The Reproductive Biology of the Diamondback Terrapin,
Malaclemys Terrapin Tequesta

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THE REPRODUCTIVE BIOLOGY OF THE DIAMONDBACK TERRAPIN, MALACLEMYS TERRAPIN TEQUESTA

BY

RICHARD A. SEIGEL
B.A., Rutgers University, 1976

THESIS

Submitted in partial fulfillment of the requirements for the degree of Master of Science: Biology in the Graduate Studies Program of the College of Natural Sciences of the University of Central Florida at Orlando, Florida

Summer Quarter
1979
ABSTRACT

The reproductive biology of the Florida east coast terrapin, Malaclemys terrapin tequesta was studied during 1977-1978 at the Merritt Island National Wildlife Refuge, Brevard County, Florida. Mating occurred in small canals and ditches during late March and April. Terrapins exhibited a poorly developed courtship behavior system; this was attributed to the relative isolation of the species due to its brackish water habitat. Nesting occurred on dike roads, rather than on sand dunes as reported for other races of Malaclemys. Air temperature was the most important factor controlling nesting activity. One to three clutches were laid each year. Malaclemys appeared to exhibit a clinal variation in clutch size between northern and southern populations. Reduced clutch size in the south is explained by a relative increase in egg and hatchling size, possibly resulting in greater survivorship of offspring in southern populations. Adult females nesting on dike roads are subject to severe predation from raccoons.
ACKNOWLEDGMENT

Numerous persons helped during the course of this study. For help with the field work, I thank E. Scott Clark, Timothy R. Clabaugh, John D. Galluzzo, Mary T. Mendonca, and Sherry E. Williams. Dale Jackson discussed the use of oxytocin, and helped examine specimens for corpora lutea. I thank J. Whitfield Gibbons for advice on the use of x-rays and Jo Curen and Alan Bosemany for use of hospital equipment. Jeffrey D. Wetherington helped with the statistical analysis. The U. S. Fish and Wildlife Service made field sites available. Rosalie Creamer typed the manuscript. My wife Nadia provided invaluable assistance both in the field and during preparation of the manuscript.

My graduate committee, composed of Drs. L. M. Ehrhart, J. L. Koevenig, P. C. H. Pritchard, and I. J. Stout provided many helpful suggestions throughout this study. I particularly thank the late James D. Anderson for advice and encouragement. This research was supported by NASA Contract NAS10-8986, to L. M. Ehrhart, who graciously made support available.
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INTRODUCTION

The life history and ecology of the diamondback terrapin, *Malaclemys terrapin* is poorly known. Of the seven sub-species currently recognized, only the northern race, *M. t. terrapin* has been studied in any detail. Information available for this race includes observations on hibernation (Lawler and Musick, 1972), nesting habits and reproductive potential (Finneran, 1948; Reid, 1955; Burger and Montevcchi, 1975; Montevcchi and Burger, 1975; Burger, 1976a), hatchling behavior (Burger, 1976b), and hatching success (Burger, 1977). Information on other races of diamondback terrapins in the wild is limited primarily to notes concerning growth in *M. t. pileata* (Cagle, 1952) and the occurrence of barnacles on *M. t. macrospilota* (Jackson and Ross, 1971; Ross and Jackson, 1972; Jackson et al., 1973).

In contrast to the above, a considerable amount of research has been conducted on captive Malaclemys. This is especially true in the areas of growth and feeding (Hildebrand, 1932; Allen and Littleford, 1955), and egg production (Hildebrand, 1929). Unfortunately, as both Carr (1952) and Burnley (1969) have pointed out, little of this information can be applied to a natural situation, because turtles in captivity often respond quite differently to environmental conditions than do wild individuals. For example, Burns and Williams (1972) found that captive *M. t. pileata* lay eggs sporadically, with no clutch being completed in a single day. Such behavior is extremely rare among wild turtles. Hildebrand (1932) forced hatchlings to grow faster than normal
by raising them in warm water tanks through the winter. It is unlikely that the growth seen in such individuals is comparable to growth under natural conditions.

The Florida east coast terrapin, M. t. tequesta was the last subspecies of Malaclemys to be described (Schwartz, 1955). With the exception of M. t. rhizophorarum, this race has the most southerly distribution of all Malaclemys. Published data for M. t. tequesta are limited to the original description and a note on mortality (Seigel, 1978). The almost complete lack of data on the biology of this subspecies indicates the need for studies of virtually any aspect of its natural history. The purpose of this study was two-fold: 1) to determine some of the basic reproductive parameters of M. t. tequesta and 2) to compare the reproductive strategies of the southern, subtropical race, with the reproductive strategies of Malaclemys from more northerly climates.
MATERIALS AND METHODS

Study Area

The general study area for this research was the Merritt Island National Wildlife Refuge, located in Brevard County, Florida. The refuge is dominated by three extremely large, brackish water lagoons, as shown in Figure 1. Until 1958, the land area of the refuge consisted primarily of salt marsh, a habitat to which Malaclemys is highly adapted. In 1958, an extensive series of mosquito-control dikes was constructed in the area, resulting in the virtual elimination of the salt marsh habitat. As a result, Malaclemys is now confined primarily to the brackish water lagoons at Merritt Island.

