individuals within a single clutch will have more supernumerary terata than expected. For example, on 28 September 1980 a clutch of hatchlings was discovered in the nest on Gravine Island. All three hatchlings (AUM #29449-29451) possessed several plastral and carapacial anomalies, the most obvious of which was the presence of 5 vertebral spines, rather than the usual 4. Since the nest cavity, at least at its discovery, was only a few centimeters below the surface of the sand, these individuals were probably subjected to inordinately high incubation temperatures and/or desiccating conditions. Either or both of these factors could be responsible for the deformities observed in these hatchlings.

Asymmetrical Scutes. Asymmetrical scutes were the next most common morphological anomaly encountered, representing 11.28% of all individuals examined. As with supernumerary scutes, asymmetry in scute shape was much more common in females than males (27.28% and 5.26%, respectively). That no instance of scute asymmetry was observed in hatchlings or juveniles suggest that as turtles age, interlaminal seams tend to "wander". Wandering plastral seam and laminal fusion have been reported in old *G. pulchra* (Shealy 1976) and senile *P. scripta* (Moll and Legler 1971). Scute asymmetry then appears to result as a consequence of aging.

Carapacial and Plastral Pits. Pits or cavities, averaging about 2.0 mm deep and 2.0-4.0 mm in diameter occuring in the shell, were fairly common adult anomalies (9.5%), particularly in older individuals. Similar pits were reported by Carpenter (1956) and have presumed to be related to aging. Their exact cause is not known.

Head or Limb Deformities. Head and limb terata in this wild caught sample were the least common form of abnormality and were found in only one individual (AUM #09271, adult female) among the 95 specimens examined. Her deformity was a minor one, consisting of a upturned claw on the right forelimb, rather than downturned, as is normally the case.

Under natural situations, individuals with severe deformities such as encephalocoele, cyclopia, monophthalmia, anophthalmia and limb loss probably would not survive even if they hatched successfully. Ewert (1979) reported that 2% of the turtle embryos of many species he studied possessed head deformities.

Only one individual in the sample displayed severe abnormalities. This hatchling (AUM #29258) possessed a warped and twisted shell with numerous supernumerary vertebral, costal, and plastral scutes. The left posterior set of marginals was bent upward at 90 degrees from the adjacent marginals. The tail was kinked, and the neck twisted so that the head appeared perpetually cocked to one side. Unlike the case where all members of one clutch displayed abnormalities, three other siblings were normal in shape. The deformed member was uppermost in the clutch, and thus probably experienced more variable thermal and moisture related conditions than did its siblings. Probably due to its warped shell, this individual was unable to retract its yolk sac completely and still possessed a broad yolk patch four weeks after hatching.

<u>Physical Injuries</u>. Injuries, in the form of missing extremities, or parts thereof, such as claws, toes, postanal tails, etc., or chips, holes and cracks in the shell,

were recorded for the sample. Males suffered significantly more accidents than did females (28.89% vs 4.54%; $X^2=5.19$*, $P<0.05$, 2x2 contingency table). The reasons for this are unknown, but may perhaps be related to some routine behavioral difference between sexes, or size related differences in vulnerability to predation.

Food Habits

Data regarding food preferences in turtles are abundant. Most of the earlier studies were purely qualitative, some recent workers have attempted to quantify their findings to better ellucidate species specific differences in food preferences in terms of food resource partitioning (Berry 1975, Vogt 1981).

Within the genus Graptemys, sexually dimorphic jaw differences occur in some species. Consequently, diets may be quite different between males and females within the same species. This phenomenon is conspicuous within the "broad-headed" group which includes G. geographica, G. barbouri, G. pulchra, and some G. p. kohni. Adult females of these species possess enlarged heads, broad, flat alveolar surfaces, and massive jaw musculature which adapt them well to their molluscivorous diet. Males of these species, on the other hand, have "normal-sized", unspecialized heads and feed primarily on insects (*G. barbouri*, Wahlquist 1970; *G. pulchra*, Shealy 1976); *G. geographica*, Vogt 1980,1981). Some species of *Graptemys* are omnivorous. These include *G. p. pseudogeographica*, *G.p. kohni*, and *G. o. ouachitensis* (Ernst and Barbour 1972, Mount 1975, Behler and King 1979, Vogt 1981). Webb (1961) found no sexual differences in food preferences between male and female *G. ouachitensis*, both consuming mostly insects. Female *Graptemys caglei*, the most recently described member of the genus, consume small, thin shelled gastropods, whereas males feed mainly on tricopteran larvae (Haynes and Mckown (1974).

Except for a few qualitative statements, little is known of the food habits in "narrow-headed" *Graptemys*. Cagle (1953) thought that *G. oculifera* fed exclusively on insects, although Ernst and Barbour (1972) reported insects and mollusks as preferred food. Behler and King (1979) reported a diet of insects and aquatic plants for this species. *Graptemys flavimaculata* is known to be primarily insectivorous, but snails are taken as well (Ernst and Barbour 1972). Wahlquist (1970) provides the only direct observation on feeding in *G. nigrinoda*. He observed this species pursuing and consuming beetles and dragonflys that had fallen into the river. Mount (1975) stated, based on the examination of fecal material, that the black-knobbed sawback is mostly, if not entirely, carnivorous, but that details of food preferences are lacking.

Aside from direct observation, there are basically three ways in which food habits in turtles are studied; through direct examination of stomach contents by dissection (most studies), through stomach flushing techniques (Legler 1977, Vogt 1981), and through the examiniation of fecal material (Folkerts 1968). Each method has various drawbacks, but the first method yields the most reliable quantitative results (Graham 1979). Consequently direct examination through dissection was used in the present study.

Gastro-intestinal contents were examined in a total of 37 _G. nigrinoda_ of various ages and both sexes. Of these, 32 (15 males and 17 females) contained food material and and were from the study area. To determine sexual differences in food preferences, diets of males and females were analyzed independently. The importance of items was determined as a function of average percent volume and percent frequency of occurrence. A summary of the results from the volumetric analysis is provided in Figure 54, and results expressed as percent frequency appear in Table 14.

Seasonal and Age-specific Differences

Substantial amounts of food material were present in the gastro-intestinal tracts during all months for which turtles

