LATITUDINAL REPRODUCTIVE VARIATION OF THE SALT MARSH TURTLE, THE DIAMONDBACK TERRAPIN (Malaclemys terrapin)

Timothy D. Zimmerman
B.S., Southeastern Massachusetts University, 1989

Thesis
Submitted in partial fulfillment of the requirements for the Master of Science Degree in Marine Biology from the University of Charleston, Charleston, SC

18 December 1992

[Signatures and dates for Major Advisor, Committee, and Dates]
ACKNOWLEDGMENTS

I would like to take this opportunity to thank all those whose abilities, efforts, facilities or funds allowed the completion of this project. My graduate committee members, Drs. Julian Harrison, J. Whitfield Gibbons, Zhexi Luo, and Carl Whitney, provided invaluable comments, suggestions and thought provoking questions throughout my thesis project. The University of Georgia's Savannah River Ecology Lab (SREL) supplied boats and manpower during parts of both nesting seasons. For help with the fieldwork, I thank Madelyn Robinson, Shaughn Polensky, Amy Fornier, and all those who helped a day or two including countless Earthwatch Volunteers and SREL employees. Dr. Jeffrey Lovich, Anton Tucker and Nancy Fitzsimmons of the SREL provided field support, comments and untold amounts of knowledge for which I am very thankful. Dr. Richard Seigel provided raw data and helpful suggestions. I would like to thank Kiawah Island Associates and Kiawah Island Community Association, especially Sylvia Armstrong and Tammy McAdory, for their cooperation and assistance in arranging access to the island. Al Sanders, of the Charleston Museum, helped with the turtle X-raying. The Medical University of South Carolina allowed me the use of their autodeveloper which greatly eased the X-ray development process. Frances Brigman of the Grice Marine
Biological Laboratory for all her help the past 3 years. Finally, I would like to thank my fellow graduate students for their support, especially Augustine DiNovo for his comments, suggestions and assistance.

This study was partially funded through the Short-term Graduate Research Assistantship Program at the SREL and by a grant from the Slocum-Lunz Foundation.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACKNOWLEDGMENTS</td>
<td>ii</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>v</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>vi</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>vii</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>MATERIALS AND METHODS</td>
<td>12</td>
</tr>
<tr>
<td>Nesting Study</td>
<td>12</td>
</tr>
<tr>
<td>X-ray Study</td>
<td>14</td>
</tr>
<tr>
<td>RESULTS</td>
<td>17</td>
</tr>
<tr>
<td>Nests and Eggs</td>
<td>17</td>
</tr>
<tr>
<td>X-ray data</td>
<td>22</td>
</tr>
<tr>
<td>Hatchling data</td>
<td>27</td>
</tr>
<tr>
<td>DISCUSSION</td>
<td>30</td>
</tr>
<tr>
<td>Predation</td>
<td>30</td>
</tr>
<tr>
<td>Nesting behavior</td>
<td>30</td>
</tr>
<tr>
<td>Clutch Size</td>
<td>33</td>
</tr>
<tr>
<td>Egg Data</td>
<td>35</td>
</tr>
<tr>
<td>Hatchlings</td>
<td>36</td>
</tr>
<tr>
<td>Female Body Size</td>
<td>38</td>
</tr>
<tr>
<td>Pelvic Aperture Constraint</td>
<td>39</td>
</tr>
<tr>
<td>Possible Causes</td>
<td>40</td>
</tr>
</tbody>
</table>
LIST OF TABLES

Table 1 - Reproductive characteristics of *Malaclemys terrapin* from various locations.........................................................6

Table 2 - Statistical results from latitudinal comparisons..............21

Table 3 - *Malaclemys terrapin* hatchling data from Kiawah Island, SC.................................................................................28
LIST OF FIGURES

Fig. 1 - Study site on Kiawah Island, South Carolina .......................13

Fig. 2 - Egg width to egg length correlation ........................................19

Fig. 3 - Relationship of egg mass to egg width (a) and egg mass to egg length (b) .................................................................20

Fig. 4 - Regression for total clutch mass on clutch size .........................23

Fig. 5 - Pelvic girdle aperture width to female plastral length correlation ...............................................................24

Fig. 6 - Correlation of mean egg width to pelvic girdle aperture width ...............................................................25

Fig. 7 - Correlation of egg width to female plastral length .......................26

Fig. 8 - Correlation of pelvic girdle aperture width and egg width to female plastral length ...............................................................42
ABSTRACT

Diamondback terrapins, *Malaclemys terrapin*, are brackish water turtles inhabiting salt marshes along the Atlantic coast from Massachusetts to Texas. Their nesting activity and parameters (clutch size, egg size, egg mass, etc.) were monitored during the summers of 1990 and 1991 on the southwestern end of Kiawah Island, SC. Nesting beaches were walked daily April-September at high tide. Crawl marks were followed to nest sites. Nests were uncovered to obtain egg measurements and caged to deter predation and allow for measurement of hatchlings. X-rays were used to determine clutch size and if pelvic aperture restriction is occurring for gravid females caught near the study site. Mean clutch size was 6.9 with egg length, egg width, egg mass, and total clutch mass being 36.9 mm, 22.2 mm, 11.2 g and 76.5 g respectively. Hatchling mass was 8.0 g. These data were then compared to data reported for more northerly (New Jersey) and more southerly (Florida) nesting populations of *Malaclemys terrapin*.

Comparisons of data between the three sites shows an apparent latitudinal trend in reproduction with clutch size increasing and egg size decreasing as latitude increases (i.e., traveling south to north). Clutch size and egg width differed significantly between New Jersey (NJ) and Florida (FL), and between NJ and South Carolina (SC), but not between SC and FL. Egg length, egg mass and hatchling mass differed significantly
between all three populations. Total clutch mass and midline plastral lengths were not significantly different. Using X-ray techniques, it was determined that terrapins from South Carolina do not exhibit a pelvic girdle aperture restriction on egg size. It is also believed that pelvic aperture restriction is not occurring in NJ or FL due to the high correlation ($r=0.84$, $p<0.0005$) of pelvic aperture to plastral length for SC terrapins and the lack of a significant difference of plastral lengths among the three populations.
INTRODUCTION

From the late 1800's to the early 1900's, diamondback terrapins [*Malaclemys terrapin* (Schoepff, 1792)] were favored items on the menu at many banquets and dinner parties, causing a sharp decline in their numbers (Carr, 1952). During the mid- to late 1920's the fad of dining on diamondbacks passed, and the terrapins have made a strong comeback in most areas (Carr, 1952; Pritchard, 1979).

Diamondback terrapins belong to the family Emydidae, which contains more genera and species than any other family of living turtles (Pritchard, 1979). *Malaclemys terrapin*, the only species belonging to this genus, is thought to contain several subspecies (Ernst and Barbour, 1989), although authorities disagree on the number (Lovich, pers. comm.). *Malaclemys terrapin centrata* is the subspecies found from Cape Hatteras, North Carolina to northern Florida (Ernst and Barbour, 1989) and is a common resident in the *Spartina* marshes of South Carolina (Martof et al., 1980).