Mating Studies

Observations of mating behavior were taken whenever possible in the spring and fall of 1977-1978 by surveying areas (chiefly the borders of the lagoons) that support large Malaclemys populations. Surveys were made three to five times weekly in the spring, and one or two times weekly in the fall, from 0700-2400 hours. Observations were made from natural blinds, using 7 x 26 binoculars to aid in viewing, making every effort to disturb the turtles as little as possible. The following data was recorded for each observation: date, time of day, general climatic conditions, and behavior of individual turtles. Air and water temperatures were recorded with a Schultheis quick-reading thermometer, accurate to ± 0.1°C.
Fig. 1. Merritt Island National Wildlife Refuge.
Nesting Studies

Study Site.-- Numerous areas were surveyed for evidence of nesting activity, including the banks of the lagoons, spoil islands, sand dunes, and various dikes. One dike, known locally as the Shiloh road was selected as the major study site for the nesting portion of the study (Figure 1). This dike is located at the northern boundary of Merritt Island, at the northern edge of the Indian River, the lagoon bordering Merritt Island on the west. The dike is rather narrow, the greatest width being about 20 m, and is dominated primarily by red mangrove (Rhizophora mangle). The dike is 5 km long and traverses two distinct habitats, each of which contains substantial populations of Malaclemys. The first section borders the Indian River, being separated from the river by a narrow (3-6 m) ditch, which is permanently filled with water. The second section borders a small salt marsh, one of the few such marshes left at Merritt Island.

Nesting Surveys.-- I collected data on nesting ecology by walking two standardized census routes, each 1.6 km long, along each section of the Shiloh road described above. Census routes were walked three to five times daily from 0700-0100 hours throughout the nesting season (late April to early July). The following data was recorded for each turtle collected along the census route: date; time; location; cloacal, substrate, and air temperatures; and straight-line carapace and plastron length. The presence of marks or injuries and the animal's activity were also recorded. Lengths were recorded to the nearest .1 cm using a foresters calipers. Weight was measured on a portable spring balance, accurate to ± 10 g. Temperatures were measured with a Schultheis...
thermometer. Turtles were marked by drilling holes in marginal scutes, following Ernst et al. (1974). Turtles found in the process of nesting were allowed to complete their activities before being captured. Data recorded for these individuals included location, type of nesting soil, distance to nearest vegetation, percent vegetation cover at the nest site, degree of slope, compass direction and distance to nearest water.

Nesting Activity.—In order to detect patterns in daily and seasonal nesting activity, it is necessary to quantify and compare activities in a relative manner. Most studies of nesting activity have considered only numbers of turtles caught per day, without regard to the amount of effort expended to obtain the sample. Examples of such studies are those of Ernest (1971) and Burger and Montevecchi (1975). For comparative observations to be valid, collecting effort must be equal between sample periods, a requirement which is not often met. Unstandardized collecting effort can easily produce biased results. For example, it is clear that if on day X, five turtles are captured in 10 hours of effort, the activity on that day is not equal to day Y, when five turtles were captured in five hours effort. Therefore, studies which do not take into account collecting effort can be misleading.

In order to quantify nesting activity, an "index of turtle nesting activity" was calculated. This index is calculated as the numbers of turtles found nesting in a given time unit (hour, day, etc.) divided by the number of search hours in that time unit. For example, if five turtles were found in 10 hours effort, the index would be .5. Although simple in its approach, this index allows for more accurate comparisons between nesting activity during different time periods. Similar indexes
have been used to analyze trapping results (Cagle, 1946), and to determine relative species abundance (Tinkle, 1959).

Clutch Size Determination.-- Three separate methods were used to determine clutch size. The simplest and most direct method was to count eggs obtained from natural nests. Unfortunately the difficulty of finding females actually in the process of nesting limited the usefulness of this method. A second method involved injecting turtles with the hormone oxytocin, in order to induce premature egg-laying in the laboratory (Ewert and Legler, 1978). This method was especially useful in obtaining eggs for size measurements and incubation. The primary method used to determine clutch size in this study was through x-ray examination of gravid females. This technique has been used successfully by Gibbons and Greene (1979) for a variety of species, with no ill effects to the individuals examined. Turtles were examined with standard hospital equipment, using a dosage of 100 ma at 60 kv for 1/30 second.

Determination of Annual Reproductive Potential.-- While the above methods are useful for determining clutch size, they provide little or no useful information regarding annual reproductive potential, i.e., the number of clutches produced by an individual female per year. The only technique which is currently available to determine reproductive potential accurately, involves the examination of enlarged follicles and corpora lutea from dissected specimens. This method has been used successfully to determine the annual reproductive potential of a number of species, including *Chrysemys picta* (Ernst, 1971; Christiansen and Moll, 1973; Moll, 1973), *Sternotherus minor* (Cox and Marion, 1978;
Iverson, 1978), *Trionyx spiniferus* (Robinson and Murphy, 1978), and *Chelydra serpentina* (White and Murphy, 1973). A limited number of *Malaclemys* were chosen for dissection, and killed with 2 cc of T-61 euthanasia solution. Following dissection, the ovaries and oviducts were removed and examined for corpora lutea. Presence of corpora lutea of more than one size class was assumed to indicate that more than one clutch had been laid that season.