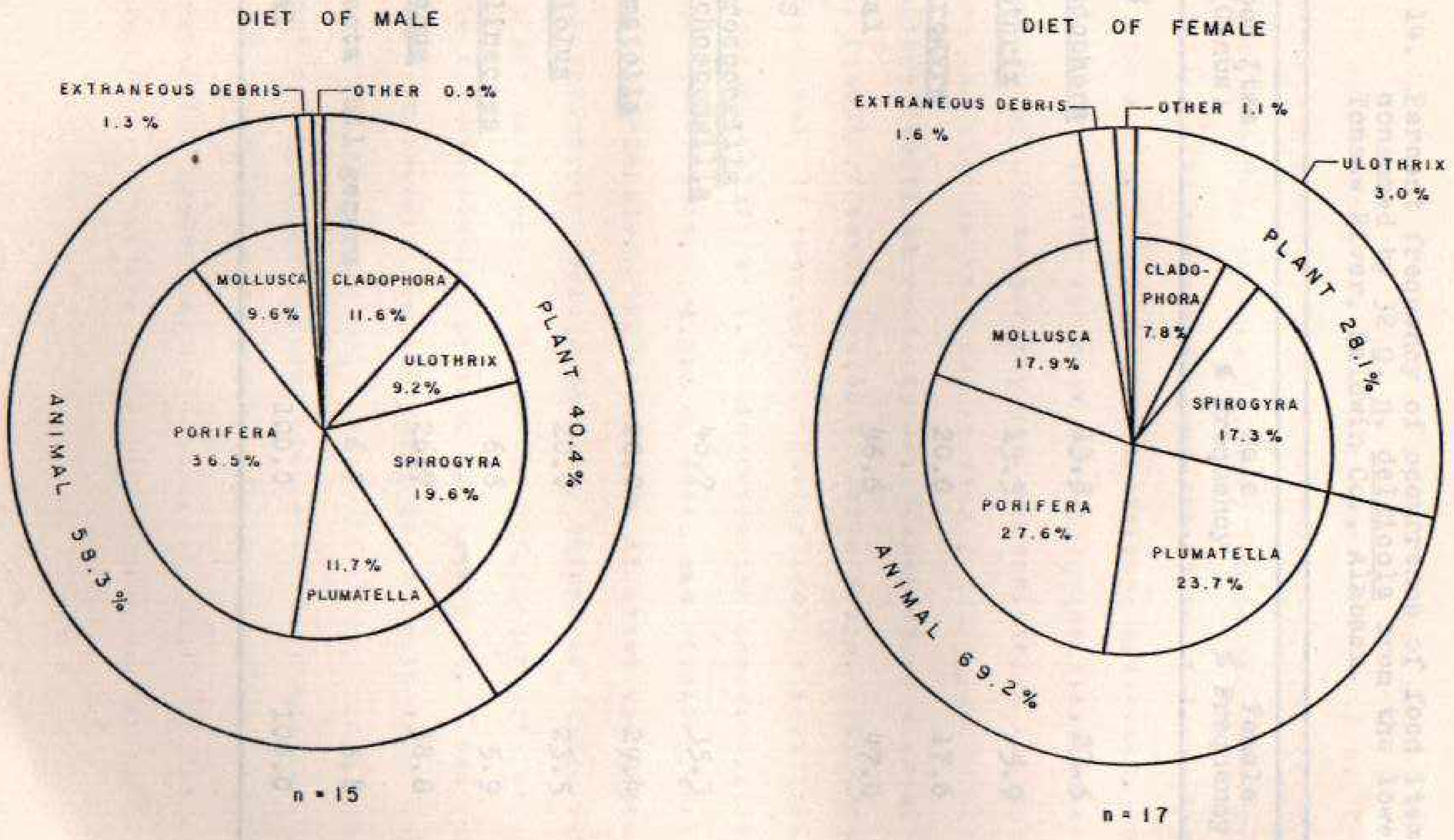


Figure 54. Diet of G. n. delticola from the lower Tensaw River, Baldwin Co., Alabama, as expressed in average percent volume of food item.

Table 14. Percent frequency of occurrence of food items consumed by 32 *G. n. delticola* from the lower Tensaw River, Baldwin Co., Alabama.

Food Item (Genus)	Male % Frequency	Female % Frequency
PLANTS		
Cladophora	13.3	23.5
Ulothrix	13.3	5.9
Spirogyra	20.0	17.6
Total	46.6	47.0
ANIMALS		
Corrospongilla *Trochospongilla*	46.7	35.3
Plumatella	20.0	29.4
Moliolus	20.0	23.5
Callinectes	6.6	5.9
Balanus	26.7	58.8
Insecta (all genera)	6.7	5.8
Total	100.0	100.0

were collected. Feeding therefore must begin upon or shortly after emergence from brumation in April and continues through November. Vogt (1981) reported that *G. pseudogeographica* and *G. o. ouachitensis* females did not begin to feed until after they deposited their first clutch of the year, generally in late May, and occasionally as late as 9 June. Shealy (1976) reported that *G. pulchra* begins to feed in May and ceases in October.

Small sample size did not permit a quantitative analysis of seasonal differences in types of food consumed. All food types, however, seemed similarly proportioned throughout the feeding period in both sexes. Several worker have noticed a substantial shift in diet with the attainment of sexual maturity, which, in most cases, involves a move from a predominantly carnivorous diet (mostly insects) to a predominantly herbivorous one (Pope 1939, Marchand 1942, Tinkle 1958, Clark and Gibbons 1969). In *G. pulchra* from the Conecuh River, the shift is to a greater proportions of the imported oriental mussel, *Corbicula maniliensis* (Shealy 1976). No *G. nigrinoda* below two years of age were examined for food contents, but approximately 38% were immature. No significant qualitative differences in diet between adults and juveniles were detected.

Sexual Differences

In both male and female black-knobbed sawbacks the same six major food items were consumed, but in different proportions. Because some differences were evident, Morista's Index (Morisita 1959) as modified by Horn (1966) for use with proportions, was used to measure the degree of food resource overlap between sexes. Niche overlap (Cx) is determined by the formula:

$$Cx = \frac{2\ E\ xi\ yi}{E\ xi + E\ yi}$$

where xi is the proportion food type species i in sample (x) (=males) and yi is the proportion of species i in (y) (=females). Where no overlap is present, Cx would equal zero, while with complete overlap, Cx equals one.

Diet overlap in *G. p. delticola* was determined for both percent volume and percent frequency, and Cx values were found to be 0.92 and 0.95, respectively. These exceptionally high values indicate that both sexes have essentially the same diet. As such, these results differ from those of all other *Graptemys* for which comparable data are available.

Food Type Proportions

Six food types accounted for 97.3% and 98.2% by volume of total food taken by females and males, respectively. Generally, stomachs and intestines were filled predominantly, or completely with only one type of food, indicating that once an individual begins to feed on a particular food item, it does so until satiated.

Vegetation, exclusively in the form of freshwater algae, made up a signifiant component for male and female _G. nigrinoda_, accounting for 40.4%/46.6% and 28.1%/44.4% by volume/frequency, respectively. Three major genera are represented, including _Spirogyra_, _Cladophora_, and _Ulothrix_. Algae have not previously been reported as a major food source in any turtle species. Vogt (1981) reported that the genera _Potamogeton_, _Lemna_, and _Vallisneria_, and algae, were plants most frequently consumed by _G. pseudogeographica_ and _G. o. ouachitensis_ in Wisconsin. Webb (1961) noted that algae occurred in the diet of _G. ouachitensis_ only incidentally. Why other plants are not eaten by _G. nigrinoda_ is unclear. It may be related to the fact that black-knobbed sawbacks are deep-water, riverine animals and as such would encounter vascular aquatic plants only rarely, at least when adult.

Various animals collectively represented the larger compontent of the sawback's diet, accounting for 58.3%/80.0% and 69.2%/82.4% by volume/frequency in males and females, respectively. Only three groups are among the major items represented: sponges, bryozoans, and mollusks. Surprisingly, encrusting Porifera represented the single most important food item both in percent volume and percent frequency of occurrence in males and females. Two species are utilized, *Trochospongilla leidyi*, a common species found in many brackish water locations, and *Corrospongilla becki*. The latter was formerly known only from the Atchafalaya River Basin of Louisiana and constitutes a considerable range extension for this species (Kenneth Manuel, pers. comm.). Sponge feeding as exhibited in *G. nigrinoda* is unusual because few vertebrates appear to be able to utilize sponges as a primary food source, perhaps due to the sponges toxicity or their penetrating spicules. Legler and Cann (1980) reported that one Australian chelid turtle (*Rheodytes leukops*) they examined contained fragments of freshwater sponge, but that the turtle was primarily insectivorous. When sawbacks consume sponges, the spicules are not digested, but pass out with the feces, appearently leaving the gastro-intestinal mucosa unharmed. The food value of the sponges consumed is not known, but considering the volumes injested (32.$\overset{05}{4}$%) and the frequency consumption (41.0%)

(average of both sexes), it is believed they make a substantial contribution to the turtle's nutritional requirements.

Bryozoans were the second most important animal food in both males and females. Two species were identified (Table 15) but only *Plumatella repens*, a form common in fresh and brackish water, was well represented. This animal was found in 20% of the males and 29.4% of the females and accounted for 11.7% and 23.7% , respectively, of their diet by volume. Bryzoans have not been reported as a regular food source in any other turtle species. Webb (1961) reported that large portions of a bryozoan colony were found in the stomach of one immature female *G. o. ouachitensis*.

Graptemys nigrinoda consume some mollusks, and although females eat relatively more than males (17.9% vs 9.6% by volume) they cannot be regarded as mollusk specialists. Only one *Modiolus* species, a colonial mussel of the family, Mytelicidae, was utilized. This bivalve was substantially represented in only 7 (22.0%) animals, but it was apparent by inspection that larger individuals selected larger mussels. Linear regression indicates that maximum bivalve length and turtle carapace length (Fig. 55) are strongly and directly correlated (r=0.98). A similar relationship was found in *G. pulchra* (Shealy, 1976) with respect to the imported oriental mussel.

Table 15. Taxonomic listing of rarely encountered food items consumed by *G. nigrinoda*.

- ENTOPROCTA
  - Urnatellidae
    - *Urnatella gracelis*
- MOLLUSCA
  - Bivalvia
    - *Corbicula maniliensis**
- CRUSTACEA
  - Cirripedia
    - *Balanus* sp.
  - Malacostraca
    - *Callinectes sapidus*
- INSECTA
  - Diptera
    - Chironomidae
    - *Stenochironomus* sp.
    - *Phenopsectra* sp.
    - *Dicrotendipes* sp.
    - *Xenochironomis xenolabis*
  - Trichoptera
    - Hydropsychidae
    - *Hydropsyche* sp.
- INSECTA (Cont.)
  - Coleoptera
    - Carabidae*
    - Chrysomelidae*
  - Hymenoptera
    - Formicidae
    - Vespidae*
  - Odonata
    - Libelullidae*
  - Lepidoptera*
  - Hemiptera
    - Coriidae*

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*Only from specimens from Clarke and Bibb Counties.