*Malaclemys terrapin* is the only turtle in North America known to inhabit, almost exclusively, brackish waters (Ernst and Barbour, 1989; Gibbons and Harrison, 1975). *Malaclemys* inhabits coastal marshes and estuaries from Wellfleet, Massachusetts to Corpus Christi, Texas (Ernst and Bury, 1982). The carapace color ranges from light brown to gray to black,
with the plastron having a honey-yellow to greenish color (Carr, 1952). The large scutes have concentric rings, and a dorsal keel is often present and varies in height from prominent to absent (Ernst and Barbour, 1989). Other distinguishing characteristics include the flecked or spotted skin, pronounced webbing on the feet, and the upward curling of the posterior margin of the carapace on males (Pritchard, 1979).

These turtles exhibit sexual size dimorphism (Lovich and Gibbons, 1990), with the females growing to about 200 mm in plastral length and the males to 140 mm (Carr, 1952). Lovich and Gibbons (1990) and Bishop (1983) report mean plastral lengths of adult terrapins from South Carolina as females=148 mm, males=102 mm (n=414 turtles; F=149, M=265), and F=121 mm, M=100 mm (n=281 turtles; F=86, M=195) respectively. Other expressions of sexual dimorphism in Malaclemys are longer tails on males, with the cloacal opening posterior to the shell margin, and females having larger heads than males (Carr, 1952).

Most behavioral studies have focused on the mating, nesting, and reproductive habits of Malaclemys (Reid, 1955; Burger and Montevecchi, 1975; Montevecchi and Burger, 1975; Burger, 1976a,b; Burger, 1977; Seigel, 1979, 1980a,b; Sachsse, 1984). Aquatic courtship and mating take place during the morning hours in April and May (Carr, 1952; Seigel, 1979, 1980b; Ernst and Barbour, 1989). The male approaches,
nuzzles and mounts the female while she floats at the surface of the water until copulation is complete (Seigel, 1980b). Nests are dug in sandy dunes above the high tide mark where 4–18 pinkish-white eggs are laid. Incubation period is a function of nest temperature and may take nine to twelve weeks in the wild for New Jersey populations (Montevecchi and Burger, 1975; Burger, 1976b) the only wild population for which these data have been recorded. Environmental sex determination, where males develop if the incubation temperature is relatively low and females develop if it is relatively high, may exist in diamondback terrapins (Sacche, 1984; Auger, pers. comm.; Roosenberg, pers. comm.), but as yet has not been conclusively documented.

Nesting studies of terrapins on the Atlantic coast have been performed in New Jersey (Burger, 1976a,b; Burger, 1977; Burger and Montevecchi, 1975; Montevecchi and Burger, 1975) and in Florida (Seigel, 1979 and 1980a). If latitudinal comparisons are made between these two study sites, there is a difference in reproductive parameters of northern and southern populations of diamondback terrapins. The general trend is one in which terrapins from the lower latitudes lay nests with fewer but larger eggs when compared to terrapin nests from higher latitudes. Such a latitudinal trend in reproductive variation is known to occur in some birds, mammals (Lack, 1954) and lizards (Sceloporus occidentalis - Minervo, 1990) and reproductive latitudinal variation has been
reported for other turtle species (*Sternotherus odoratus* – Tinkle, 1961; *Chrysemys picta* – Moll, 1973) and even within subspecies (*Chrysemys picta bellii* – Christiansen and Moll, 1973). Montevecchi and Burger (1975) and Seigel (1980a) both suggested that *Malaclemys terrapin* may show latitudinal variation.

Several comparisons were made between the Florida and New Jersey populations by Seigel (1979 and 1980a). He found that *Malaclemys terrapin* from Florida laid clutches with significantly fewer eggs and eggs that were significantly heavier and longer than those of *Malaclemys terrapin* from New Jersey. Clutch mass and egg width were not found to be significantly different. It has been suggested that egg width, not egg length, is a better estimator of egg mass in some species where body size is related to egg size (Congdon and Tinkle, 1982; Congdon and Gibbons, 1983; Congdon et al., 1983) but neither Montevecchi and Burger (1975) nor Seigel (1979, 1980a) found any significant correlation between plastron size and any measure of egg size (i.e., mass, length or width). No significant difference was found between plastral lengths of laying females from Florida and New Jersey (Seigel, 1979). Terrapins from both studies showed a significant positive correlation of plastral length to clutch size (Montevecchi and Burger, 1975; Seigel, 1979, 1980a).

Comparisons using other published data on reproductive parameters of *Malaclemys* are presented in Table 1 along with
data from New Jersey, Florida and data from Kiawah Island, South Carolina from this study. Some of the data presented in Table 1 must be viewed with extra caution because, in addition to wild population data, data from captive populations are included (i.e., Burns and Williams, 1972; Hildebrand, 1932). Animals in captivity behave differently, with regard to reproduction, from those in the wild (Cagle, 1950; Carr, 1952; Seigel, 1980a) and may receive supplementary feeding (Coker, 1906) which could affect reproductive characteristics. The data presented by McCauley (1945) and Reid (1955) are from only 1 nest each.