**Eggs and Hatchlings.**—All eggs obtained during this study were measured within one hour of laying, so that changes in egg size due to water absorption were minimal. Egg length and width were measured to the nearest .1 mm using vernier calipers. Weight was measured on a Mettler balance, accurate to ± .1 g. Eggs were incubated in an open, outdoor house trailer, in plastic bags containing moist soil, following Stebbins (1966). Measurements of hatchlings were taken 24-72 hours after hatching, after the yolk sac had been completely absorbed. The following data were recorded for each hatchling: carapace length, carapace width, body depth, plastron length, and weight. Lengths were measured with vernier calipers; weight on a Mettler torsion balance.

**Statistical Analysis.**—Differences between sample means were tested using a Students t-test (Ott, 1977). All measurements are followed by one standard deviation of the mean.
RESULTS AND DISCUSSION

Mating Studies

Habitat Utilization. -- Numerous areas were searched for evidence of *Malaclemys* mating activity, including open lagoonal waters, brackish water impoundments, and canals. Mating activity, however, was only observed in quiet canals and ditches which border Mosquito Lagoon and Indian River. A typical canal is illustrated in Figure 2.

Mating Behavior. -- Diamondback terrapins form large aggregations for breeding, with turtles assembling in canals and ditches in late March and early April. Aggregations which I observed ranged from 6-75 individuals, but local residents have reported as many as 250 terrapins in a single narrow canal, having an area of 100 m^2^. Aggregations probably serve to increase the probability of a successful mating, since it would be difficult for turtles to find and secure mates in the large, open waters of the lagoons. As mentioned above, no mating activity was ever seen in the lagoons proper.

Courtship and mating were observed on eight days, from 26 March - 25 April. All mating was seen during daylight hours, from 1040-1610 hours. Water temperatures ranged from 24.8-27.0°C ($\bar{X} = 26.5 \pm 1.2$), while air temperatures ranged from 22.8-27.0°C ($\bar{X} = 25.5 \pm 1.3$). Hay (1904), in the only other report of *Malaclemys* mating in the wild, noted that terrapins (locality unknown) mate soon after emerging from hibernation, usually at night or in the early morning. Diamondback terrapins at Merritt Island became active in mid-February, and I saw no
Fig. 2. Mating habitat of diamondback terrapins at Merritt Island.
examples of night time or early morning mating behavior.

Although the complete sequence of courtship and copulation was never seen sufficient partial observations were made to provide a reasonably complete description of mating behavior. Courtship begins with the female floating on the surface of the water; males approach from the rear, and nuzzle or nudge the female's cloacal region with their snouts. If the female remains motionless, the male will mount, and copulation will occur immediately, with both individuals floating on the water's surface. Females that swam away from approaching males were often actively pursued through the water, sometimes for long distances. The entire process is rather short: the approach phase lasting 30-60 seconds, with copulation taking only 1-2 minutes to complete. However, since copulation was never seen in full, it may last somewhat longer.

The mating behavior of *M. t. tequesta* is notable for its lack of complexity. Many species of emydine turtles exhibit a rather complex courtship behavior, with females responding only to specific visual and tactile stimuli (Ernst and Barbour, 1972). Such behavior is probably important in species recognition, and may serve to prevent interbreeding between closely related species. There is evidence to suggest that in species where contact with other emydine forms is limited, complex courtship behavior has failed to evolve. Davis and Jackson (1973) found that males of *Chrysemys scripta taytori* lack the enlarged foreclaws used by other members of the genus in mating displays, and consequently does not exhibit typical courtship behavior. Instead, courtship is unspecialized, with males copulating with any available
female, regardless of species. This was attributed to the geographical isolation of the race.

It seems likely that a similar situation has evolved in *Malaclemys t. tequesta*. Since few emydine turtles regularly enter brackish water, (Ernst and Barbour, 1972), *Malaclemys* is effectively isolated from contact with other turtles, and the chances for interbreeding are minimal. As a result, there has been no selective pressure to evolve the complex courtship behavior seen in other species.

These observations represent the first report of mating behavior in *M. t. tequesta*, and the first detailed report of mating in any wild *Malaclemys*, since the observations of Hay (1904) were anecdotal. It is not possible, therefore, to compare the mating behavior of *M. t. tequesta* to other races of *Malaclemys* at this time.

**Nesting Studies**

Nest Site Selection.—Most nesting of *Malaclemys* at Merritt Island occurs on dike roads, especially on those bordering lagoonal waters. There is also some evidence (dug-up nests, Baker, pers. comm.) that nesting may occasionally occur on small spoil islands found in the lagoons, although the frequency of such nesting is not known. A typical dike is shown in Figure 3.

Other races of *Malaclemys* usually nest on sand dunes, or in disturbed areas where sand dunes were once present (Carr, 1952; Reid, 1955; Burger and Montevecchi, 1975; Wood, pers. comm.). Although considerable time was spent searching for nesting turtles on sand dunes at Merritt Island, no evidence for such nesting was found. Since at least one lagoon (Mosquito Lagoon, Figure 1), borders the sand dunes quite
Fig. 3. Nesting habitat of *Malaclemys* at Merritt Island. Nests are dug only on the edges of the dike, between the hard soil in the center, and the thick vegetation along the sides.
closely (<100 m), distance from the water is not a significant factor. The failure for at least some *Malaclemys* to nest on sand dunes is difficult to explain. Conceivably, the soil of Merritt Island sand dunes is unsuitable for nesting, although there is no evidence to confirm this.

