Aspects of the Reproductive Biology of the Northern Diamondback Terrapin Malaclemys terrapin terrapin

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ABSTRACT: The characteristics, interrelationships and seasonal variation of the nests, eggs, clutches and plastron sizes of a population of northern diamondback terrapins (*Malaclemys terrapin terrapin*) nesting on a barrier beach island in southern New Jersey were studied during the 1973 breeding season. Positive correlations were obtained between (a) egg length and egg breadth; (b) clutch size and clutch weight; (c) plastron length and clutch size, and (d) plastron length and clutch weight. No significant correlations were found between (a) clutch size and any egg dimension (length, breadth, weight); (b) plastron length and any egg dimension; (c) plastron length and any nest dimension (depth, egg compartment depth, egg compartment width). The mean, median and modal clutch size of 10 eggs suggested that clutch size of northern populations may be larger than those of more southerly situated populations and subspecies. Mean egg size (length, breadth, weight) tended to decrease as the laying season advanced. Comparisons with findings from avian biology concerning eggs and egg-related phenomena were made.

INTRODUCTION

The seven subspecies of the diamondback terrapin (*Malaclemys terrapin*) are clinally distributed along the eastern and Gulf coastal salt marsh estuarine regions of North America from southern New England to Mexico (Hay, 1904; Carr, 1952; Pritchard, 1967; Ernst and Barbour, 1972). Very little is known of the breeding biology and ecology of these turtles in nature (Coker, 1906, 1951; McCauley, 1945; Cagle, 1952; Allen and Littleford, 1955; Reid, 1955; Lawler and Musick, 1972). During the early decades of this century hybrid diamondback terrapins (*terrapin* x *centrata*) were cultivated on "terrapin farms" because of their economic value as a food delicacy. As a result, much information has been collected on the growth and reproductive characteristics of captive animals (Hay, 1904, 1917; Coker, 1906, 1920; Barney, 1922; Hildebrand, 1929, 1932). Economic incentive, however, led to overexploitation and resulted in a drastic reduction in the population of diamondbacks on the East Coast of the United States during the early 1900's (Hay, 1904, 1917; Coker, 1906; Babcock, 1926; Hildebrand, 1929; McCauley, 1945; Finneran, 1948). Partially as a result of legislative protection, the population levels of *M. t. terrapin* and *M. t. centrata* appear to have gradually recovered (Coker, 1951; Ernst and Barbour, 1972), even though the destruction of East Coast salt marshes during the last 50 years (Teal and Teal, 1969) has greatly reduced the natural habitat of these turtles.

The present investigation reports on reproductive data concerning the nest, eggs, clutch sizes, sizes of nesting females and the seasonal trends of these factors among a population of northern diamondback terrapins, *M. t. terrapin*. Our findings were also compared with hypotheses concerning oological tendencies generated from research in avian biology.

METHODS

Research was conducted during June, July and early August 1973, on an *M. t. terrapin* nesting area on Little Beach (39° 29′N, 74° 21′W), a barrier beach island which protects a large salt marsh within the Brigantine Wildlife Refuge, New Jersey (for description of habitat, *see* Burger and Montevecchi, 1975). The nesting area was censused 2-4 times daily throughout the laying season. Any turtle seen digging or laying was observed from a distance. After laying was completed, the nest covered, and the turtle began to move away from the nest site, the animal was captured, its midplastron length measured to the nearest mm, and released. The nests were marked and the following recorded: (a) nest depth (ground surface level to the lower surface of the bottom egg of the clutch); (b) egg compartment depth (nest depth less the sand depth to the top surface of the uppermost egg of the clutch); (c) widest breadth of the egg compartment; (d) clutch size; (e) length of each egg; (f) maximum transverse breadth of each egg (to nearest 0.05 mm, Helios dial vernier calipers); (g) egg weight (Pisola portable 10 g scale), and (h) egg volume (water displacement technique using a 100 ml graduated cylinder). *M. t. terrapin* pack sand over their eggs upon termination of laying, and we defined the egg compartment as the outer surface of the clutch mass (Fig. 1).

Data were collected from 46 nests (40 on the main nesting area, six from other locations on the island). Some measurements were not collected at all nests. For instance, data on the depth and width of the nest were not taken when the hand excavation of the eggs extended noticeably beyond the outer clutch surface. After the data were recorded from each nest, the eggs were carefully packed back into the nest, and the cavity was hand-packed with sand. This disturbance did not appear to have any serious effects upon the hatching success of these nests.

RESULTS

Nests.—Egg compartments were on the average wider than they were deep (Table 1). No significant correlation was obtained between the width and depth of the egg compartments. Many abandoned nest cavities were found in the nesting area, but these were not measured.