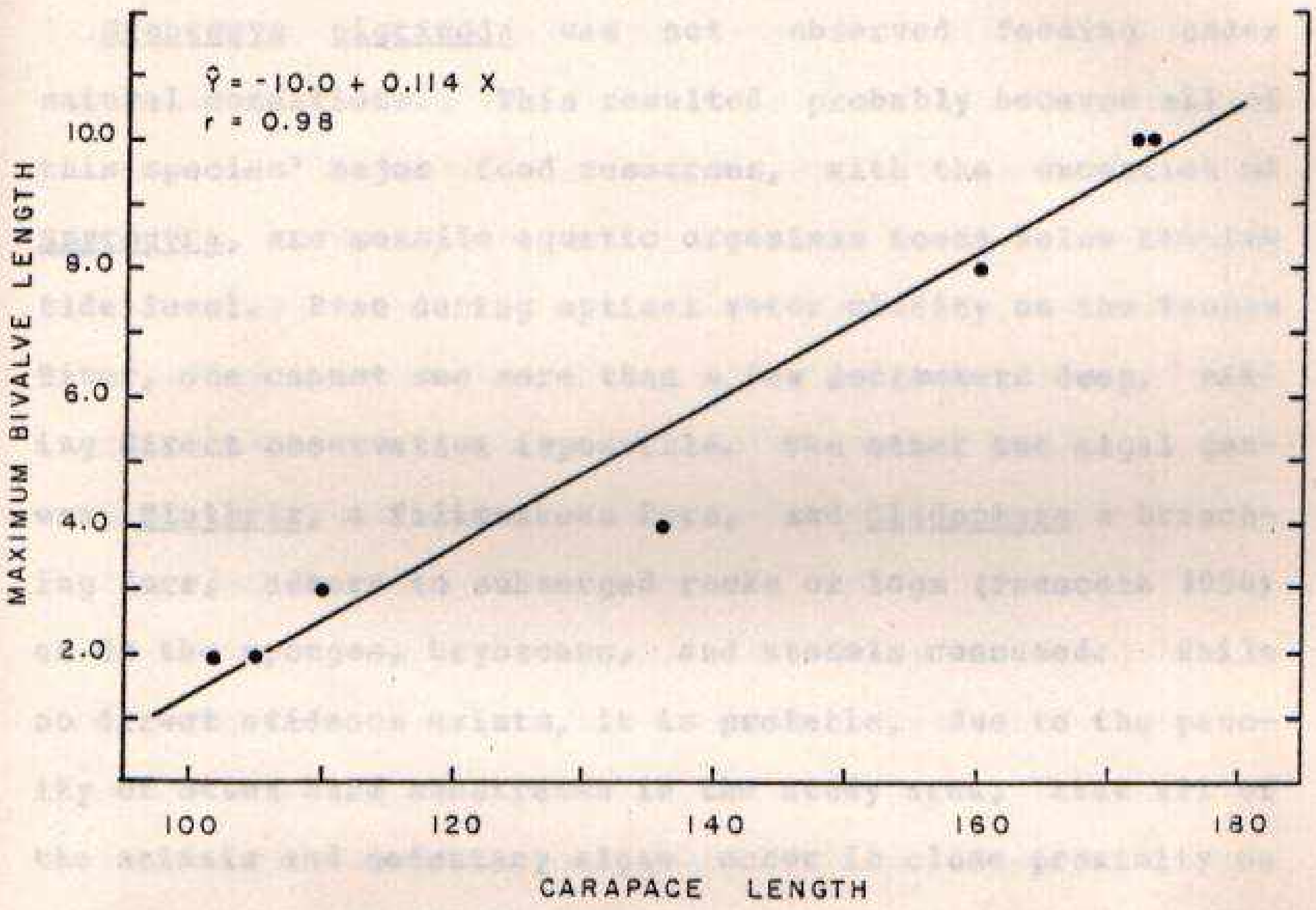

Figure 55. Selection for mullusk (Modiolus sp.) size by male and female G. n. delticola from the lower Tensaw River, Baldwin Co., Alabama.

Feeding Behavior

Graptemys nigrinoda was not observed feeding under natural conditions. This resulted probably because all of this species' major food resourses, with the exception of *Spyrogyra*, are sessile aquatic organisms found below the low tide level. Even during optimal water clarity on the Tensaw River, one cannot see more than a few decimeters deep, making direct observation impossible. The other two algal genera, *Ulothrix*, a filimentous form, and *Cladophora* a branching form, adhere to submerged rocks or logs (Prescott 1954) as do the sponges, bryozoans, and mussels consumed. While no direct evidence exists, it is probable, due to the paucity of other hard substrates in the study area, that all of the animals and sedentary algae occur in close proximity on the same log. Twenty-five percent of the black-knobbed sawbacks examined contained two or more of these sessile species. By contrast, in all instances where *Spyrogyra* was present, this plant made up 98-100% of the total food volume taken by the individual.

Terrestrial insects were seldom encountered in the gut contents. In view of this, it seems likely that *G. n. delticola* may occassionally feed at the surface, but that this species is predominantly a browser on submerged logs or other objects. Both types of feeding behavior were observed often in the lab and can probably be considered indicative of this behavior under natural conditions. Mahmoud and Klicka (1979) agreed that the study of feeding in captivity may be suggestive of the kind of feeding behavior exhibited in nature. The following observations were made in connection with and under the same conditions as the observations of courtship behavior. When first placed in a new tank, both individuals swam directly to the bottom and remained there motionless for approximately five minutes. Once aroused, the turtles began to investigate the aquarium. The inclination to feed was obvious in these animals as indicated by the stereotypic appetitive behavior of continuously moving the lower jaw. A conch shell, encrusted with barnacles and bryozoa, was closely examined by the sawbacks and several times bitten as they moved over the shell's surface. Objects of intrest, such as any protuberance, was closely approached, and after the tip of the snout was pressed against the object, it was either bitten or ignored. An algae-coated branch was similarly investigated and bitten.

Olfactory cues may be important to turtles in recognizing food (Harless 1979), but in many instances non-food items were bitten at as well. That G. nigrinoda will sometimes consume nonfood items was demnostrated in two individuals, an adult female engorged with pink string, and an adult male containing bits of styrofoam. Laboratory observations suggest that turtles are attracted to possible food first through visual cues, such as some distinctive object in the immediate environment, and then recognizes it through olfaction. Harless (1979) observed that moving food was preferentially selected over stationary food of the same type.

This mode of feeding, as exhibited in *G. nigrinoda*, is different from feeding behavior reported for other emydines. Sexton (1959) reported that *C. picta* hunted by dislodging prey from aquatic vegetation, and subsequently gave chase. Neotropical *P. scripta* is reported to spread aquatic vegetation apart with its forelimbs and to bite at the plant material indiscriminantly (Moll and Legle 1971). Neustophagia, the act of skimming organisms off the surface, was observed in *G. ouachitensis* by Vogt (1981).

In the laboratory, juvenile black-knobbed sawbacks consumed raw and cooked beef, pork, chicken, dead fish, insects, and on occasionally, *Elodea* sp. When a morsel of food was located, either at the surface or on the bottom of the tank, turtles would take it into the mouth and if small enough, swallow the food whole. If too large to be swallowed whole, the food item was held in the jaws and torn into smaller sizes with the foreclaws. Individuals without food would often attempt to "steal" it from another, often resulting in chases.

To summarize, *G. nigrinoda* has omnivorous feeding habits which are similar in both sexes. Additionally, that 78% of the animals examined contained only one type of food, suggests that black-knobbed sawbacks are opportunistic feeders, consuming to capacity whatever is most abundant and readily accessible. The food habits of *G. nigrinoda* in the lower reaches of the Mobile Bay drainage are believed to be unusual. Turtles of this species occurring elsewhere within the range, in purely fresh water, are likely to differ markely in food habits. Indeed, diet within *G. n. delticola* may change abruptly only a few miles above the level of tidal influence, as suggested by the examination of gut contents of two individuals from Clarke County; one an adult male and the other a juvenile male, which contained only insects of various orders (Table 15). Similarly, one adult female collected from the Cahaba River in Bibb County contained only the bivalve *Corbicula maniliensis* as determined from fecal material.