The above scenario of turtles from the North laying larger clutches with smaller eggs compared to those in the South is consistent with optimal egg size (OES) theories (Congdon, 1989). In OES models, egg size is optimized through natural selection; therefore, reproductive variation within a population should occur primarily in clutch size and secondarily in egg size (Congdon, 1989; Congdon and Gibbons, 1990). In other words, as parental investment per individual offspring increases, the concomitant clutch size (number of offspring) must be reduced (Smith and Fretwell, 1974). Parental investment is defined for turtles as the total energy put into producing the egg, including the energy placed within the egg (Congdon and Tinkle, 1982; Congdon et al., 1983; Congdon and Gibbons, 1987; Congdon, 1989; Congdon and Gibbons, 1989; Congdon and Gibbons, 1990) since turtles do not exhibit parental care.
Table 1 - Means of various reproductive characteristics of *Malaclemys terrapin* from both wild and captive populations. #Nests=number of nests used in the analysis, unless noted otherwise in (); #Eggs=number of eggs used in the analysis, unless noted otherwise in (); Female PL=curved plastral length; Masses in g; Lengths and Widths in mm.
<table>
<thead>
<tr>
<th>Loc.</th>
<th>Authority</th>
<th># Nests</th>
<th># Eggs</th>
<th>Clutch Size</th>
<th>Clutch Mass</th>
<th>Egg Mass</th>
<th>Egg Length</th>
<th>Hatch. Female</th>
<th>Female PL</th>
</tr>
</thead>
<tbody>
<tr>
<td>MA</td>
<td>Shipley, Pers. Comm.</td>
<td>40</td>
<td>336</td>
<td>12</td>
<td>9.7</td>
<td>7.7</td>
<td>31.7</td>
<td>7.7</td>
<td>6.8</td>
</tr>
<tr>
<td>NJ</td>
<td>Montvecchi and Burger, 1975</td>
<td>37</td>
<td></td>
<td>1</td>
<td>12</td>
<td>7.0</td>
<td>31.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>NJ</td>
<td>Burger, 1977</td>
<td></td>
<td></td>
<td>1</td>
<td>12</td>
<td>7.0</td>
<td>31.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MD</td>
<td>McCauley, 1945</td>
<td>1</td>
<td>14</td>
<td>36</td>
<td>6.9</td>
<td>8.0</td>
<td>21.2</td>
<td>22.2</td>
<td>11.2(48)</td>
</tr>
<tr>
<td>VA</td>
<td>Reid, 1955</td>
<td>1</td>
<td></td>
<td></td>
<td>6.9</td>
<td>8.0</td>
<td>21.2</td>
<td>22.2</td>
<td>11.2(48)</td>
</tr>
<tr>
<td>NC</td>
<td>Hildebrand, 1932</td>
<td></td>
<td></td>
<td></td>
<td>6.9</td>
<td>8.0</td>
<td>21.2</td>
<td>22.2</td>
<td>11.2(48)</td>
</tr>
<tr>
<td>SC</td>
<td>Zimmerman, this study</td>
<td>14</td>
<td>96</td>
<td>11</td>
<td>95</td>
<td>36.9</td>
<td>37.3</td>
<td>39.0</td>
<td>12.5</td>
</tr>
<tr>
<td>LA</td>
<td>Burns and Williams, 1972</td>
<td>14</td>
<td>41</td>
<td>14</td>
<td>41</td>
<td>6.7</td>
<td>66.6</td>
<td>22.3</td>
<td>8.8</td>
</tr>
<tr>
<td>FL</td>
<td>Seigel, 1979, 1980a</td>
<td>14</td>
<td>41</td>
<td>14</td>
<td>41</td>
<td>6.7</td>
<td>66.6</td>
<td>22.3</td>
<td>8.8</td>
</tr>
</tbody>
</table>
Congdon (1989) suggested that the term "optimal offspring-quality model" may be more appropriate than the "optimal egg size model". In the optimal offspring model, the parental investment is apportioned so as to optimize the quality of the offspring, not the size of the egg (Congdon, 1989). Given the implicit assumption that there is a limit on maximum reproductive effort, I hypothesize that increasing the individual investment to increase the offspring's quality would necessitate a reduction in the clutch size (number, not total weight) in order to maintain a constant reproductive effort. Unfortunately, a decisive way to determine the quality of an offspring has yet to be formulated. Larger hatchling size in turtles has been suggested, though never documented, to increase survivorship (quality?) (Seigel, 1979; Congdon et al, 1983). This increase in hatchling size may lead to increased survivorship through one, or a combination, of several means (see below).

Several authors (Congdon and Tinkle, 1982; Congdon et al., 1983; Congdon and Gibbons, 1987) have suggested that morphological constraints, such as pelvic girdle aperture, may limit egg size, which would allow for results inconsistent with predictions of OES models to be obtained. This pelvic aperture constraint has been demonstrated for *Chrysemys picta* and *Deirochelys reticularia* in which egg size is positively related to body size (Congdon and Gibbons, 1987). On the other hand, *Trachemys scripta* did not show a significant relationship
between increased egg size and pelvic aperture (Congdon and Gibbons, 1987) even though a significant relationship has been shown between body size and egg size for this species (Congdon and Gibbons, 1983). This morphological constraint on egg size, along with a lack of evidence for egg size–clutch size trade offs, has cast a shadow of doubt on the optimal egg size model, although a few life history studies support it (Congdon, 1989; Congdon and Gibbons, 1990).

Clutch frequency is viewed as a “key variable” by Gibbons and Greene (1990) in determining reproductive characteristics of turtle life histories. Unfortunately, a firm understanding of clutch frequency is difficult to obtain. Variation of clutch frequency has been reported for some turtle species both among geographically separate populations (e.g., C. picta - Christiansen and Moll, 1973; S. odoratus - Tinkle, 1961; Kinosternon subrubrum - Gibbons, 1983) and populations within a geographic locality (e.g., D. reticularia, S. odoratus, T. scripta, K. subrubrum, Gibbons et al, 1982). Resource availability and acquisition during the present and previous year and the length of the laying season are thought to be important variables in determining the number of clutches to be laid per nesting season. In general, it is assumed that turtles in cooler regions will lay fewer clutches due to the shorter nesting season (Gibbons, 1983). A clear determination of clutch frequency for Malaclemys has not yet been established.
There are several sources of reproductive variation which may cause variation both within and among turtle populations. Adult female body size is known to affect clutch size. Larger females have larger body cavities and therefore can carry a larger number of eggs (Congdon and Tinkle, 1982; Gibbons et al., 1982; Congdon and Gibbons, 1985; Congdon and Gibbons, 1987). Females may also vary the amount of energy put into a clutch. This variation in energy allocated to reproduction may necessitate a change in clutch size or egg size, thus causing reproductive variation due to parental investment. Since turtles do not exhibit post-hatching parental care, total clutch mass can be used as a measure of parental investment. A third possible source of reproductive variation is morphological constraint in the form of pelvic girdle aperture restriction (see above and below). This constraint may cause egg size variation if the amount of restriction varies from female to female or population to population. This egg size variation may possibly cause a concomitant clutch size variation.

The main objective of my study was to determine if a latitudinal reproductive trend exists for *Malaclemys terrapin* living along the Atlantic coast of the U.S.A. To meet this objective, comparisons were made between my data from South Carolina and literature data. Since data from the studies from New Jersey (Montevecchi and Burger, 1975) and Florida (Seigel, 1979, 1980a,b) are from non-captive populations and are the most complete, they were chosen to represent data
points to the north and south of my study site. To date, no single model can fully explain the variation of egg size, clutch size or an egg size/clutch size trade-off in all species of turtles. I do not presume my data will fit one model perfectly, but increasing the data sets for turtle species both within and among geographic localities will aid in the understanding of reproductive strategies in the order Testudines. With the above factors in mind the following hypotheses were formulated and tested:

**Hypothesis 1:** Terrapins living at lower latitudes produce nests with smaller clutch sizes but with relatively larger egg sizes (length, width, and mass) than their more northerly counterparts from higher latitudes.

**Hypothesis 2:** In order to rule out size differences as a contributing factor to reproductive variation (e.g., in clutch size, egg size, hatchling size, etc.), the size of reproductively active females should not differ among the populations at different latitudes.

**Hypothesis 3:** To show that parental investment is not causing variation in clutch size or egg size, parental investment should not differ among the three latitudes compared. If the total clutch mass is the best approximation to parental investment
for turtles, then a lack of clutch mass variation would indicate that there is no latitudinal variation in parental investment.

**Hypothesis 4:** Pelvic aperture restrictions on egg width may cause variation in egg sizes. If pelvic aperture restriction is to be ruled out as a possible cause of egg size variation, then egg width should not be correlated to pelvic girdle aperture width.
MATERIALS AND METHODS

Nesting Study

I conducted my nesting study on Kiawah Island, SC (32°35'N, 80°08'W), a small barrier island located about 25 km southwest of Charleston, SC. The southwestern tip of the island contains a series of sand dunes used by *M. terrapin* for nesting (Fig. 1). Terrapins nested on a stretch of beach (approximately 2.5 km long) along the Kiawah River. I surveyed these beaches daily from April through September during 1990 and 1991. After boating to the beaches, I walked along the high tide line looking for crawls of nesting females. When a crawl was found I would follow it into the dunes, sometimes for several hundred meters, in an attempt to find the nest. If I found the possible nest site, I would probe the ground to find the nest cavity.