Eggs.—*M. t. terrapin* lay pinkish-white, dimpled, leathery-shelled eggs which fill out during the early stages of incubation. The egg shapes are symmetrical with positive bicone, *i.e.,* poles blunter than the curvature of a true ellipsoid (Preston, 1953; Palmer, 1962). The mean standard deviation, coefficient of variation (*i.e.*, standard deviation expressed as a percentage of the mean, Simpson *et al.*, 1960), and range of the length, breadth, elongation (length/breadth, Preston, 1968), weight and volume of the eggs are presented in Table 2. The

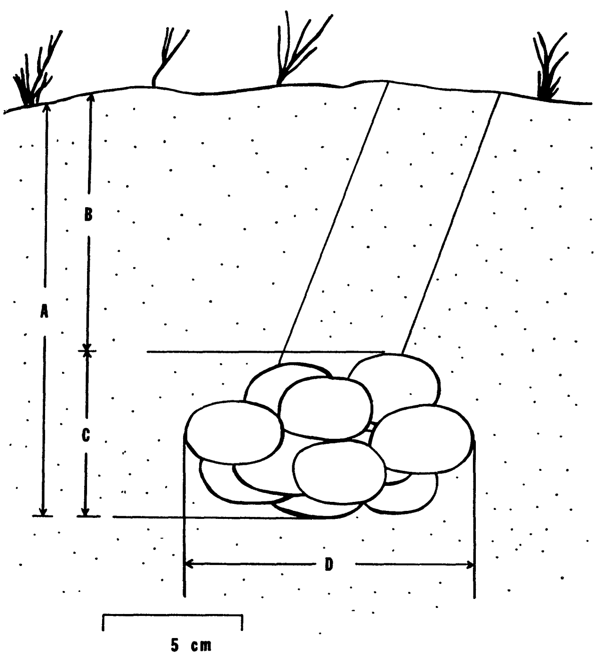

Fig. 1.—Scaled nest diagram. Measurements: (A) nest depth; (B) depth to top egg; (C) egg compartment depth = A-B; (D) egg compartment width

TABLE 1.—Nest dimensions (cm) of *Malaclemys t. terrapin*

Measurement	N	Mean	SD	Range
Nest depth (A)	43	14.98	2.08	10.80 - 20.30
Depth to top egg (B)	32	10.65	2.16	5.08 - 14.61
Egg compartment depth (C)	28	4.67	1.76	2.21 - 8.89
Egg compartment width (D)	32	7.29	1.41	4.45 - 10.15

TABLE 2.—Egg characteristics of *Malaclemys t. terrapin*

Measurement	N	Mean	SD	Range	Coefficient of variation
Length	336	31.65 mm	1.80 mm	26.30 - 36.50 mm	5.73
Breadth	336	19.79 mm	1.08 mm	15.90 - 21.95 mm	5.44
Elongation	336	1.60	0.09	1.41 - 2.13	5.72
Weight	300	7.7 g	1.1 g	5.0 - 11.0 g	14.34
Volume	54	6.43 ml	1.22 ml	4.0 - 9.5 ml	19.01

dimensions of the eggs of extreme length and breadth are *36.50* x 19.65, *26.30* x 17.40, 33.70 x *21.95*, 34.00 x *15.90* mm. There was a high positive correlation between the mean egg lengths and breadths of each clutch ($r = +0.62$, $df = 33$, $P < .01$). The variability was much greater between individual clutches than within them. One-way analyses of variance based upon 320 eggs from 34 complete clutches were highly significant for length ($F = 24.85$, $df = 33, 286$, $P < .005$) and for breadth ($F = 39.76$, $df = 33, 286$, $P < .005$). The between-groups variation accounted for 74% and 82% of the total variation for the length and breadth analyses, respectively.

The nesting area can be topographically partitioned into high dunes, low dunes and level grassy areas (*see* Burger and Montevecchi, 1975). Neither the mean egg length nor the mean egg breadth of the clutches laid in these areas was significantly different from each other.

Clutch size.—Based on 40 complete clutches, the mean clutch size was 9.76 ± 2.61, while the median and modal (15 clutches) clutch sizes were 10 eggs. Clutches ranged from 4-18 eggs. The mean clutch weight for 30 clutches with a mean of 9.5 eggs was 71.77 ± 17.69 g.

Clutch size and weight were highly correlated with each other ($r = +0.90$, $df = 29$, $P < .01$), while clutch weight showed no linear relationship with the mean egg weight of the eggs which comprised the clutch. No significant correlations were found between clutch and size of mean egg length, mean egg breadth, coefficients of variation of egg breadth, mean egg elongation or mean egg weight.