Since the dikes currently used for nesting were built in 1958, terrapins must have nested in different areas prior to that time. The only other suitable nesting habitat would have been the sandy shores of the lagoons, although no nesting in this area was noted during this study. Other races of *Malaclemys* have been reported to occasionally utilize similar areas (such as the edges of tidal marshes), for nesting (Finneran, 1948; Carr, 1952).

Burger and Montevecchi (1976) found that *M. t. terrapin* nesting on sand dunes exhibited a complex nest site selection mechanism, particularly in regard to such factors as type of dune, slope, and percent vegetation cover at the nest site. Various parameters of the nest site preferences of Merritt Island terrapins are presented in Table 1. The wide variability in some factors, particularly distance from water, slope, and percent vegetation cover indicate that *M. t. tequesta* has a much less sophisticated nest site selection mechanism than does *M. t. terrapin*. This is primarily due to the type of nesting habitat utilized at Merritt Island, as seen in Figure 3. Nests can only be dug in a narrow strip, between the hard soil in the center of the dike and the thick vegetation along the sides. Lacking wide availability of suitable nest sites, terrapins nest opportunistically wherever loose soil and an open canopy can be found. A typical nest site is shown in Figure 4.
Table 1. Nest Site Selection Parameters for *Malaclemys terrapin tequesta* at Merritt Island.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean</th>
<th>Std. Dev.</th>
<th>Range</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance from water (m)</td>
<td>14.3</td>
<td>16.5</td>
<td>3.0-30.0</td>
<td>9</td>
</tr>
<tr>
<td>Percent Cover</td>
<td>20.0</td>
<td>32.9</td>
<td>0-75.0</td>
<td>10</td>
</tr>
<tr>
<td>Distance to vegetation (cm)</td>
<td>1</td>
<td>1.2</td>
<td>0-0.5</td>
<td>10</td>
</tr>
<tr>
<td>Slope (degree)</td>
<td>9.0</td>
<td>12.8</td>
<td>0-30.0</td>
<td>10</td>
</tr>
</tbody>
</table>
Fig. 4. Typical nest site of diamondback terrapin at Merritt Island, showing the characteristic open canopy and loose soil.
Some of the data in Table 1 must be interpreted with caution. For example, the data concerning distance from water might be taken to mean that turtles preferred to nest in close proximity to the water. However, considering that the Shiloh dike is relatively narrow (20-30 c), turtles were incapable of nesting very far from the water. In addition, the data concerning slope at the nest site shows that turtles never nested on slopes greater than 30°. It should be pointed out, however, that the maximum slope on the Shiloh dike exceeded 30° (maximum = 40°) and then only in areas where the vegetation was too thick for nesting to occur. A chi-square test showed that turtles exhibited no preference in terms of which compass direction the nest site faced ($X^2 = 3.0$, df = 3, p>.10). Since the vegetation along the dike was relatively uniform, this result should be expected.

Nesting Behavior.-- The nesting behavior of *P. t. tequesta* is very similar to that reported for northern terrapins (Burger, 1977). After locating a suitable nest site, the female begins to dig, using the hind legs alternately to excavate the nest chamber. This process takes from 5-10 minutes. After the nest chamber is complete egg deposition begins, and takes no more than 5 minutes to complete. Covering activity begins immediately upon completion of egg deposition and is a rather vigorous process, as the female often pounds the dirt above the nest chamber flat with her plastron. This process lasts from 5-10 minutes. The entire process, from the time the female leaves the water, to the time she returns, takes from 30-45 minutes.

After nesting, most terrapins returned to the water by the shortest route. On several occasions, however, terrapins ignored the nearest
water, choosing instead to walk along the dike for distances of up to 50 m before turning into the water. It is possible that these individuals were following some visual landmarks, and were returning to the water via the same route they emerged, in order to insure returning to the proper locality. Because few females were observed while emerging and returning to the water, these speculations cannot be confirmed.

Seasonal Aspects.-- The nesting season for the terrapins at Merritt Island extends from late April through early July. Gravid females were seen from 6 May - 1 July in 1977 (57 days) and from 28 April - 18 June in 1978 (54 days). The later start of the nesting season in 1978 was probably due to the extremely cold winter of 1976-1977. No seasonal peak of nesting activity was noted. The 54-57 day nesting season for *M. t. tequesta* is somewhat longer than the 44 day season reported for *M. t. terrapin* from New Jersey (Burger and Montevecchi, 1975). Southern turtles often have longer nesting seasons than their northern counterparts, due to the less severe environmental conditions in the south (Christianson and Noll, 1973; Noll, 1973).

Daily Timing and Environmental Influence on Nesting Activity.-- All nesting at Merritt Island takes place during daylight hours. No nighttime nesting was observed, and no evidence for such nesting (e.g. freshly dug or preyed upon nests) was seen. However, since visibility during nighttime surveys was greatly reduced, it is possible that some nocturnal nesting does occur. Wood (pers. comm.) has noted nighttime nesting by *M. t. terrapin* in New Jersey, although Burger and Montevecchi (1975) reported only daytime nesting in a terrapin population located only 40 km from Wood's. The majority of nesting at Merritt Island
occurred in the late morning, from 1000-1200 hours. The earliest observed nesting was at 1030 hours, the latest at 1610. The daily cycle of nesting activity is presented in Figure 5.