When a nest was found, I carefully uncovered and removed the eggs. I measured egg length and width to the nearest mm using vernier calipers. For nests found in 1991, egg mass was also measured, measuring to the nearest 0.1 g on an Ohaus portable electronic balance (Model #C305) placed in a Plexiglass box to shield it from the wind. Nest depth and width were measured to the nearest mm using a plastic ruler. During the summer of 1991, wire nest cages made from 1/4 inch mesh hardware cloth were placed in the nest cavity, the eggs placed
Fig. 1. - Diamondback terrapin nesting beaches on Kiawah Island, South Carolina, USA. The stippled areas are dune habitat nesting beaches which were surveyed during the 1990 and 1991 nesting seasons. Inset shows the site location in relation to the state of South Carolina.
inside, maintaining order and orientation, and the cage wired shut. This was to deter predation, allow for determination of incubation times in situ and to allow for the measurement and marking of hatchlings. I marked nest sites with surveyor's flags containing the date and time of nesting along with the nest number that was sequentially assigned in order of discovery.

Starting fifty days after discovery, I checked nests daily by uncovering and opening the cages to expose the first one or two eggs. If the eggs had hatched, hatchlings were removed and carapace length, plastral length, width, and height were measured to the nearest mm with vernier calipers. Hatchling mass (measured to the nearest 0.1 g) was determined on the portable balance. Hatchlings were marked with individual codes by notching marginal scutes with a scalpel, using the same method used for adults (see below). I then returned the hatchlings to the nest site and released them.

**X-ray Study**

Adult female terrapins were captured at two sites in Charleston County, SC, (1) Kiawah Island and (2) behind the Grice Marine Biological Laboratory on James Island, using trammel nets, stop nets and a 15 m, 3 inch stretch mesh purse seine. Turtles were also hand captured as they traveled to and from nesting. Terrapins determined to be gravid through palpation and those captured on the nesting beaches were
brought back to the Grice lab for measurement, marking and X-raying (see below).

I measured straightline carapace length (to the nearest 1 mm) using Haglof tree calipers and curved plastral length (to the nearest 1 mm) with a clear plastic ruler. Terrapins were given individual 3 or 4 letter codes and marked by notching the marginal scutes with a triangular file following the method of Cagle (1939). Turtles were then X-rayed using a technique adapted from that described by Gibbons and Greene (1979). I placed the live terrapins in a plastic bag and taped it shut to keep them still during X-raying. Once in the bag, turtles were placed in a Hewlett Packard 43805N Faxitron series X-ray machine and X-rayed for 3-5 seconds at 70 kvp at a distance of 45 cm using Kodak X-Omat AR film plates. X-ray radiographs were developed using an auto developer (Konica Medical Film Processor) in the Medical University of South Carolina's Radiology department. Egg widths and pelvic girdle aperture width were measured to the nearest 1 mm using vernier calipers. These measurements were made directly from the radiographs on all radiographs where terrapins had not moved and were perpendicular to the film plane. The number of eggs was counted on all the radiographs of turtles with eggs.

I compared my data with data from Little Beach, NJ (39°29'N, 74°21'W) (Montevecchi and Burger, 1975), and from Merrit Island, FL (28°35'N, 80°40'W) (Seigel, 1980a), using a one-way Model I ANOVA. If the means were determined to be
significantly different (p<0.05), then a Tukey test was performed to determine which of the three possible combinations (New Jersey-South Carolina; New Jersey-Florida; South Carolina-Florida) were significantly different. All ANOVAs and Tukey tests were calculated by hand. Statview 512+ version 1.01 was used on a Macintosh Classic PC for correlation and regressional analysis of X-ray data, nesting data, and for calculating means, counts and standard deviations of raw data from South Carolina.
RESULTS

See Table 2 for data compared from the three latitudes used.

Nests and Eggs

I found a total of 14 nests, 7 each summer, after following 106 crawls over both summers, resulting in a nest finding success rate of 13%. Mean nest width and depth were $7.1 \pm 1.5$ cm and $16.8 \pm 1.8$ cm, respectively. The nesting season lasted approximately 60 days each year with terrapins nesting as early as May 7 and as late as July 10 with most nesting occurring around mid-May through early June. Nesting terrapins seemed to have a preference for fair weather. I found 92% of the crawls on sunny or mostly sunny days while only 8% were found on partly cloudy days. No terrapins nested on overcast or rainy days. Eighty-six percent of the time (12 of 14), terrapins laid nests next to some form of vegetation. Length of crawls varied from about 10 m to more than 200 m total crawl length (measured as the distance from the point of departure from the water up to the nest and back to the water). Terrapins had a tendency toward nesting around high tide. The earliest crawl was found at 0600 hrs and the latest at 1830 hrs. Nesting also occurred on salt marsh islands, but dense vegetative cover precluded following crawls to the nests.
Predated nests and remains from predated female terrapins were the only evidence of nesting on these islands.

I found the mean egg length to be 36.9 mm with a standard deviation of ± 2.3 mm and mean egg width to be 22.2 ± 1.3 mm for 96 eggs from the 14 nests found. Egg length and egg width were significantly positively correlated (r=0.536, p<0.0005) (Fig. 2); therefore, egg width increases with an increase in egg length. Egg mass was measured for 48 eggs from 7 nests and resulted in a mean egg mass of 11.2 ± 0.8 g. Individual egg mass varied significantly (One-way ANOVA, p=0.0001) among nests. Mean total clutch mass was 76.5 ± 19.5 g (n=7). Egg mass is significantly correlated to both egg width (r=0.74, p<0.0005), and egg length (r=0.538, p<0.0005) (Fig. 3). Mean clutch size, using both nest and X-ray data, was 6.9 ± 1.5 eggs (range 4 - 9) from a sample size of 25 (14 from nests, 11 from X-rays). Egg length and egg mass were found to be significantly different among all three latitudes compared (i.e., for all pairwise comparisons) (Table 2). Egg width and clutch size are significantly different between New Jersey and South Carolina, and New Jersey and Florida, the latitudes further apart, but are not significantly different between South Carolina and Florida. The total clutch mass does not differ significantly among the three populations (p>0.25).
Fig. 2. - Relationship of egg width (mm) to egg length (mm) for eggs measured from *Malaclemys terrapin* nests from Kiawah Island, SC during the 1990 and 1991 nesting seasons. NOTE: on all graphs and tables, * indicates "significant" with p values less than 0.005.
$r = 0.536, \ p < 0.0005^*$

**Egg Length (mm)**
Fig. 3. - (a) Regression of egg mass on egg width. (b) Regression of egg mass on egg length. Note the higher $r^2$ value for egg width, indicating a better fit between egg width and egg mass than between egg length and egg mass.
\( r = 0.74, \quad p < 0.0005^* \)
\( r^2 = 0.547, \quad p = 0.0001^* \)