Populations

Dispersion of Adults, Juveniles, and Hatchlings

Most workers who have conducted field studies on turtle populations have noticed that habitats prefered by adults and juveniles may differ markedly. Moll and Legler (1971) for example, listed three different habitats for P. scripta in Panama. In this species hatchlings prefered the edges of floating mats of grass, whereas open lotic situations attracted juveniles and subadults. With maturity, turtles moved into fluviatile protions of the river which contained the plant Elodea.

Based on basking observations, G. nigrinoda was found to utilize two different habitats in the lower Mobile Bay delta region. Adults and juvenile females were most often observed in the main channels of the Tensaw, Mobile, and Raft rivers (Fig. 1). Adults often congregate on preferred basking sites which were invariably adjacent to deep, swift-flowing water. Furthermore, adult turtles apparently find log jams less attractive for basking, preferring instead single logs jutting from the water. Waters (1974) examined in detail the basking habits of G. nigrinoda on the Cahaba River of Alabama and found that preferred basking sites were stationary and well separated from shore by an expanse of open water. Although no detailed analysis was made in the present study, there seemed to be a direct relationship between current and the abundance of adult G. nigrinoda. Fôr example, the greatest number of black-knobbed sawbacks observed at any one location was a group of 12 individuals located on a large emergent log some distance from the south shore of the Raft River approximately 500 m east of its confluence with the Tensaw. This stretch of water represents an outside bend in the river, creating a swift current. When the observation was made, surface speed of the water was estimated at 1.5 m/sec at the basking site. Vogt (1980) reported that in G. pseudogeographica and G. o. ouachitensis, males were found primarily along the sloughs in moving water whereas females prefered quiet backwaters adjacent to islands and sloughs. No sexual difference was noted in habitat preference for adult G. nigrinoda, as both males and females were frequently observed basking on the same log in equal numbers. Waters (1974) reports similar findings for this species on the Cahaba River.

Hatchlings and young juveniles (1-3 years old judging from size) appear to prefer the relatively quiet and shallow waters of sloughs, bayous, and backwaters such as Gravine Island slough, Byrne's Lake, and Hurricane Bayou (Fig. 1). These areas were generally less than 20 m across and were well supplied with aquatic and shoreline vegetation. Because these habitats are sheltered from strong winds and have only weak currents, small limbs and branches remain along the shore where they fall, providing ideal basking platforms for small G. nigrinoda. During late fall (October and November), hatchlings were sometimes encountered basking on emergent branches along quieter stretches of the main river channels. Temporary occupancy of these habitats results because all known nesting beaches are adjacent to main river channels. Just how long hatchlings remain in these areas or how much time is required to make the journey from the nesting beach to backwater areas, is not known. Habitat separation between adults and juveniles probably has several adaptive advantages, but may in part be due to differences in food, basking site, and water current requirements, or may be predator related. Moll and Legler (1971) list reduction of intraspecific competition for food and basking sites as major advantages to differential microhabitat utilization between hatchlings and adults.

Population Density

An estimate of population density by conventional mark-recapture methods was not possible due to the extremely low incidence of recapture.

Although an absolute population estimate was not possible, relative abundance as determined by collecting can be equally meaningful. Cagle (1954a) noted that the black-knobbed sawback was the most common turtle in the Black Warrior and Alabâma River systems. Similarly, Mount (1975) reports that this species is the dominant turtle in the delta region of the Mobile Bay drainage. McCoy and Vogt

(1980), who determined population densities throughout its range, found that *G. nigrinoda* to be the most abundant species in both basking and spot trapping surveys.

The relative abundance of various species of turtles sharing the main river channels with *G. nigrinoda* was estimated from trapping records. Because traps were not baited, turtles were not differentially attracted to them. As such, this trapping method represents a nearly unbiased sampling technique for adult emydines.

Between August 1979 and September 1980, a total of 186 turtles were traped in the vicinity of Gravine Island. Of these 77 (41.4%) were *G. nigrinoda*, 56 (30.1%) were *P. alabamensis*, 46 (24.7%) were *P. concinna*, and 7 (3.8%) were *P. scripta*. The black-knobbed sawback is clearly the dominant emydine species in the study area, but *P. alabamensis* and *P. concinna* are well represented also. That all three species are relatively abundant in this region is as expected because they share fluviatile habitat preferences, but why *G. nigrinoda* are more numerous than any of the other species, is not at all certain. *Pseudemys scripta*, on the other hand is primarily a lotic species (Ernst and Barbour 1972, Mount 1975) and apparently only rarely enters rapidly flowing water.

Other turtle species known to share habitat with *G. n. delticola* includes *M. temmincki*, *C. serpentina*, *T. spiniferus*, *K. subrubrum*, and *S. minor*, and *G. pulchra*.

In some areas the black-knobbed sawback is exceedingly abundant. The heaviest concentration that McCoy and Vogt (1980) observed was on the lower Tensaw between its confluence with the Middle River and Bryant's upper landing, Baldwin County, Alabama. In this stretch of river, they observed more than 150 basking individuals per hour. They believed that this area was particularly attractive to *G. nigrinoda* because it is above the effect of the tide and is well supplied with optimal basking sites. No such densities were observed in the vicinity of Gravine Island, but this species does occur there in relative abundance despite the brackish water.

Population Composition

Of the 77 *G. nigrinoda* collected from trapping efforts, 31 (40.2%) were adult males (CL>83 mm), 29 (37.7%) were adult females (CL>183 mm), and 17 (22.1%) were juvenile females.

Sex Ratios

There have been many reports of unequal sex ratios in natural populations of turtles, with females generally outnumbering males (*G. agassiz* Woodbury and Hardy 1948, *Sternotherus odoratus* Risely 1933, *Sternotherus depressus* and *S.*

carinatus Tinkle 1958, *M. terrapin* Hildebrand 1932, *T. ornata* Legler 1960, *G. pseudogeographica* and *G. o. ouachitensis* Vogt 1980) but sometimes the reverse is true (*M. terrapin* Cagle 1952, *C. picta* Ream and Ream 1966, *P. scripta* Moll and Legler 1971). In many of these instances unequal sex ratios may have resulted from improper methodology and selective sampling (Ream and Ream 1966, Gibbons 1970b). In view of this, Bury (1979) encouraged caution in accepting evidence of unequal sex ratios in natural populations of turtles. Bury found that in 39 studies representing 20 different species, 71% showed sex ratios not significantly different from 1:1. In the present study, sex ratio of adults (male:female) was essentially equal (1:0.94). Hatchlings resulting from the 1980 nesting season on Gravine Island were represented by 11 males and 10 females or, essentially 1:1. Vogt (1980) found a slightly different sex ratio for *G. nigrinoda* on the Cahaba River, Perry County, Alabama, where males were less abundant than females (1:1.7) but offered no indication as to whether these results were for all age groups or exclusively adults. In *G. pseudogeographica* and *G. o. ouachitensis*, Vogt (1980) observed sex ratios highly skewed towards females, but attributes this to biased sampling. Timkin (1968) found a 1:1 sex ratio in *G. pseudogeographica* in the upper Missouri River.

Size Distributions

Because turtle nets were constucted with 7.6 cm nylon mesh and set in main river channels, only animals that were larger than 80 mm CL were caught. Consequently, the sampling method was highly biased towards adult turtles.

Of the total collected, adults represented 77.9% of the sample, and juveniles (all females) made up the difference. No juvenile males or hatchlings were collected in the nets. An assumption could be made that juvenile males occur at the same density as juvenile females. In view of the fact that adult and hatchling sex ratios approach unity, there is no a priori reason to suspect that this assumption is invalid. The lower delta population of G. nigrinoda in the vicinity of Gravine Island would, then, be composed of 33% males, 31% females, and 36% juveniles. This juvenile estimated proportion is very close to the 31% reported by Bury (1979) as a composite average for 6637 individuals of several species.