The most important factor controlling nesting activity was air temperature. Turtles nested within a relatively high and restricted range of air temperatures, from 28.0-36.0°C ($\bar{X} = 31.0 \pm 1.92$), with 83% of all nesting occurring between 29.0-33.0°C. There was a significant correlation between air and cloacal temperatures ($r = +.53$, $p<.005$), and body temperatures paralleled air temperatures rather closely ($\bar{X} = 30.7 \pm 2.09$, range = 27.2-34.8°C.). The distribution of these temperatures is shown in Figures 6 and 7 respectively. The control of air temperature on nesting activity is reflected in Figure 5, which shows that all nesting occurred between 1000-1600 hours, the time periods when air temperatures reached their maximum. In contrast, nesting activity in New Jersey M. t. terrapin has been reported to be controlled mainly by tidal influences (Burger and Montevecchi, 1975), and time of day (Wood, pers. comm.).

Diamondback terrapins at Merritt Island nest under much higher temperatures than those reported for other species of turtles. Hammer (1969) found that rising air temperatures in the range of 10.0-15.5°C, stimulated nesting activity in snapping turtles, Chelydra serpentina. Unpublished data (Seigel and Mendonca, in preparation), on four species of northern turtles (Chelydra serpentina, Clemmys guttata, Clemmys insculpta, and Chrysemys picta) shows that these turtles nest at mean body temperatures of 19.0-25.0°C, and mean air temperatures of 18.9-23.1°C.
Fig. 5. Daily cycle of nesting activity for Malaclemys at Merritt Island. Vertical bars represent ranges of air temperatures, dots represent means.
Fig. 6. Distribution of air temperatures for nesting Malaclemys, 1977-1978.
AIR TEMPERATURES

(N) 31.0
X = 31.0

NUMBER OF TURTLES

N = 24
Fig. 7. Distribution of cloacal temperatures for nesting *Malaclemys*, 1977-1978.
CLOACAL TEMPERATURES

Temperature (°C)

24.0 - 26.0 - 28.0 - 30.0 - 32.0 - 34.0 - 36.0 -

25.9 27.9 29.9 31.9 33.9 35.9 37.9

NUMBER OF TURTLES

N = 24

= 30.7 °C
The differences in preferred nesting temperatures between these species and Florida Malaclemys can probably be explained by the southern distribution of M. t. tequesta, which results in its exposure to much higher temperatures than any of the above species. Hutchinson et al. (1966) reported that Malaclemys from Florida have one of the highest critical thermal maxima of any aquatic turtle, indicating that the race is physiologically well-adapted to the higher temperatures found in the south. It is not surprising, therefore, that M. t. tequesta nests at relatively higher temperatures than other species.

Other environmental factors that might influence nesting activity were also noted. Rainfall, particularly late afternoon thunderstorms which sharply reduced air temperatures, also appeared to reduce nesting activity. Turtles also showed a significant preference for nesting during fair weather rather than during periods of cloudy or overcast skies ($X^2 = 5.11$, df = 1, p<.05). Other turtle species, including M. t. terrapin (Burger and Montevecchi, 1975) and Trionyx muticus (Plummer, 1976) have also been reported to nest primarily during fair weather.

Size Structure of the Nesting Population.---Measurements were taken on both nesting females and freshly killed individuals preyed on while attempting to nest (see Predation, below). Since there was no significant difference between the two samples, the data were combined. The mean plastron length of 33 females was $15.8 \pm 1.04$ cm. The distribution of these sizes was quite normal (Figure 8). Females ranged in size from 13.7-17.5 cm. Insufficient data were available to detect any seasonal trends in the size of the nesting animals.
Clutch Size and Reproductive Potential.-- The mean size of 14 clutches taken from natural nests, or counted from x-ray data and oviducal egg counts was $6.71 \pm 1.43$ (range, 5-10). There was a significant correlation between plastron length and clutch size ($r = +.53$, $p < .05$), i.e., larger females produced larger clutches. Examination of corpora lutea in a small number of specimens, indicates that 30% of the Merritt Island population produces two clutches each year, and 15% produces three. Since relatively few turtles were examined ($N = 8$), this conclusion must be regarded as tentative. Other races of *Malaclemys* have also been reported to lay multiple clutches, including *M. t. terrapin* (Hildebrand, 1932; Wood, pers. comm.), and *M. t. macrospilota* (Jackson, pers. comm.).

Eggs and Hatchlings.-- Measurements of eggs and hatchlings are presented in Table 2. No significant correlations were found between clutch size and egg size, nor between female plastron length and egg size. Montevecchi and Burger (1975) also found no correlations between those measurements in a population of *M. t. terrapin*.

Eggs were incubated under artificial conditions, at temperatures ranging from 15.0-34.0°C. Mean incubation time for five clutches was $65.6 \pm 5.3$ days (range 60-73). Burger (1977) reported a mean incubation period of 76.2 days for *M. t. terrapin* eggs incubated under natural conditions. Because eggs from this study were incubated artificially, comparisons of incubation times between the two sub-species cannot be made.

Geographic Variation in Reproduction.-- Various authors have noted the existence of a clinal variation in clutch size between northern and
Table 2. Size of eggs and hatchlings of various races of *Malaclemys*.