\( r = 0.538, \quad p < 0.0005^* \)
\( r^2 = 0.289, \quad p = 0.0001^* \)
Table 2 - Results of ANOVAs and Tukey tests for comparisons of reproductive data (X=mean, s=standard deviation, n=number of observations) from New Jersey (Montevecchi and Burger, 1975), Florida (Seigel, 1979, 1980a) and South Carolina (this study).
<table>
<thead>
<tr>
<th>Female Plastral Length (mm)</th>
<th>X</th>
<th>S</th>
<th>N</th>
<th>Results from One-way ANOVA</th>
<th>Results from Tukey Test</th>
</tr>
</thead>
<tbody>
<tr>
<td>NJ</td>
<td>154</td>
<td>9.9</td>
<td>221</td>
<td>Accept Ho 0.25&lt;P&lt;0.10</td>
<td>N/A</td>
</tr>
<tr>
<td>SC</td>
<td>157</td>
<td>12.1</td>
<td>40</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FL</td>
<td>154</td>
<td>10.0</td>
<td>113</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Total Clutch Mass (g)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NJ</td>
<td>71.8</td>
<td>17.7</td>
<td>30</td>
<td>Accept Ho P&gt;0.25</td>
<td>N/A</td>
</tr>
<tr>
<td>SC</td>
<td>76.5</td>
<td>19.5</td>
<td>7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FL</td>
<td>73.3</td>
<td>13.1</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Clutch Size</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NJ</td>
<td>9.8</td>
<td>2.6</td>
<td>40</td>
<td>Reject Ho P&lt;0.0005</td>
<td>NJ≠FL* P&lt;0.001</td>
</tr>
<tr>
<td>SC</td>
<td>6.9</td>
<td>1.5</td>
<td>25</td>
<td>SC≠NJ* P&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>FL</td>
<td>6.7</td>
<td>1.4</td>
<td>14</td>
<td>FL≠SC P&gt;0.50</td>
<td></td>
</tr>
<tr>
<td><strong>Egg Length (mm)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NJ</td>
<td>31.7</td>
<td>1.8</td>
<td>336</td>
<td>Reject Ho P&lt;0.0005</td>
<td>NJ≠FL* P&lt;0.001</td>
</tr>
<tr>
<td>SC</td>
<td>36.9</td>
<td>2.3</td>
<td>96</td>
<td>SC≠NJ* P&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>FL</td>
<td>39.0</td>
<td>1.3</td>
<td>31</td>
<td>FL≠SC P&gt;0.05</td>
<td></td>
</tr>
<tr>
<td><strong>Egg Width (mm)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NJ</td>
<td>19.8</td>
<td>1.1</td>
<td>336</td>
<td>Reject Ho P&lt;0.0005</td>
<td>NJ≠FL* P&lt;0.001</td>
</tr>
<tr>
<td>SC</td>
<td>22.2</td>
<td>1.3</td>
<td>96</td>
<td>SC≠NJ* P&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>FL</td>
<td>22.3</td>
<td>1.2</td>
<td>31</td>
<td>FL=SC P&gt;0.05</td>
<td></td>
</tr>
<tr>
<td><strong>Egg Mass (g)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NJ</td>
<td>7.7</td>
<td>1.1</td>
<td>300</td>
<td>Reject Ho P&lt;0.0005</td>
<td>NJ≠FL* P&lt;0.001</td>
</tr>
<tr>
<td>SC</td>
<td>11.2</td>
<td>0.8</td>
<td>48</td>
<td>SC≠NJ* P&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>FL</td>
<td>12.5</td>
<td>0.7</td>
<td>31</td>
<td>FL=SC* P&gt;0.001</td>
<td></td>
</tr>
<tr>
<td><strong>Hatchling Mass (g)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NJ</td>
<td>6.8</td>
<td>0.9</td>
<td>207</td>
<td>Reject Ho P&lt;0.0005</td>
<td>NJ≠FL* P&lt;0.001</td>
</tr>
<tr>
<td>SC</td>
<td>8.0</td>
<td>0.4</td>
<td>16</td>
<td>SC≠NJ* P&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>FL</td>
<td>8.8</td>
<td>0.2</td>
<td>29</td>
<td>FL=SC* 0.005&lt;P&lt;0.001</td>
<td></td>
</tr>
<tr>
<td><strong>Hatchling Plastral Length (mm)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NJ</td>
<td>24.4</td>
<td>1.1</td>
<td>207</td>
<td>Reject Ho P&lt;0.0005</td>
<td>NJ≠FL* P&lt;0.001</td>
</tr>
<tr>
<td>SC</td>
<td>28.3</td>
<td>1.0</td>
<td>16</td>
<td>SC≠NJ* P&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>FL</td>
<td>27.9</td>
<td>0.1</td>
<td>29</td>
<td>FL=SC 0.5&lt;P&lt;0.2</td>
<td></td>
</tr>
</tbody>
</table>
Size of Reproductively Active Females

Mean curved plastral length of reproductively active females from South Carolina was $157 \pm 12.1$ mm. Plastral lengths were not significantly different between New Jersey, South Carolina and Florida ($0.25<p<0.10$) (Table 2). Clutch size increased with plastral length but was not significantly correlated to it ($r=0.48$, $0.05<p<0.10$). Total clutch mass increased significantly with increased clutch size ($r=0.97$, $p<0.0005$) (Fig. 4).

X-ray data

I X-rayed 41 turtles from Kiawah Island and James Island, SC. Only 14 accurate measurements could be made of pelvic apertures on radiographs due to movement of terrapins during X-raying. These measurements resulted in a mean pelvic aperture of $26.0 \pm 2.5$ mm with the corresponding females having a mean plastral length of $157 \pm 15.9$ mm (based on 40 measurements). Comparing the pelvic girdle aperture to the plastral lengths (Fig. 5) of these terrapins yields a significant positive correlation ($n=14$, $r=0.84$, $p<0.0005$). Of the X-rays with measurable pelvic apertures, 6 had all eggs measurable. The mean egg width for the previously mentioned terrapins appears to show no correlation to pelvic aperture ($r=0.048$, $p>0.25$) (Fig. 6). Egg width was not significantly correlated to plastral length for X-rayed turtles ($r=-0.048$, $p>0.25$) (Fig. 7).
Fig. 4. - Regression of total clutch mass (g) on clutch size. The regression is significant (p=0.0003) and clutch mass is significantly correlated to clutch size (r=0.97, p<0.0005).
Fig. 5. - Correlation of pelvic girdle aperture width (mm) to plastral length (mm) as measured from X-ray radiographs for adult females from Kiawah Island and James Island, SC (n=14).
Fig. 6. - Correlation of mean egg width (mm) to pelvic girdle aperture width (mm) for X-rayed terrapins from South Carolina (n=6).
$r = 0.048, \ p > 0.25$
$r^2 = 0.012, \ p = 0.833$
Fig. 7. - Correlation of egg width (mm) to adult female plastral length (mm) as measured from X-ray radiographs for terrapins from Kiawah Island and James Island, SC (n=6).
Hatchling data

Mean nest incubation time, time from laying to hatching of the first egg, for the four successful nests from 1991 was 54.5 ± 2.4 days (range 52-57 days). Mean egg hatching time, time from laying to hatching of an individual egg, was 56.3 ± 2.5 days (range 53-59 days) (n=16). Hatchling plastral length (n=16) was negatively correlated to time to hatching (r=-0.366) but this was not significant (0.05<p<0.10). Hatchling carapace length and mass were both positively correlated to time to hatching, but neither was significant (r=0.392, 0.05<p<0.10; r=0.161, p>0.25, respectively). Of the 48 eggs caged in 7 nests during 1991, 18 eggs (56.3%) hatched. A total of 27 hatchlings were measured for plastral and carapace lengths (16 from 1991 nests, 11 from data for incubated 1990 terrapins), while 16 were measured for height, width and mass. Mean plastral length, carapace length, height, weight and mass were 32.3 ± 1.4 mm, 28.7 ± 1.2 mm, 15.9 ± 0.9 mm, 26.6 ± 1.1 mm and 8.0 ± 0.4 g, respectively (Table 3).