The distribution of size classes in the male sample was normal, with individuals in the 106-110 mm CL class most numerous (Fig. 56). The sample of females displayed much wider variation due to the inclusion of juveniles, but adults also show a normally distributed curve. The most frequently observed size class in adult females was 201-210 mm CL (Fig. 57). Shealy (1976) found a similar distribution in male G. pulchra, but females of this species between

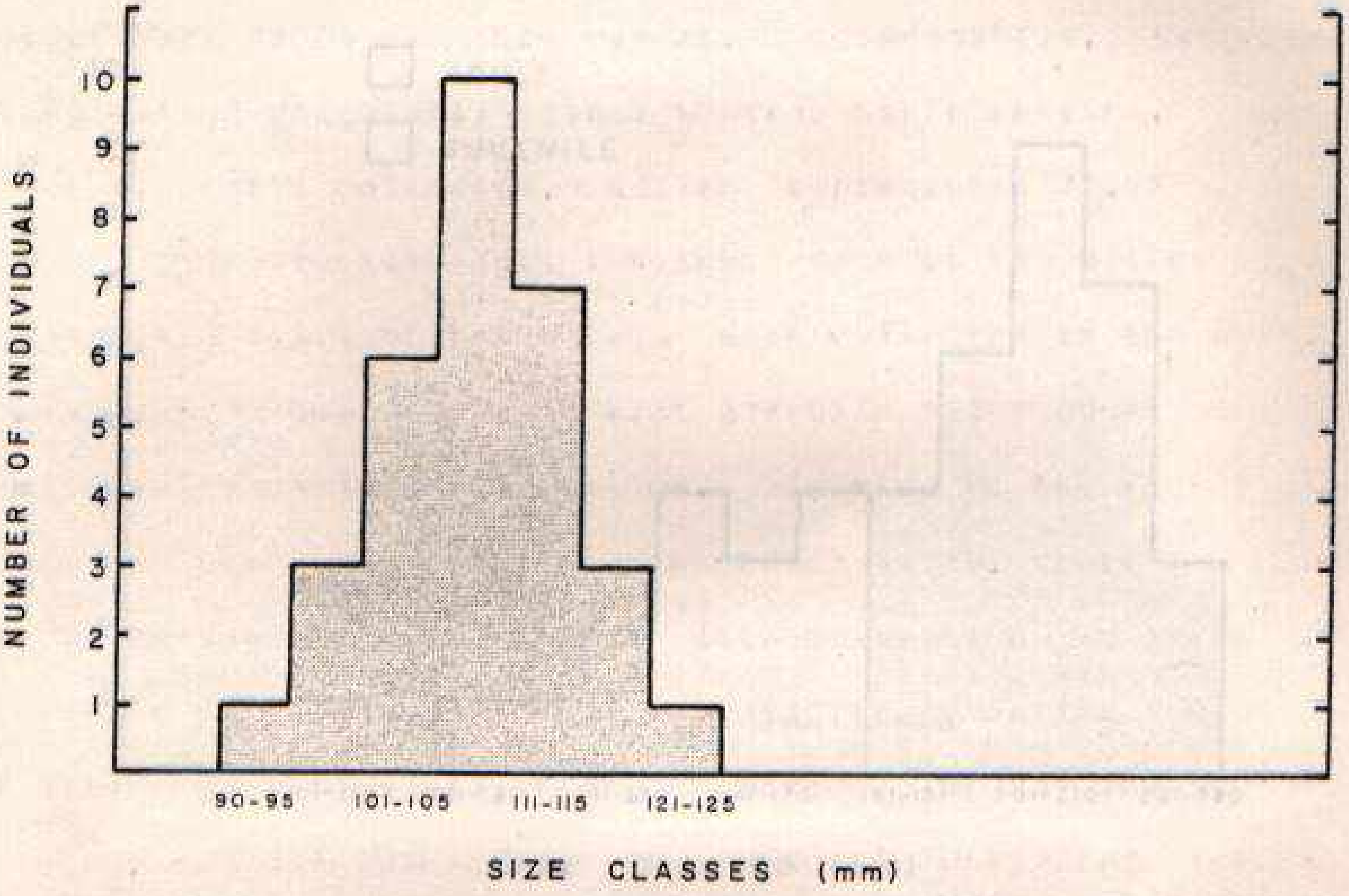

Figure 56. Size distribution in male *G. n. delticola* collected from traps; Tensaw River, Baldwin Co., Alabama.

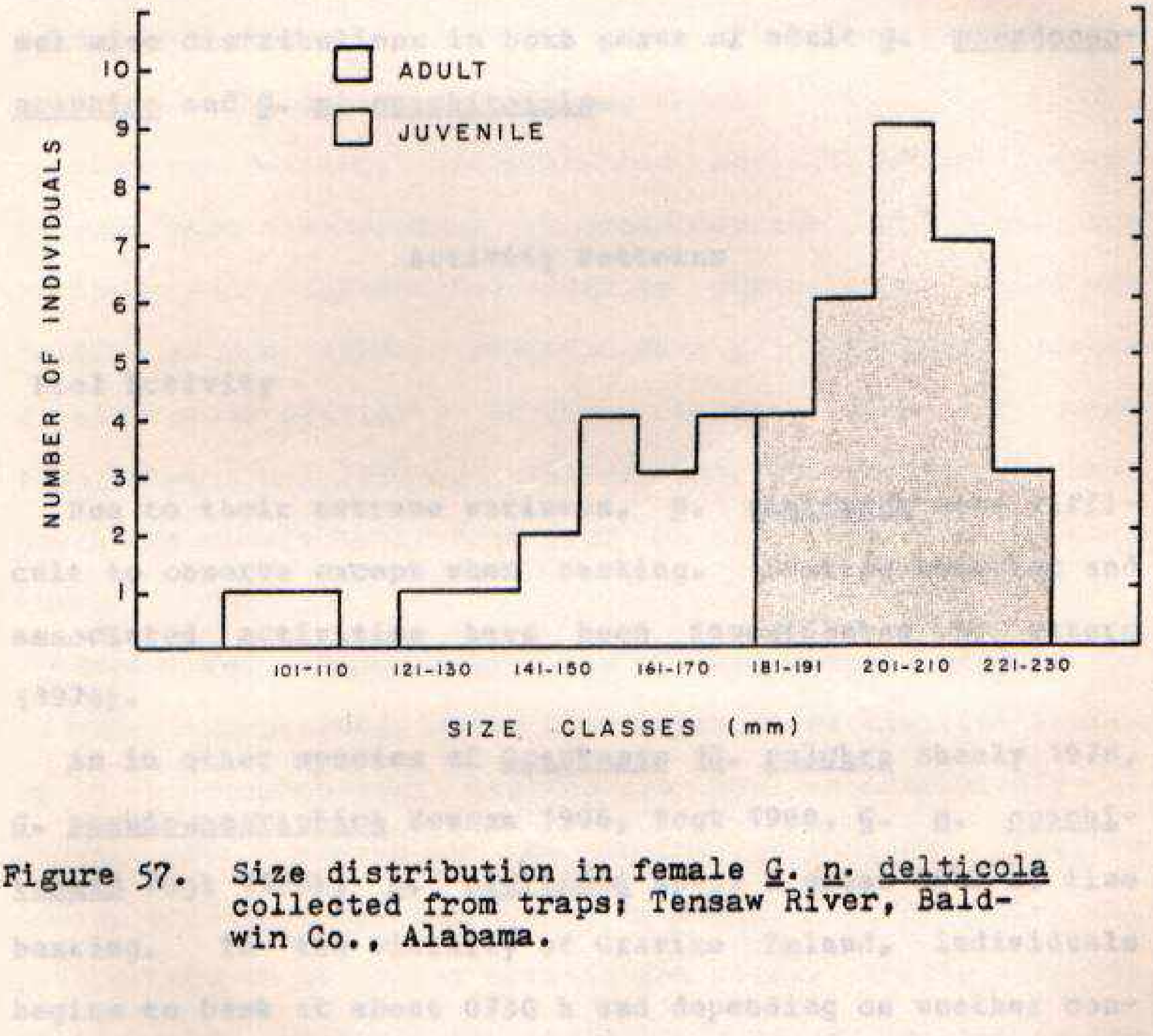

Figure 57. Size distribution in female G. n. delticola collected from traps; Tensaw River, Baldwin Co., Alabama.

125-175 mm CL were rare. Shealy attributed this to the rapid transition of individuals from one size class to another as a result of rapid growth. Vogt (1980) found normal size distributions in both sexes of adult G. pseudogeographica and G. o. ouachitensis.

Activity Patterns

Diel Activity

Due to their extreme wariness, G. nigrinoda were difficult to observe except when basking. Basking behavior and associated activities have been investigated by Waters (1974).

As in other species of Graptemys (G. pulchra Shealy 1976, G. pseudogeographica Newman 1906, Vogt 1980, G. o. ouachitensis Vogt 1980), G. nigrinoda spend a great deal of time basking. In the vicinity of Gravine Island, individuals begins to bask at about 0730 h and depending on weather conditions and time of year, may be seen basking all day. In the spring, turtles emerge from the water earlier and remain on the basking sites for longer periods of time. In late summer, a few individuals can be observed basking anytime during the day, but most cease this activity by late morning. Waters (1974) noticed in the Cahaba River population he studied, that basking activity had two peak periods of activity, one during mid-morning, and another in the early afternoon. Generally speaking, the same was observed in the Tensaw population, except that fewer turtles basked in the afternoon than during the morning hours.