<table>
<thead>
<tr>
<th>Locality</th>
<th>tequesta</th>
<th>pileata</th>
<th>terrapin</th>
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<tr>
<td>Brevard County, Fla.</td>
<td>St. Bernard Parish, La.</td>
<td>Little Beach Is., N.J.</td>
<td></td>
</tr>
<tr>
<td>This study</td>
<td>Burns and Williams, 1972</td>
<td>Montevecchi and Burger, 1975, Burger, 1977</td>
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<tr>
<th>Egg Diameter (cm)</th>
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<tr>
<td>(X, range)</td>
<td>3.90 (3.61-4.08)</td>
<td>3.73 (3.40-4.01)</td>
<td>3.16 (2.60-3.65)</td>
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<th>Egg Width (cm)</th>
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<tbody>
<tr>
<td>(X, range)</td>
<td>2.23 (1.90-2.40)</td>
<td>2.39 (2.19-2.70)</td>
<td>1.97 (1.59-2.19)</td>
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<tr>
<th>Egg Weight (g)</th>
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<th></th>
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<tr>
<td>(X, range)</td>
<td>12.48 (11.2-13.2)</td>
<td>....</td>
<td>7.7 (5.0-11.0)</td>
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<thead>
<tr>
<th>Carapace (cm)</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>(X, range)</td>
<td>3.19 (2.88-3.40)</td>
<td>2.99 (2.94-3.04)</td>
<td>2.75 (2.5-3.07)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Plastron (cm)</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>(X, range)</td>
<td>2.79 (2.42-3.02)</td>
<td>2.55 (2.48-2.61)</td>
<td>2.44 (2.1-2.69)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Weight (g)</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>(X, range)</td>
<td>8.83 (6.0-10.8)</td>
<td>8.1 (7.2-9.1)</td>
<td>6.8 (5.0-9.0)</td>
</tr>
</tbody>
</table>
southern populations of turtles. Such variation has been reported for the following species: *Sternotherus odoratus* (Tinkle, 1961), *Chrysemys picta* (Powell, 1967; Christiansen and Moll, 1973; Moll, 1973), and *Chrysemys scripta* (Moll and Legler, 1971). In general, northern populations of these species produce larger clutches than their southern counterparts. Tropical *C. scripta* is an exception to this rule, producing more eggs per clutch than northern sub-species.

This trend toward smaller clutch size in the south is puzzling. Lack (1954), Tinkle (1961), and Williams (1966) have pointed out that small clutch size within a species should not evolve unless there is some selective advantage to producing a smaller clutch rather than a larger one. Moll (1973) explained the small clutch size among southern populations of *C. picta* by pointing out that such populations were constrained by small body size into producing small clutches. However, since these southern populations produced more clutches per year than did northern populations, there was no net difference in annual reproductive potential, and thus no disadvantage in producing smaller clutches. Tinkle (1961) used a similar hypothesis to explain small clutch size in southern populations of *Sternotherus odoratus*.

Diamondback terrapins exhibit a similar clinal variation in clutch size. The mean clutch size of *M. t. tequesta* (6.7) is significantly smaller (p < .05) than the 9.8 mean clutch size of *M. t. terrapin* (Montevecchi and Burger, 1975), or the 8.5 clutch size reported for *M. t. pileata* from Louisiana (Burns and Williams, 1972). This is shown in Table 3.
Table 3. Comparison of reproductive potential in various races of *Malaclemys.*

<table>
<thead>
<tr>
<th>Subspecies</th>
<th>Locality</th>
<th>Authority</th>
<th>Clutch size (X, range)</th>
<th># of Clutches</th>
</tr>
</thead>
<tbody>
<tr>
<td>tequesta</td>
<td>Brevard County, Fla.</td>
<td>This study</td>
<td>6.7 (5-10)</td>
<td>1-3</td>
</tr>
<tr>
<td><em>terrapin</em></td>
<td>Beaufort, N.C.</td>
<td>Hildebrand</td>
<td>8.0 (....)</td>
<td>1-5</td>
</tr>
<tr>
<td>X centrata</td>
<td></td>
<td>(1932)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>terrapin</td>
<td>Little Beach, Is., N.J.</td>
<td>Monteverchic</td>
<td>9.7 (4-18)</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>and Burger</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1975)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>pileata</em></td>
<td>St. Bernard, Parish, La.</td>
<td>Williams</td>
<td>8.5 (5-12)</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1972)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Denotes captive population*
The reduced clutch size in southern populations of *Malaclemys* cannot be explained by either small body size or equal reproductive potentials. First, Florida *Malaclemys* are not constrained by small body size into producing smaller clutches, since there is no significant difference between the midline plastral lengths of turtles from this study (15.7 ± 1.1 cm) and the 15.4 cm plastral length of terrapins from New Jersey (Montevecchi and Burger, 1975). Secondly, the annual reproductive potential of *M. t. tequesta* does not appear to equal that of northern terrapins. Less than one-third of the turtles from this study were found to produce a second clutch. Captive *M. t. terrapin* have been reported to produce as many as five clutches per year (Hildebrand, 1932), and Wood (pers. comm.) has reported multiple nesting in a wild population of the same sub-species. The large difference in clutch size between the two populations (6.7 vs 9.7), as well as the fact that multiple clutches may be produced with equal frequency, suggests that the reproductive potential of *M. t. terrapin* is somewhat higher than that of *M. t. tequesta*. However, until more extensive data on the reproductive potential of northern terrapins in the wild become available, these speculations cannot be verified.