Of the 18 eggs that hatched, 1 turtle died while hatching and 2 were predated upon in the nest, resulting in a hatchling mortality rate of 16.7%. Plastral length was positively correlated to carapace length, height, width and hatchling mass, but plastral length to carapace length was the only significant comparison (Table 3). Carapace length was significantly positively correlated to hatchling mass, and positively, but not
Table 3 - Hatchling data for *Malaclemys terrapin* from Kiawah Island. Correlation coefficients and significance levels for comparisons noted. Plastral Length=curved plastral length; Carapace Length=straightline carapace length; Masses in g; Lengths and Widths in mm.
<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>X</th>
<th>s</th>
<th>range</th>
<th>Plastral Length</th>
<th>Carapace Length</th>
<th>Height</th>
<th>Width</th>
<th>Mass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plastral Length</td>
<td>27</td>
<td>28.7</td>
<td>1.2</td>
<td>27.0-32.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carapace Length</td>
<td>27</td>
<td>32.3</td>
<td>1.4</td>
<td>30.0-36.0</td>
<td></td>
<td>r=0.772</td>
<td>r=0.021</td>
<td>r=0.113</td>
<td>r=0.155</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>p&lt;0.001*</td>
<td>p&gt;0.50</td>
<td>p&gt;0.50</td>
<td>p&gt;0.50</td>
</tr>
<tr>
<td>Height</td>
<td>16</td>
<td>15.9</td>
<td>0.9</td>
<td>15.0-19.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Width</td>
<td>16</td>
<td>26.6</td>
<td>1.1</td>
<td>24.0-28.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mass</td>
<td>16</td>
<td>8.0</td>
<td>0.4</td>
<td>6.9-8.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
significantly, correlated to carapace width and height. Of the 16 hatchlings for which data were recorded, 38% (6 individuals) had scutation that deviated from normal (e.g., split nuchal, 5 pleurals, 25 marginals, etc.). Four of the six with abnormal scutation, or 25% of the total, were from the same nest.
DISCUSSION

Predation

All 7 nests found during the first summer (1990) were destroyed by predators. Raccoons seemed to be the most predominant predator on terrapin nests, but bobcats, foxes and ghost crabs all contributed to nest destruction. Caging nests the second summer helped to reduce, but not completely eliminate, predation. Even with the wire mesh cages in place, I lost 1 nest to a ghost crab and 1 nest to plant "predation." Plant predation occurs when an egg or nest gets completely consumed by plant stolons or rhizomes. Predation of terrapin nests by plants (Ammophila breviligulata) has been reported for Malaclemys in Massachusetts (Lazell and Auger, 1981), but was not mentioned for the New Jersey or Florida populations.

Nesting behavior

Seigel (1979) noted that the nesting season he observed in Florida (54-57 days) was longer than the nesting season in New Jersey (44 days), as reported by Montevecchi and Burger, 1975. The 60-day nesting season for terrapins on Kiawah Island was approximately 3-4 days longer than that in Florida and just over two weeks longer than New Jersey's. A longer nesting season with decreasing latitude is expected due to warmer spring and fall temperatures, and the discrepancy
between South Carolina and Florida could merely be due to yearly fluctuations between my study in 1990, 1991 and Seigel's in 1977-1979. Some authors (Moll, 1979; Gibbons, 1983) suggest the shorter nesting season at higher latitudes may cause northern turtles to lay fewer clutches. This may be a factor with terrapins.

Montevecchi and Burger (1975) could not document multiple clutches for their population, but speculated it may occur. Through examination of corpora lutea of eight turtles, Seigel (1979, 1980a) found some evidence that Florida terrapins may lay two or three clutches per year. No terrapins were sacrificed for corpora lutea examination at Kiawah so as not to disrupt the long-term study on terrapins currently being conducted there. A two year total of 38 terrapins were known to have had eggs (based on X-raying or palpation techniques) or to have laid eggs (based on capture on the nesting beaches) and were later recaptured that same year by seine or trammel net. None of these were determined to have a second clutch. Although it may not be conclusive data, the paucity of terrapins being captured twice in a season with eggs lends support to the notion that terrapins in South Carolina may only lay one clutch per season. Clutch frequency was positively correlated to body size in Chrysemys picta in Illinois (Thornhill, 1982), but body size should not cause clutch frequency differences in Malaclemys along the Atlantic coast since no significant difference was noted in plastral lengths from New
Jersey to Florida, Table 2. It is also unknown whether female terrapins reproduce annually or otherwise. During this two year study, no terrapins were determined through palpation to have eggs in two consecutive seasons. A more comprehensive understanding of clutch frequency for terrapins is needed before comparisons of this parameter can be made among the three study sites.

Tidal periodicity appears to be the most important factor controlling nesting activity on Kiawah Island where terrapins came out primarily at high tide to nest. This connection between nesting activity and high tide on Kiawah is similar to that observed by Burger and Montevecchi (1975) in New Jersey where nesting was positively correlated to the time of high tide (p=0.001). Florida terrapins showed a temperature preference, and therefore a time of day preference, for nesting. The number of females nesting was correlated to air temperature with all nesting occurring when air temperatures were at their highest (Seigel, 1979). This correlation to temperature was not apparent in South Carolina (this study) or New Jersey (Montevecchi and Burger, 1975). Diamondback terrapins from all three study sites show a preference for nesting in close proximity to vegetation and for nesting during fair weather. Terrapins nesting on the dunes at Kiawah seemed to have a tendency toward nesting on the slope of a dune, although I have no quantitative data to support this. In contrast, Burger and Montevecchi (1975) noted a significant
correlation (p=0.001) for terrapins "choosing" a flat slope for nesting in the New Jersey dune habitat. The terrapins nesting on Kiawah travel further into the dunes than reported elsewhere. This long distance travel may be typical of South Carolina diamondbacks or, more likely, it may be due to the dune nesting habitat at Kiawah and restricted to this population. The low nest finding success rate of the author is attributed to the nesting habitat. Crawls would often get obliterated by wind or rain showers, making tracking impossible.

Clutch Size

Clutch size is known to vary in emydid turtle populations of the same species both within the same geographic location (Gibbons and Tinkle, 1969; Gibbons et al., 1978; Gibbons et al., 1982; Gibbons, 1983) and among different geographic locations (Tinkle, 1961; Christiansen and Moll, 1973; Moll, 1973; Seigel, 1979). The significant difference in clutch size among the more distant latitudes (NJ and SC; NJ and FL) supports a latitudinal reproductive trend for *Malaclemys*. The lack of a significant difference between South Carolina and Florida may be due to their proximity and hence greater climatic similarities. In both geographic locations the more stable climate may be causing "K" rather than "r" selection (see below). Soil moisture plays an important role in egg development and survival (Congdon and Gibbons, 1990) and similarities in rainfall amounts and
possibly concomitant soil moisture may be causing similarities in clutch size (see below). Even though clutch size increased with plastral length for all three locations, differences in clutch size are not due to body size differences among latitudes (see below).