We could find no evidence that any eggs were laid before dawn or after sunset (Burger and Montevecchi, 1975). There was no significant difference between the clutches of females which laid their eggs in the morning and those which laid their eggs in the afternoon. The sizes of the eggs laid in the three topographic areas were not significantly different from one another.

Size of laying females.—The mean midplastron length of 221 females which were captured ashore during the nesting season was 15.44 ± 0.99 cm (range from 13.20 to 18.40 cm). The size distribution of these females appears quite normal (Fig. 2). The mean midplastron lengths of the turtles found in the three topographic areas were not significantly different.

Larger females tended to lay larger clutches ($r = +0.46$, $df = 27$, $P < .02$) of greater weight ($r = +0.55$, $df = 27$, $P < .01$). No significant correlations were obtained between plastron length and mean egg length, mean egg breadth, mean egg weight, the coefficient of variation of egg length, the coefficient of variation of egg breadth, nest depth, egg compartment depth or egg compartment width.

Seasonal trends.—The data on seasonal trends are presented in Table 3. Egg size tended to decrease as the laying season advanced. Significant negative correlations were obtained between laying data and mean egg length, mean egg breadth and mean egg weight. The plastron lengths of laying females, clutch size and clutch weight did not yield significant correlations with the date of egg laying.

DISCUSSION

Nests.—Hay (1904, 1917) reported that nests of East Coast diamondback terrapins are 5 or 6 inches (approximately 13-15 cm) deep and from 2.5 to 3.5 inches (approximately 6-9 cm) at the widest diam, while Coker (1906) and Ernst and Barbour (1972) reported that diamondback terrapin nests range from 4-8 inches (approximately 10-20 cm) deep. Reid (1955) reported that a single *M. t. terrapin* nest found in nature in Virginia had a nest depth of approximately 7.5 inches (19 cm) and an egg compartment depth (which we calculated) of about 2 cm. These figures are in good agreement with the range of nest dimensions found on Little Beach Island.

The type of soil in which reptiles dig their nests is an important nest characteristic which should be reported with the presentation of nest parameters. Nest measurements should be taken as soon as possible after egg laying for species which deposit their eggs under loose surfaces such as sand, since nest depth measurements may fluctuate with time.

Eggs.—The systematic study of avian egg characters has long been, and remains, an important priority of ornithologists and poultry

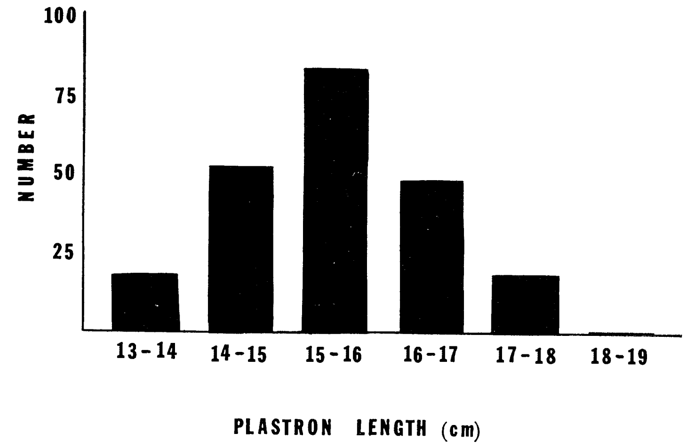

Fig. 2.—Frequency distribution of plastron lengths of females found ashore during the laying season (N = 221)

TABLE 3.—Seasonal trends of *Malaclemys t. terrapin* reproductive data

Variable	Correlation with laying date	DF	P
Clutch size	+0.29	40	<.10
Clutch weight	+0.06	29	NS
Mean egg length	—0.56	34	<.01
Mean egg breadth	—0.52	34	<.01
Mean egg weight	—0.38	29	<.05
Plastron length	+0.03	27	NS

scientists (*e.g.,* Ingersoll, 1897; Russell, 1925; Rehkugler, 1973). Reptilian eggs, however, have received less scientific attention (*e.g.,* Nichols, 1920; Conant and Downs, 1940; Edgren, 1949, 1956). *M. t. terrapin* eggs, like those of other reptiles, are symmetrical, possessing positive bicone, in contrast to avian eggs which are generally asymmetrical with a negative bicone (Preston, 1953, 1969). The average elongation of *M. t. terrapin* eggs (1.60) falls within the range (1.04-2.42) which Preston (1969) calculated for some other reptiles. The high positive correlation obtained between the length and the breadth of the terrapin eggs may be interpreted to indicate that, as egg length or breadth increases, egg shape is a more conservative trait than egg volume. If egg volume were the more conservative, a negative correlation would be expected between egg length and breadth, one increasing at the expense of the other. A similar trend can be found among the eggs of many birds (van Bree, 1957; Coulson *et al.,* 1969; Preston, 1969), and Preston (1969) has advanced this argument for avian eggs.