The most likely explanation for the smaller clutch size in *M. t. tequesta* is found by examining relative egg and hatchling sizes. The size of *M. t. tequesta* offspring is compared to those of other sub-species in Table 2. Eggs and hatchlings from this study are significantly larger (p<.05) in all dimensions than eggs and hatchlings of *M. t. terrapin*. When compared to *M. t. pileata*, Florida offspring were larger in all dimensions except egg width and hatchling weight. The
reasons for this discrepancy in egg width are not known, but the
difference in hatchling weight may be explained by the fact that the
*M. t. pileata* young were weighed with the yolk sac still attached,
which may have influenced the measurements. Larger eggs and young in
southern populations of turtles have also been reported for various
races of *Chrysemys scripta* (Moll and Legler, 1971).

Although it has not been proven conclusively, it seems reasonable
to assume that larger eggs and hatchlings have a greater survival value
than smaller offspring. Larger eggs may provide additional resources
during development. Despite expectations to the contrary, Burger (1977)
found that larger eggs of *M. t. terrapin* had a shorter incubation time
than did smaller eggs. This might reduce chances for predation during
incubation, and would allow more time for growth of young before the
onset of winter. Larger hatchlings might have greater strength and
maneuverability, allowing them to elude some predators more efficiently.
If the increased survival value of *M. t. tequesta* offspring results in
equivalent reproductive success between the three races (i.e. if the
number of offspring surviving to the next generation is the same) then
there would be no selective disadvantage to the small clutch size
strategy of Florida terrapins. Moll (1979) indirectly supports this
view by noting the adaptive value of small clutches of large eggs, in
such tropical genera as *Rhinoclemys*.

The difference in clutch and egg size between various populations
of *Malaclemys* may be interpreted as an example of r- and K-selection
operating within a species. It has been suggested (Tinkle, 1961;
Tinkle, et al., 1970; Pianka, 1970) that due to the high abiotic
mortality (chiefly severe winter mortality) in the north, selection there should favor increased reproduction, i.e. r-selection. In tropical or southern areas, abiotic mortality may be less important, and populations may closely approach the carrying capacity. Selection should, therefore, favor fewer but larger and more competitive offspring, i.e. K-selection. If this is true, then parental investment per offspring should be somewhat higher in southern areas. If mean clutch weight is used as a rough approximation to reproductive investment, then it appears that both M. t. terrapin and M. t. tequesta invest similar amounts of energy per clutch, since there is no significant difference (p > .10) between the mean clutch weight of Florida terrapins (66.6 g/clutch) and the mean weight (71.7 g) reported for New Jersey clutches (Montevecchi and Burger, 1975). There are no clutch weight data available for M. t. pileata. Because Florida terrapins produce fewer eggs per clutch than do northern terrapins, the amount of parental investment per offspring (as expressed by egg weight) is almost 40% larger in M. t. tequesta than in northern terrapins. If this increased parental investment results in increased survivorship and competitive ability of the offspring, these results would strongly support the r- and K-selection model stated above.

It should be pointed out that since considerable variation may exist in reproductive potential between local populations of the same species (Gibbons and Tinkle, 1969), the reproductive potential of Malaclemys at Merritt Island may not be typical of the race. Studies on the reproductive biology of Malaclemys from other parts of its range are badly needed.
Predation

When this study began, it was not expected that predation would be part of the nesting biology of *Malaclemys*. As the study progressed, however, it became apparent that predation on adult terrapins was indeed an integral part of the nesting ecology of *Malaclemys* at Merritt Island. Therefore, a brief summary of the effects of such predation is presented below.

Except for occasional attacks by alligators, predation on adult turtles appears to be a relatively rare phenomenon. Of the 43 freshwater species listed by Ernst and Barbour (1972), adult predation is listed for only 19, and in all but 9 of these cases, alligators were the predator. Most records of adult predation are anecdotal, usually describing attacks on only one or a few individuals. Predation of this kind has been reported for the following species: *Chrysemys picta* (Ernst, 1974), *Chrysemys scripta* (Minickly, 1966), *Clemmys guttata* (Ernst, 1976), *Graptemys pulchra* (Shealy, 1976), *Gopherus polyphemus* (Causey and Cude, 1978), and *Podocnemis expansa* (Pritchard, pers. comm). To date, only Wilbur (1975) has reported a case of consistent adult predation. In this instance, man-made changes in a pond habitat forced painted turtles (*Chrysemys picta*) to bask on the banks of the pond, where they were exposed to predation by raccoons (*Procyon lotor*).

The sole predator on *Malaclemys* at Merritt Island also appears to be the raccoon. All turtles found dead during this study were surrounded by raccoon tracks, and in one case, an attack was observed in full. Raccoons apparently kill terrapins by severing one or more limbs, causing the turtle to weaken rapidly from blood loss. After the turtle becomes
limp the neck is broken, killing the turtle. Although actual attacks on other individuals were not observed, the following evidence indicates that raccoons were the cause of death. First, in virtually all cases, the dead turtles were surrounded by raccoon tracks, and showed body damage similar to that described above. Second, despite the fact that the dikes the turtles were found on were surveyed constantly (see Materials and Methods), no evidence was noted to suggest that the turtles died from natural causes (e.g. overheating or dessication), nor that other predators were involved. The only other likely predators of adult _Malaclemys_ at Merritt Island are the bobcat and river otter, neither of which were ever observed on the study area.