When not basking, black-knobbed sawbacks probably spend considerable time feeding, whereas courtship and mating may be the primary non-basking activity during early spring and fall. Waters (1974) reported that _G._ _nigrinoda_ forages within close proximity of their basking sites and cease feeding at about 2200 h. Indeed, near Gravine Island, sawbacks may obtain their food from the same logs on which they bask.

Except for females during the nesting season, black-knobbed sawbacks probably spend the night in an inactive state. It is unknown whether turtles can manuver effectively at night. As reported in the section on nesting, females appear to locate the beach they intend to nest on during the late afternoon or early evening and remain in the vicinity until dark. Where these individuals go on reentering the water after nesting is not known. Perhaps they remain in shallow water near where they entered and disperse in the morning. Telemetric studies would be an effective means by which these and related questions might be answered.

Chaney and Smith (1950) reported that *Graptemys* can be easily taken at night from shallowly submerged branches and logs. Similarly, Waters (1974) observed that *G. nigrinoda* "bed down" in shallow water on submerged logs or vegetation. On the Tensaw River, several attempts to locate sleeping turtles at night with the use of a spotlight proved unsuccessful. Ren Loenhefner (pers. comm.) was similarly unsuccessful in attempts to locate *G. pulchra* and *G. oculifera* on the Pearl River of Mississippi and Louisiana.

Seasonal Activity

Details of the various aspects and timing of seasonal activity have been described in the preceeding sections in there appropriate places. For convenience, seasonal activity patterns as well as associated physiological and morphological changes, are summarized in Figure 58.

Predation

Eggs

Eighty-two percent of all *G. nigrinoda* nests discovered on Gravine Island were destroyed by predators. High rates

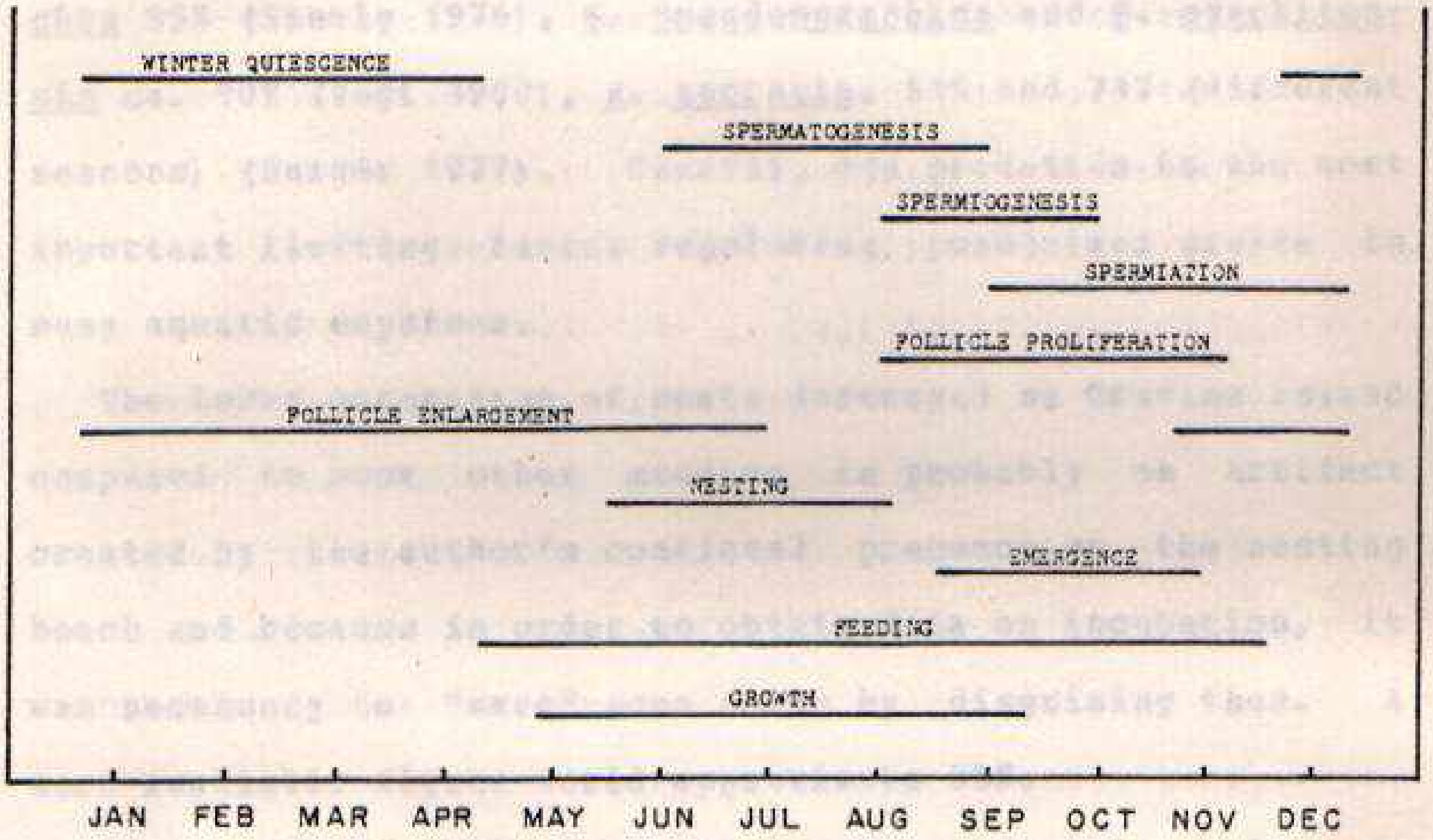

Figure 58. Seasonal activity patterns and associated physiological and morphological changes in G. n. delticola from the Tensaw River, Baldwin Co., Alabama.

of predation have also been reported for P. *floridana*, 95% (Allen 1938), P. *scripta* ca. 100% (Cagle 1950), and 97% and 97% (different localities) (Moll and Legler 1971), G. *pulchra* 95% (Shealy 1976), G. *pseudeographica* and G. *ouachitensis* ca. 90% (Vogt 1980), M. *terrapin*, 51% and 71% (different seasons) (Burger 1977). Clearly, egg predation is the most important limiting factor regulating population growth in many aquatic emydines.

The lower percentage of nests destroyed on Gravine island compared to most other studies is probably an artifact created by the author's continual presence on the nesting beach and because in order to obtain data on incubation, it was necessary to "save" some nests by disguising them. A more realistic figure would approximate 95%.

Of several potential egg predators suspected, only one, the Fish Crow (*Corvus ossifragus*) proved important. This animal alone accounted for 100% of the predator-robbed turtle nests on Gravine Island. Working in flocks of 5-10 birds, Fish Crows attack nests early in the morning between first light and sunrise (0500-0600 h), within 12 hrs of deposition. Nests which escaped notice the first day were generally safe from subsequent predation. Moll and Legler (1971), Shealy (1976), and Vogt (1980) noticed a similar decrease in predation rate with nest age. No direct observations of crow predation were made because the slightest disturbance (such as a person walking on the opposite side of the nesting beach) caused them to cease their activities.

Several experiments and observations were made to illucidate the menthod by which fish crows locate turtle eggs, and are enumerated here.

1) Crows were often attracted to and subsequently excavated test nests.

2) Crows were attracted to false "nests" which had neither turtle tracks leading to or away from them.

3) In a few instances where turtle nests were particularly well camouflaged, crows walked directly over them without discovering their location.

4) In one instance crows excavated a nest but because the nest cavity was slightly off center from the surface disturbance, crows were unsuccessful in finding the eggs. These crows dug down along side the nest chamber to within 10 mm of the eggs but were appearently unable to detect their presence.

5) Twice, when turtles were discovered in the process of ovipositing, the nest when completed, as well a 1 m length of turtle track in both directions from the nest was disguised by carefully smoothing the ground surface. A surface disturbance resembling an area where a nest had been made was constructed at one of the turtle tracks new end point.

In the morning it was discovered that the false nest had been attacked by crows while the real nest remained undisturbed.

6) In the late afternoon on 13 July 1980, a clutch of four turtle eggs was buried at normal egg depth (ca. 13 cm) in a open expanse of level Type I sand and the surface was smoothed as previously described. Five meters away a false nest was constructed, as described in #4. Five meters from both the false and real nest, an adult female _G. nigrinoda_ collected nesting the night before was allowed to crawl away from this area, leaving behind a conspicuous trail. Except for a few cautiously placed foot prints, no other irregularities were present in the immediate area.