Although they are rare "runts," or abnormally small (often yolkless) eggs, have been found among many turtle species (*e.g.,* Bustard and Greenham, 1969; Caldwell, 1959; Hendrickson, 1958; LeBuff and Beatty, 1971; Limpus, 1971). Others have noticed that runt eggs also occur infrequently in the clutches of many passerine (Rothstein, 1973) and nonpasserine birds (Romanoff and Romanoff, 1949). No abnormally small eggs were found among the 350 terrapin eggs which we examined.

The coefficients of variation showed breadth is a less variable egg character than either the length or elongation of the eggs of *M. t. terrapin.* Egg breadth is also the most stable measurement of birds' eggs (Bergtold, 1929; Preston, 1958, 1969; Coulson, 1963; Garrett *et al.,* 1972; Beason and Franks, 1973). The egg dimensions of *M. t. terrapin* are more variable between the clutches of different females than within the clutches of individual females. This is probably attributable in large part to the physical constraints which the oviducts of the individual females impose upon the eggs. Preston and Preston (1953) reported that egg breadth, although not egg length, was significantly more variable between than within the clutches of laughing gulls, *Larus atricilla.*

Many birds also show a predictable trend in the dimensions of sequentially laid eggs within a clutch (Kendeigh *et al.,* 1956; Koskimies, 1957; Barth, 1968; Vermeer, 1969). Although these data were not collected on the terrapins, since it would have been impossible to do so without disturbing the laying females, it would be interesting to investigate this in reptiles.

There were no differences in the sizes or shapes of the eggs deposited in the different topographic regions of the nesting area. Although a correlation between topographic region and egg size has not yet been reported for any reptile, it has been found for two avian species (van Bree, 1957; Coulson *et al.,* 1969).

Clutch size.—The average (9.78±2.61), mode (10) and range (4-18) of the clutch sizes of *M. t. terrapin* nesting on Little Beach Island are slightly higher than the average (8.5±2.2) and range (5-12) of clutch sizes reported for captive *M. t. pileata* from Louisiana (Burns and Williams, 1972) and than the average or "usual" (eight or nine) and range (up to 15 or 16) of clutch sizes reported for captive hybrid and *M. t. centrata* reared in North Carolina (Hay, 1917; Hildebrand, 1932; Coker, 1951). A single nest of *M. t. terrapin* found in nature in Virginia contained seven eggs (Reid, 1955). The mean clutch size for seven nests found in nature in North Carolina was 5.29 eggs (Coker, 1906). These findings suggest a possible geographic increase in the clutch size of *Malaclemys* in more temperate, northerly regions. Such a geographic trend in clutch size is well-documented for other turtles (Cagle, 1954; Tinkle, 1961; Milstead and Tinkle, 1967; Powell, 1967), *Pseudemys scripta* being an exception in that its clutch size tends to decrease from tropical to more temperate regions (Moll and Legler, 1971). Many birds and mammals are known to average higher clutch and litter sizes at higher latitudes (Lack, 1954; Lord, 1960; Beer, 1965; Cody, 1966; Klomp, 1970). Increased clutch size in more temperate regions may be attributed in part to environmental pressures which often impose greater difficulties upon the successful rearing of young in these areas (*e.g.*, Price, 1974).

Barney (1922) and Hildebrand (1929, 1932) reported that captive hybrid terrapins lay multiple clutches (up to five), while Burns and Williams (1972) reported that captive *M. t. pileata* never lay a complete clutch on the same day, requiring approximately five layings over a period of 2-7 weeks to do so, depositing an average of two eggs at each laying. Our observation that *M. t. terrapin* lay a mean clutch of over nine eggs during a single laying in the wild gives indirect support to Burns and Williams' (1972) contention that conditions of captivity may induce the sporadic laying of diamondbacks. Other turtles lay irregularly in captivity, seemingly a result of egg retention in the absence of favorable nest sites (Cagle, 1944, 1950; Cagle and Tihen, 1948), and Risley (1933) reported that musk turtles, *Sternotherus odoratus,* lay smaller clutches in captivity than in nature. Although we have not yet documented whether *M. t. terrapin* produces multiple clutches in nature, this seems likely, since the mean clutch size of the terrapins on Little Beach Island is well below the annual egg production of captive terrapins (Barney, 1922; Hildebrand, 1929).