Clutch size is significantly positively correlated to clutch mass both in South Carolina (this study) and New Jersey (Montevecchi and Burger, 1975). It is interesting to note, however, that the total clutch mass does not differ significantly among the three latitudes even though mean clutch size changes, and clutch size and clutch mass co-vary. Although clutch frequency data are weak, if, as stated earlier, shorter nesting seasons in the north cause decreased clutch frequency, then the total clutch mass for northern terrapins would be larger if annual reproductive potential (clutch mass x clutch frequency) is to remain constant. Since the total clutch mass does not differ significantly, parental investment per clutch is thought to be the same for terrapins from New Jersey, South Carolina and Florida. The annual reproductive potential (Seigel, 1979; Iverson, 1992) cannot be calculated due to lack of sufficient clutch frequency data for *Malaclemys*. Iverson (1992) found no correlation between latitude and body-size-adjusted annual clutch mass across many turtle species. He states that this suggests that latitude does not affect body-size-adjusted annual reproductive output. The lack of variation in parental investment for terrapins rules out parental
investment as a source of reproductive variation. This lends support to a latitudinal reproductive trend for turtles exhibiting little parental investment (i.e., total clutch mass) variation as is true for *Malaclemys*.

**Egg Data**

Egg sizes were different among the latitudes compared. The length of the eggs increases significantly with decreasing latitude (Table 2). This significant difference in egg length among New Jersey, South Carolina and Florida terrapin populations suggests larger eggs are being produced by the more southerly turtles. This change in egg size, as measured by egg length, should be viewed cautiously, for egg width is thought to be a better measure of "egg quality" than egg length due to more consistent correlations of egg width to egg mass (Congdon and Gibbons, 1983; Congdon et al., 1983; Congdon and Gibbons, 1985, 1987). The egg width to egg mass relationship reported in the aforementioned studies also seems to hold for *Malaclemys* from Kiawah. Even though egg length and egg width were both significantly positively correlated to egg mass, regressing egg mass on egg width resulted in a tighter fit ($r^2=0.547$, $p=0.0001$) than did egg mass on egg length ($r^2=0.289$, $p=0.0001$) (see Fig. 3). Egg width was significantly different between only two of the three latitudinal comparisons. Egg widths from South Carolina and Florida were not significantly different ($p>0.05$). The lack of a significant
difference in egg width among the two lower latitude sites may be related to the lack of difference in clutch size (see above and below) and its possible environmental causes (soil moisture?, similarities in climate?). Although egg width is correlated to plastral length for some freshwater emydid turtles (Tucker et al., 1978; Congdon and Tinkle, 1982; Congdon and Gibbons, 1983; Congdon et al., 1983; Congdon and Gibbons, 1987; Congdon et al., 1987), it is not for diamondback terrapins in South Carolina (p>0.25) (this study), New Jersey (Montevecchi and Burger, 1975) or Florida (Seigel, 1980a).

Egg mass increases significantly with a decrease in latitude as would be expected if a latitudinal trend exists. Egg mass has been shown to be positively correlated to hatchling mass for terrapins from New Jersey (Burger, 1977) and for other freshwater turtles (Congdon et al., 1983), but this statistic was not calculated for South Carolina terrapins, due to lack of sufficient data.

Hatchlings

Hatchling mass differed significantly among the study sites, with a tendency toward increasing mass with decreasing latitude. This makes intuitive sense since egg mass increased significantly with decreasing latitude and we would expect a heavier egg to give rise to a heavier hatchling (see above). This idea is supported by the data from Congdon et al. (1983) who found the wet mass of hatchlings to be highly correlated to wet
egg mass for Deirochelys reticularia. Even though egg mass differed significantly in my comparisons (Table 2), plastral lengths of hatchlings from the South Carolina and Florida populations did not. The New Jersey-South Carolina and New Jersey-Florida comparisons showed a significant difference. Again, we see no significant difference between the South Carolina and Florida populations. Congdon et al. (1983) found a similar discrepancy when they noted a difference in hatchling mass but not plastral lengths when comparing hatchling D. reticularia from spring and fall clutches. In both cases, this study and Congdon et al. (1983), comparisons were made between laboratory-incubated (i.e., Florida and "spring") and natural (i.e., New Jersey, South Carolina and "fall") nests. Laboratory incubation may have altered hatchling development due to laboratory conditions (e.g., temperature, soil moisture, movement of the eggs) not properly simulating the in situ conditions, which may, partially or completely, explain this unexpected difference. Another, and I believe a more likely, explanation for the similarity of hatchling plastral lengths for South Carolina and Florida terrapins refers back to the egg width and clutch size similarities and the possibly comparable environments for these two populations.

Incubation time differed significantly between the New Jersey and South Carolina populations (p<0.001). Comparisons using the Florida data were not performed because available incubation times for this population (Seigel, 1979) are from
eggs incubated in the laboratory. The difference in incubation time for the New Jersey-South Carolina comparison is most likely due to differences in nest temperature. It has been shown that increased nest temperature will reduce the incubation time for many turtle species (Congdon and Gibbons, 1990) including *Malaclemys terrapin* (Burger, 1976b). Terrapins from Kiawah tended to have shorter incubation times for hatchlings with larger plastral lengths. Burger, 1977, also reported this trend not only for plastral length but also for carapace length and hatchling mass. I cannot explain why South Carolina terrapins had a positive instead of negative correlation to incubation time for carapace length and hatchling mass. Hatchling turtles from both populations (New Jersey and South Carolina) exhibited a positive correlation of plastral length to hatchling mass (this study; Burger, 1977).

**Female Body Size**

Many authors have suggested adult female body size plays an important role in turtle reproduction (Congdon and Tinkle, 1982; Gibbons et al., 1982; Congdon and Gibbons, 1985; Congdon and Gibbons, 1987). This holds true for many emydid turtles in which body size (plastral length and/or wet body mass) is correlated to clutch size, clutch mass, egg size and pelvic girdle aperture. Therefore, it follows that if body size of reproductively active females differs between populations there may be variation in these reproductive characters due
simply to body size variation. Plastral lengths of reproductively active female terrapins from the three sites being compared are not significantly different (0.25<p<0.10). This lack of body size variation then rules out the possibility of the reproductive variation, for example in clutch size, clutch mass, egg size, etc., being caused by differences in body size of adult, reproductively active terrapins among these populations.