At 0800 h the following morning, this area was examined for signs of fish crow activity. The disguised real nest was not discovered, nor was the slightest attention paid to the turtle tracks. The false nest, however, had been "robbed" by fish crows.

Seemingly, Fish Crows locate turtle nests simply by being attracted to a concentrated ground surface disturbance and then excavating a hole directly in the center of it. Crows apparently do not utilize olfactory cues (observation #2.) and probably do not follow turtle tracks to the nest (i.e. to where the tracks end). That crow tracks are abundant and concentrated in some areas suggests that they may be attracted to many different ground surface irregularities, but excavate only those that in some way resemble a turtle's nest.

How Fish Crows learn to associate a ground surface disturbance with an available food source is not known. They could not possibly have learned this behavior by watching female turtles nest because crows are decidedly diurnal, whereas oviposition in _G. nigrinoda_ occurs invariably at night. It is possible that crows, having observed a diurnal nester, learned to recognize buried turtle nests and subsequently transferred this ability to black-knobbed sawback nests. Mount (pers. comm.) has observed Boat-tailed Grackles standing behind nesting _P. scripta_ removing eggs as they are released. Burger (1977) found that Laughing Gulls remove eggs of _M. terrapin_ after they have frightened turtles from the nest. But even if nest-finding behavior was learned by watching nesting turtles, only a very small percetage of crows would be likely to observe such an event. That many crows appear to share the ability in locating nests suggests that this behavior is transferred from one individual to another, probably by watching conspecifics perform.

It was noticed that the ability, or at least the tendency of crows to rob turtle nests waned as the frequency of nesting activity decreased late in the season. During the last

16 days of the 1980 nesting season (20 July through 5 August) only 40% of the nests were taken by crows, compared to an estimated 95% at the peak of the season. Crows probably give up searching for turtle nest when the rewards for this activity no longer equal the energy expended, and spend more time exploiting other more plentiful food resources.

Once nests are located by crows, excavation is rapid, possibly requiring no more than 5-10 minutes. Nests preyed upon by crows are conspicuous and readily identifiable (Fig. 59). After exhuming the eggs, crows generally (74%) carry them in their bills away from the nest to nearby trees to be consumed. Eggshells litter the ground beneath such perches.

Shealy (1976) found that the fish crow was the major diurnal predator and that the racoon was the most frequent nocturnal predator, but did not specify their relative importance. Burger (1977) and Vogt (1980) listed red foxes and raccoons as the primary predators of *M. terrapin* and *Graptemys* eggs, respectively. Moll and Legler (1971) found that the teiid, *Amevia ameiva*, and the armadillo, *Dasypus novemcinctus*, were the most important predators on neotropical slider eggs. They determined that both of these predators locate nests by using olfactory cues resulting from the turtles urine. Likewise, Shealy (1976) reported that raccoons can, presumably by odor, locate *G. pulchra* nests up to 4 days after deposition. Shealy does not comment, however,

Figure 59. Typical appearence of G. n. delticola nest after predation by fish crows (Corvus ossifragus).

whether or not *G. pulchra* urinate on nests. Racoons (*Procyon lotor* were extremely abundant in the delta region and were commonly seen foraging even during the day, yet, they did not prey on turtle eggs on Gravine Island. This might be explained by the fact that unlike *P. scripta*, *G. nigrinoda* females do not urinate while constructing nest.

Several authors have reported ants as occasional predators on turtle eggs (Cagle 1937, Hammer 1969, Moll and Legler 1971, Burger 1977). Moll and Legler, (1971) found that fire ants entered eggs though small pin-sized holes which these authors presumed ants make themselves. Mount (1981) and Mount and Trauth (1981) demonstrated the likelyhood that the fire ant *Solenopsis invicta* regularly prey on eggs of the lizard *Cnemidophorus sexlineatus*, and probably on the eggs of other reptile species as well. While fire ants were present on Gravine, no instance of predation by them was noted.

Hatchlings, Juveniles, and Adults

No instance of predation was observed on hatchlings. However, there are many animals residing in the study area quite capable of consuming hatchling *G. nigrinoda*. Among these in presumed order of importance are a host of preditory fishes including both fresh and marine forms, alligators, and various wading birds. The Great Blue Heron and Yellow Crowned Night Heron were particularly abundant in the delta region. The latter bird often left droppings along the beaches of Gravine Island. An examination of about a dozen of these pellets, however, yielded only crab remains. Moll and Legler (1971) thought that the caiman (Caiaman crocodilus) was the major preditor of P. scripta hatchlings, but found that the Great-tailed Grackle also preyed regularly on them. Vogt (1980) reported that Redwing Blackbirds and grackles were observed eviscerating hatchling G. pseudogeographica and G. o. ouachitensis. Crows remain on Gravine Island throughout the period of hatchling emergence but since hatchlings emerge only at night, crows would have to pick them from the water or basking sites. The liklihood of this occurring seems remote. As turtles become larger, and their shells harden, potential predators become fewer in number until when fully mature, alligators and possibly otters would be the most significant predator. Several male G. nigrinoda possessed shell injuries thought to have been made by alligators.

Relations with Man

With the exception of crows, man serves as the greatest threat to G. nigrinoda in the Tensaw. Francis Mayer, a long time resident of the area, informed me that it was once the seasonal pasttime of Tensaw River area residents to collect turtle eggs on Gravine Island for human consumption. In times past, Mr. Mayer explains, it was not unsual for an individual to fill a five gallon bucket with turtle eggs in a single night. Barring exaggeration, this indicates that turtles once nested on Gravine Island in much greater numbers than they do now. Indeed, the total number of turtle eggs deposited on Gravine during the entire 1980 season would not half fill a five gallon bucket.

Apparently, there is still a market for G. nigrinoda and other emydines in this region. A man at Cloverleaf Landing once offered me $3.00 per turtle for as many as I could provide.

The greatest threat people pose to the black-knobbed sawbacks existence and to all the delta biota stems from the recreational and commercial activities in the area. During the week, commercial fishermen setting trot lines and gill nets undoubtedly take, drown, or otherwise kill a great number of sawbacks. A commercial fisherman informed me that on one occasion he lost track of one of his nets for about a week and when it was finally located, the net was so heavy from the weight of turtle carcasses that he could not get it into his boat! On the weekends, thousands of recreationists descend on the delta for the purpose of fishing, skiing, camping, and pick-nicking. The effects on nesting activity by the presence of numerous individuals on Gravine Island has already been stated. Maliciousness is rampant not only in children but in adults as well. It is estimated that 75% of all the potential data that could have been secured during the 1980 nesting season was lost to mindless destruction of nests, nest enclosures, drift fences, and other items. Many adult turtles are probably killed by collisions with boats, particularly on weekends when human activity is greatest. Two *G. nigrinoda* and one *P. alabamensis* were discovered with their carapaces cracked from an impact with boat or motor.

Defenses

As with most turtles, the black-knobbed sawback's major defense is to withdraw into its shell. Besides this, and occassional hiss and strong swimming ability appear to be their only defenses. This species could not be induced to bite. The vertebral and marginal spines might be considered as defense structures, but the liklihood that they are employed for this purpose seems slight in view of the fact that, especially in adult females, these spines become mere nubs. Folkerts (pers. comm.) suggests that vertebral spines in hatchlings might function as disruptive camouflage, making them difficult to see among the tangles of branches in which they frequently bask.

Basking *G. nigrinoda* are extremely wary of movements not only from boats, but particularly along shore. Flight distances vary from 100 to 10 meters. Waters (1974) observed that black-knobbed sawbacks in some areas of the Cahaba River were less cautious than turtles in other parts of the river, and he attributed this to a lack of persecution.

Parasites

Virtually all *G. nigrinoda* examined harbored some parasites. Leeches (*Placobdella* sp.) found mostly in axillary and inguinal pockets, but also on the neck and tail, were present on 24% of the turtles. No difference with respect of age or sex was noted. Shealy (1976) discovered that *Placobdella* was seasonally abundant on *G. pulchra*.

The gastro-intestinal tracts were examined for internal parasites in 38 individuals. Incidence of the acanthocephalan *Neoechinorhyncus* sp. in turtles 4 years and older (n=32) from Baldwin County, was 91.4%. Since the three turtles examined under three years of age did not contain acanthocephalans, it seems likely that individuals do not contract this parasite until at least three years of age. Acanthocephalans were more concentrated in the portions of the small intestines, than in the large intestines. None were ever found in the stomach. No inter-sexual differences were noted in the degree of acanthocephalan infection.