Clutch size was highly correlated with clutch weight but showed no relationship with any measure of egg size. Thus, for *M. t. terrapin,* clutch size is not a function of egg size. Among other turtle species larger clutches are associated with larger eggs (Risley, 1933; Allard, 1935; Legler, 1960; Moll and Legler, 1971), while among avian species clutch size tends to be inversely related to egg size (Lack, 1968; Klomp, 1970).

There was no significant difference in the clutch sizes of the terrapins nesting in the grassy areas, low and high dunes. Gibbons and Tinkle (1969) found clutch size differences among populations of *Chrysemys picta* occupying different habitats in the same geographic locale, and this phenomenon occurs among many species of birds (Kluyver, 1951; Coulson, 1968; for review, *see* Lack, 1968; Klomp, 1970).

Size of laying females.—The plastron lengths of the terrapins found ashore during the nesting season are normally distributed. Although plastron length is correlated with age in *Malaclemys* and many other turtles, there is great individual variability in the growth patterns, and growth rate slows markedly at or after maturity, thus obscuring age-size relationships (Coker, 1920; Pearse, 1923; Hildebrand, 1932; Sergeev, 1937; Cagle, 1946, 1950, 1954). Diamondback terrapins raised in captivity usually begin to lay during their 7th year, and may live well over 40 years, but their precise longevity and the period of female fecundity are not known (Hildebrand, 1932). Barney (1922) reported an average plastron length of 15.40 cm for a group of females estimated to be approximately 20 years of age, although females may attain this size in fewer years (Coker, 1906; *cf.* Fig. 2). The smallest female terrapin which has been observed laying in captivity had a plastron length of 11.97 cm (4.75 inches, Hildebrand, 1932), whereas the smallest female found ashore on the nesting area on Little Beach Island had a plastron length of 13.20 cm. The largest female found ashore had a plastron length of 18.40 cm, while the largest captive hybrid female had a plastron length of 18.5 cm (Hildebrand, 1932).

Although a relationship was anticipated, none was found between the plastron length of the laying female and any of the nest dimensions. Carr (1967), Ernst (1970) and Moll and Legler (1971) reported that larger turtles dig deeper nests—as deep as their hind legs can reach. Ernst and Barbour (1972) implied this relationship for *M. t. terrapin.* It is possible that our hand excavations of the nests and the shifting sand levels distorted the true nest dimensions and obscured a relationship which may exist between turtle size and nest size.

There was no relationship between plastron length and egg sizes or shapes (elongation). Cagle (1950) also found no correlation between plastron length and egg size for the slider turtle, *Pseudemys scripta troosti.* Larger spotted turtles, *Clemmys guttata* (Ernst, 1970), and larger common snapping turtles, *Chelydra serpentina* (Yntema, 1970), tend to lay larger eggs. Many birds lay larger eggs with increasing age (*e.g.,* Romanoff and Romanoff, 1949; Serventy, 1967).

There was no relationship between plastron length and the variance of egg breadth or length. These data were analyzed in view of findings which show that the within-clutch variance of egg breadth may increase or decrease with age among different avian species (Andersen, 1957; Coulson, 1963; Coulson *et al.,* 1969).

Carr (1952) has generalized that inter- and intraspecific correlations exist between the sizes of laying females and egg complement. A positive correlation between plastron length or width and the clutch size or number of oviducal eggs and follicles has been reported for a number of turtles (*Chelydra serpentina*: Ash, 1951, Yntema, 1970, White and Murphy, 1973; *Sternotherus odoratus*: Tinkle, 1961; *Kingsternon bauri*: Einem, 1956; *Clemmys guttata*: Ernst, 1970; *Pseudemys scripta*: Cagle 1944, 1950 and Moll and Legler, 1971). We found that larger female *M. t. terrapin* also tend to lay larger clutches than do smaller females. First-year clutches tend to be smaller than subsequent clutches among many birds (Richdale, 1955, 1957; von Haartman, 1967; *see* Klomp, 1970 for review).

Seasonal trends.—Egg size (length, breadth and weight) decreased as the laying season advanced. This was the only seasonal tendency found among the egg and nest data collected from the diamondback terrapins nesting on Little Beach Island, and this trend could not be attributed to detectable seasonal fluctuations in the plastron lengths of laying females, clutch size or clutch weight. A seasonal decrease in egg size has not yet been reported for any other reptile. Three avian species have been documented as laying smaller eggs later in the laying season, and this appears to be partially accounted for by the later laying of younger animals (Coulson, 1963; Coulson *et al.*, 1969; *Larus atricilla* Montevecchi, in prep.).

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