Initial examinations of the dead _Malaclemys_ seemed to indicate that raccoons were not completely consuming the turtles since many of the individuals appeared to be only partially eaten, with only one or two limbs bitten off, and with minor external damage. Subsequent dissections, however, showed that raccoons may "gut" _Malaclemys_ by opening a small hole through a limb, and reaching in to pull out all internal organs. Wilbur (1975) reported that raccoons ate only the head and limbs of _Chrysemys picta_, but apparently did not dissect the turtles to determine if the internal organs had been eaten as well.

Adult females accounted for the majority (86%) of the individuals found dead. In contrast, Wilbur (1975) reported that both sexes of _Chrysemys picta_ were equally susceptible to predation. Adult females were more susceptible to predation in this study because the nesting season constitutes the only period of significant overland activity for _Malaclemys_ at Merritt Island. Obviously, females are more likely to be
on land at this time than are males, and they are thus more likely to be exposed to predators. Although the dikes were surveyed year-round, no evidence of predation was found outside of the nesting season.

In contrast to other reports of adult predation in which it was confined to a single pond (Minckley, 1966; Wilbur, 1975), predation at Merritt Island appears to occur wherever *Malaclemys* nesting takes place. Evidence of predation has been recorded on dike roads located 24 km apart, and it is likely that additional search efforts would broaden this area further.

A total of 19 adult females were found on a .5 km section of the Shiloh dike in 1977. Fewer individuals \( n = 3 \) were found in 1978, but this was due to a general lack of nesting activity that year, rather than a reduction in predation pressure since the ratio of turtles killed by raccoons to turtles found alive was similar in both years (1977 = 1:1.2; 1978 = 1:1.6). The dead turtles ranged in plastron length from 13.7-17.5 cm \( \bar{X} = 15.6 \pm .92 \) cm). There was no significant difference between the mean size of these turtles and the rest of the nesting population \( p > .10 \). A chi-square test showed that all size classes were equally represented among the dead individuals, corresponding to their relative frequency in the overall population \( \chi^2 = 7.59, df = 4, p > .10 \). This indicates that raccoons did not select any particular size class.

The impact of raccoon predation on *Malaclemys* populations is not yet clear. Preliminary population estimates (Seigel, unpublished) indicate that at least 10% of the adult female population at the Shiloh study site was killed by predators in 1977. The long term effects of this mortality are not known, but I noted greatly reduced mating and
nesting activity at the study site in 1978, possibly reflecting a reduction in the population size. Numerous old, decomposed Malaclemys shells found along the dike suggest that the predation there has occurred for a number of years, and that the population has been subjected to severe predation for some period of time. Wilbur (1975) found that a C. picta population was greatly reduced by raccoon predation, resulting in a decrease in the mean generation time of the population.

I suggest that the intense raccoon predation on Malaclemys at Merritt Island is peculiar to that area, and does not represent a natural occurrence for the following reasons. First, if raccoon predation on Malaclemys is common, it is difficult to explain why such a conspicuous phenomenon has not been previously reported. Second, there is indirect evidence to suggest that man-made changes in the Merritt Island habitat may have led to the predation currently seen. As previously mentioned, the construction of the mosquito control dikes in 1958 caused the destruction of most of the salt marsh on the refuge. Local residents familiar with the area claim that the raccoon population increased sharply at this time. This increase, coupled with an invasion of the new dike habitats by raccoons as feeding areas, probably led to increased contact between raccoons and Malaclemys when the latter began to use the dikes as nesting sites (see Results - Nest Site Selection). Thus, rather than being a normal part of raccoon feeding habits, severe raccoon predation on adult Malaclemys may have only begun when conditions led to increased contact between the two species.

These observations, coupled with those of Wilbur (1975) suggest that while predation on adult turtles is rare, the barriers preventing
such predation may be easily disturbed by man-made changes in habitat. Large reductions in population size, and even eradication of local populations may result from such disturbances, since turtles are poorly adapted to severe mortality at a life history stage when survivorship is generally very high. This is especially true at Merritt Island, since most of the predation was on reproducing females, the most biologically important part of the population.
SUMMARY

1. *Malaclemys* at Merritt Island mate from late March - late April in small canals and ditches bordering lagoonal waters. Terrapins formed large aggregations for mating, with up to 250 individuals in a single aggregation. These aggregations probably serve to increase the chances of a successful mating.

2. The mating behavior of *M. t. tequesta* is relatively simple. This may reflect the fact that *Malaclemys* rarely encounters other species with which to inter-breed. Therefore, there has been no selective pressure to evolve a courtship system to prevent such inter-breeding.

3. Nesting occurs on dike roads, rather than on sand dunes as has been reported for other races of *Malaclemys*.

4. Nesting occurs exclusively during daylight hours. Nesting activity is regulated primarily by air temperature.

5. The clutch size of *Malaclemys* at Merritt Island is significantly smaller than that of northern races. This small clutch size is counter-balanced by an increase in egg and hatchling size, possibly resulting in greater survivorship among southern offspring.

6. Predation on adult females by raccoons is an important part of *Malaclemys* nesting ecology.