Minute nematodes were often found within the stomachs containing algae. In view of their gastric location, it is believed that they were not parasitic but free living forms injested incidentially.

IV. SUMMARY

Life history studies were conducted on the southern black-knobbed sawback *Graptemys nigrinoda delticola* Folkerts and Mount. The black-knobbed sawback is most closely related to and shares many morphological features with *G. oculifera* and *G. flavimaculata*. Together, these three allopatric species form the "narrow-headed" *Graptemys* complex of the testudinate family, Emydidae.

Graptemys nigrinoda is desidedly fluviatile in its habitat requirements and prefers large, muddy-bottomed rivers of the Alabama and Tombigbee systems of Alabama and Mississippi, to which it is restricted. Two subspecies exist. The nominant race occurs in the Alabama River system wheras *G. n. delticola* is restricted to the delta region of the Mobile Bay drainage. Individuals from all other localities are intergradient.

Field studies, centered at Gravine Island, Tensaw River, Baldwin Co., Alabama (R1N,T2S; 30°47'W, 87°80'N) were carried out from August 1979 through September 1980. To document nesting activity, the author remained in residence on Gravine Island from June through September, 1980. A total of 102 hatchlings, juveniles, and adults were collected from the study area. Preserved specimens collected from Baldwin Co., and housed in the Auburn University Museum were utilized in part for growth analysis and related studies.

Courtship was observed in isolated, lab reared juveniles and is characterized by a series of rapid head nods (5 per sec.) performed when conspecifics face each other snout to snout. Mating was not observed.

Gonadal cycles in both sexes were similar to other North American emydines, differing only in the timing of phases. Spermatagonia are present in abundance by April, having presumably proliferated during the winter and early spring. Spermatogenesis begins in June, peaks in August, and ceases in September. Spermiogenesis initiates in August, peaks in September, and is essentially completed by late November. Spermiation begins in September and continues through early winter. Epididymides contain large amounts of sperm in all months except August, when only trace amounts are present. Relative testicular and epididymal weights are correlated with the spermatogenic cycle.

Follicular proliferation occurs in August and September. Follicules presumably enlarge during the winter and early spring, attaining preovulatory size by mid-April. Ovulation occurs from May to late July. No latent period was observed.

Nesting is strictly nocturnal, and on Gravine Island it extends from mid-May to early August with peak activity from mid-June to mid-July. Inter-nesting period could be as long as 30 days.

Most turtles stranded (91.2%) and nested (61.8%) on the north beach of the main nesting area of Gravine Island. The route taken by the female in search of a nest site is characteristically winding and significantly longer than the route taken from the nest back to the water, which is basically direct. A hormonal feedback mechanisms mediated by the hypothalamus is hypothesized to account for the variation observed in nesting activity. Nest-sites appear to be chosen at random with respect to sparsely vegetated and barren subsrates, but hillocks seem to be prefered. Optimal nest sites are in open sunny situations of fine, clean, homogeneous sand, located well above the water level, and within 50 m of shore. Turtles preparing to nest congregate at sunset from 30-50 m offshore and begin to strand shortly after dark. Pre-nesting activity is characterized by seemingly random wanderings with frequent apparent attempts to test the substrate for nesting suitability. Substrate testing behaviors include the "test-scratch", which is performed with the forelimbs and results in the carapace being covered with sand, and test nest construction. The frequency of test nests increases with the location of the actual nest.

In most cases, no differences between the test nest and the actual nest were found, with respect to the environmental parameters examined. Nest construction, which begins when the proper position has been attained, is performed entirely with alternating strokes of the hind limbs and results in a globular nest averaging 15.2 cm in total depth and 8.9 cm in cavity diameter. Eggs are deposited at a rate of 1 egg every 1-2 min and are arranged in the nest with the hind limbs. Burial commences as soon as ovoposition ends and is accomplished with alternating sweeps of the hind limbs and subsequent padding. Eggs are white, elliptical, and average 37.0 mm long and 23.8 mm wide. An average of 5.5 eggs per clutch is deposited and from two to three clutches are laid annually.

During natural incubation, eggs enlarge and undergo changes in shell morphology thought to represent water conserving adaptations. Embryos have a good tolerance to desiccation as demonstrated by two individuals which were alive and normal appearing after the eggs which contained them sustained an average water loss of 45.9% by weight. The rate of development, however, was substantially reduced, presumably a result of desiccation. Natural incubation periods average 62 days. Specific changes in the egg, including the appearence of liquid on the outer shell surface, shell collapse, and complete opacity occur from 1-3 days prior to hatching. Hatching begins in mid-August and results initially from a rip in the shell created by the caruncle or claws. Hatchlings remain within the fragmented eggshell from 2-3 days until the yolk sac is fully retracted. Approximately two days are required to burrow to the surface, an activity which is performed individually. Some individuals remain buried for up to 2 wks after hatching.

Emergence from the nest is nocturnal and probably occurs in response to thermal stimuli. Hatchlings appear to lack orienting ability and are as likely to travel away from the nearest water as towards it, when emerging on level surfaces. On a sloped surface within an experimental enclosure, emerging hatchlings crawled up hill and down, but not across the angle of slope.

Rate of growth is significantly higher in females than in males. Growth is rapid in both sexes until maturity, after which growth is minimal. Females become reproductively mature at a plastron length of about 170 mm (8-9 years) and males mature at about 70 mm (4-5 years). The period of growth extends from at least late April to September, approximately 170 days. Lack of growth during October and November suggests that food energy acquired in these months may be diverted towards deposition of body fat and gametogenesis.

Sexual dimorphism is pronounced. The seven largest females examined averaged 200.6 mm in carapace length, whereas the seven largest males averaged 113.0 mm. Females possess relatively higher shells, smaller vertebral spines and foreclaws, shorter tails, and the anus, when the tail is extended, is located at or anterior to the edge of the posterior marginals. Males have relatively flatter shells, longer vertebral spines and foreclaws, longer tails (pre-anal and post-anal), and the anus is located beyond the edge of the posterior marginals.

Females display allometry with regard to carapace width, plastron length, total shell height, tail length, and head width. Features that show allometric change in males include carapace width, plastron width, tail length, and head width. Except for head width, allometric changes are related to sexually dimorphic features or appear to occur as a consequence of a general lengthening of the shell.

Supernumerary scutes are as prevelent in adults as in hatchlings but much more common in females than males. Scute asymmetry and shell pits occur in both sexes and appear to be acquired as a consequence of aging. Males are much more susceptible to injury than females.

Habitat preference is generally related to age or size. Adults and subadult females occur primarily in the deep and swift-flowing main river channels, whereas hatchlings, juvenile males, and smaller juvenile females occupy the relatively shallow and quiet backwaters of sloughs, bayous, and "lakes".

The black-knobbed sawback is the most abundant emydine in the large channels of the delta region and made up 41.3% of all turtles collected in traps. Other emydines with which *G. nigrinoda* shares its habitat on the lower Tensaw include *P. alabamensis* (30.1%), *P. concinna* (24.7%), and *P. scripta* (3.8%). The *G. nigrinoda* population in the vicinity of Gravine Island was estimated to include 64% adults and 36% juveniles (hatchlings not considered). Size distributions of adults are normal. The most common carapace length size classes in males and females are 106-110 mm and 201-210 mm, respectively. Adult and hatchling sex ratios are both essentially 1:1.

An unusual feeding niche is exploited within the study area. Animal and plant material are consumed at a ratio of about 2:1. Animal foods, in descending order of importance by both volume and frequency, include the genera *Corrospongilla* and *Trochospongilla* (Porifera), *Plumatella* (Bryzoa), and *Modiolus* (Mollusca). Algae, the only plant material consumed, is represented by three genera, *Cladophora*, *Spirogyra*, and *Ulothrix*. The adults of both sexes and the juveniles have similar diets.

The incidence of predation was highest on eggs with the fish crow, Corvus ossifragus, causing 95% mortality in those nests discovered. Crows generally attack eggs within 12 hours after depostition and were found to destroy a greater percentage during the peak of the nesting season than near its end. Fish crows apparently locate turtle nests by being attracted to concentrated ground-surface disturbances.

Leeches (Placobdella sp.) were present on 25.3% of the turtles examined. Acanthocephalans (Neoechinorhynchus sp.) were found in the intestines in 91.4% of turtles over 3 years of age. Turtles under 3 years old were not found to contain acanthocephalans.

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