Pelvic Aperture Constraint

It has been suggested that pelvic girdle aperture width may place a morphological constraint on the size (width) of turtle eggs (see above for explanation). If pelvic aperture were restricting egg size to varying degrees in some Malaclemys populations, this would cause egg size variation and possibly clutch size variation. I believe egg size is not morphologically constrained by the pelvic girdle aperture in Malaclemys terrapin, in South Carolina or along the Atlantic seaboard. We would expect egg width to increase with increasing plastral length and increasing pelvic aperture width if pelvic aperture is positively correlated to plastral length, and if restriction is occurring. The positive correlation of pelvic aperture to plastral length for terrapins in South Carolina is highly significant (Fig. 5), but egg width is not significantly correlated to plastral length (Fig. 7) or pelvic aperture (Fig. 6). This indicates a lack of morphological egg size restriction and is supported by the difference in the slopes of the pelvic aperture width to plastral
length and mean egg width to plastral length regressions (Fig. 8). Congdon and Gibbons (1987) demonstrated pelvic girdle restriction for *C. picta* and *D. reticularia* due to the analogous slopes for pelvic girdle width and mean egg width to plastral length for these turtles. *T. scripta* was presumed to have no pelvic girdle aperture constraint on egg size because of a lack of slope similarity (Congdon and Gibbons, 1987); thus, I similarly believe terrapins from South Carolina do not have a pelvic girdle restriction on egg size. It also follows that, since pelvic aperture is highly correlated to plastral length for *Malaclemys* in South Carolina and the plastral lengths do not differ among South Carolina, New Jersey and Florida populations (this study), pelvic aperture is not restricting egg size in the terrapin populations from these sites.

**Possible Causes**

Variation in environmental factors is known to cause variation in parental investment (Congdon and Tinkle, 1982; McGinley et al., 1987; Congdon, 1989; Sinervo, 1990; Schultz, 1991). In their models of varying environmental factors, McGinley et al. (1987) demonstrated that animals are likely to show adaptive size variation of young, and that year to year environmental variation could favor offspring size variation in annually reproducing species. Terrapins may be varying offspring size in response to differing environmental pressures (e.g., resource availability, temperature (affecting activity
periods), suitable nest site availability, etc.] associated with the distinct climates at various latitudes. This is most likely a graded response and, therefore, a specific change in latitude would not correspond to a specific environmental and/or reproductive change. Due to the closer proximity of the South Carolina and Florida populations and, therefore, greater climatic similarities, I believe similar environmental selective pressure is causing terrapins in these areas to employ analogous reproductive strategies.

The pattern shown here by Atlantic coast terrapins seems to loosely fit the life history principle of \( r \) and \( K \) selection. In \( r \) and \( K \) selection, populations exhibit these life history patterns in response to the concomitant environment in which they live [i.e., \( r \)-selected individuals live in \( r \)-selected environments and vice-versa]. The \( r \)-selected populations tend to produce many, small offspring in response to a variable and "unpredictable" environment. In contrast, the \( K \)-selected populations tend to produce fewer, larger offspring in a less variable (i.e., more stable) and hence more "predictable" environment. In general, temperate climates, like in New Jersey, are thought to be more variable, while the sub-tropical, as in South Carolina and Florida, and tropical climates are considered more stable. Since turtles do not practice parental care, the two reproductive strategies for increasing offspring survivorship available to turtles are to: (1) produce many offspring, which often reduces parental investment per offspring thus reducing size and/or
Fig. 8. - The correlation of pelvic girdle aperture width (mm) and egg width (mm) to adult female plastral length (mm) for terrapins from South Carolina. Notice the dissimilarity of the slopes of the two lines. This is similar to what Congdon and Gibbons found for *Trachemys scripta* (1977) and from this concluded that the pelvic girdle aperture of *T. Scripta* was not restricting egg width in these turtles.
Pelvic Aperture Width = 8.440878E-2x + 1.337730E+1
\( r^2 = 6.597556E-1 \)

Mean Egg Width = -3.242712E-3x + 2.497910E+1
\( r^2 = 2.351857E-3 \)
fitness (r-selection) or (2) produce fewer, larger, presumably more fit offspring (K-selection). Although it has not been quantitatively demonstrated, it is often suggested that larger hatchling turtles will have increased survival rates for a variety of reasons [e.g., increased competitive ability, decreased mortality due to predation, increased foraging success, increased room for yolk stores (Congdon et al., 1983; Congdon and Gibbons, 1990), reduced surface area to volume ratio, and possibly reduced metabolic rate and therefore reduced need for food intake]. Sinervo (1990) showed an increase in sprinting speed for *Sceloporus occidentalis*, an iguanid lizard, with increased hatchling size. Turtles laying consistently larger eggs may be producing higher quality offspring (Congdon, 1989), which theoretically have a better chance of survival and contribution to the population. These females might not "need" to produce as many offspring as those producing a smaller lower quality young. On the other hand, increasing sheer numbers of offspring can increase overall survivorship simply due to probabilities, but this increase is not considered to be as substantial as that gained by increased size.

It has been suggested that decreased length of nesting season in the colder climates may cause decreased nesting frequency simply due to time constraints and the increased developmental time necessary in cooler climates. If this is occurring in *Malaclemys* along the Atlantic coast, we might attribute the increased number of offspring produced per
female (clutch size) in more northern latitudes as a counterbalance to a decreased clutch frequency. This trade-off between clutch frequency and clutch size is only speculative, for there is no real evidence to support it. Further studies of clutch frequency in terrapins are necessary before any conclusions on the effect of clutch frequency on varying reproductive characters can be made.

From an evolutionary standpoint, soil moisture may be causing the north to south differences, and possibly the South Carolina-Florida similarities. The moisture of the incubating substrate affects the survivorship and development of embryos in flexible-shelled eggs (Congdon and Gibbons, 1990). Increased soil moisture increases hatchling size, decreases incubation time and the amount of yolk stores (see Congdon and Gibbons, 1990). Although soil moisture data were not obtained for any of the terrapin nesting populations, it may be reasonable to assume rainfall amounts approximate relative soil moistures. If this is true, then we would expect, in general, drier soil at the higher latitudes with increasing soil moisture as we move south. Drier soil in New Jersey may cause decreased hatchling size, increased incubation time, and higher egg mortality rates (lower hatching rates). Burger (1977) reported a hatching rate of 21% over 2 nesting seasons, while I had a hatching rate of 56% for 1 season. The lower rate in New Jersey may be due to year to year fluctuations (in New Jersey the rate was 39% in 1973 and 18% in 1974, '73-74 was 21%;
Burger, 1977) not apparent in my single season of data. If these hatching rate differences do reflect a lower hatching rate in New Jersey because of soil moisture, this may explain the larger clutch size in New Jersey, again as a counterbalance to offspring mortality, and also the similar clutch sizes among the South Carolina and Florida populations.

Hatchling survival may also be an important contributing factor to reproductive variation. Little is known about hatchling terrapins, and available data (Burger, 1977; Pitler, 1985; Lovich et al., 1991) are not related to survivorship of hatchlings after leaving the nest. Is competition (either inter- or intraspecific) high? Does hatchling competition vary with latitude (habitat, climate, environment)? How does hatchling size affect predator-escape success, foraging success, growth rate, or age to sexual maturity? Any one or a combination of these factors may be causing selection for "optimal" hatchling size or number.
LITERATURE CITED


PERSONAL COMMUNICATIONS WITH:

Peter Auger – Barnstable High School, Barnstable MA.
Jeffrey Lovich - Savannah River Ecology Lab, Aiken, SC.
Willem Roosenberg – University of Pennsylvania, PA.
Stephanie Shipley - Mass. Audubon Society, Wellfleet, MA.