

The Effect of Egg Size and Incubation Temperature on Growth in the Turtle, *Malaclemys terrapin*

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ABSTRACT.— We conducted an incubation and rearing experiment to test the effects of incubation temperature and egg size on hatchling size and growth of the emydid turtle, *Malaclemys terrapin*. Eggs from four clutches were assigned randomly to two incubation temperatures, 26 C and 32 C. Half of the hatchlings were sacrificed and sexed after five months and the remainder were raised for three years in a common environment. Similar to other studies of emydid turtles, low and high temperature treatments produced exclusively males and females, respectively. Egg size was more variable among the four clutches than within each clutch. Egg mass accounted for 96% and 97% of the variance in hatchling mass for females and males, respectively. Both clutch and incubation temperature influenced post-hatching growth. The clutch effect was due to both differences in egg mass among clutches and the effects of egg size on hatchling size. Egg mass explained 59% of the variation in size among 3 year old females, but did not explain size variation among 3 year old males. Differences in female growth attributable to egg size could result in as much as a three year difference in age at first reproduction based on the growth trajectories of terrapins from a natural population.

Growth rate can influence age at first reproduction and thus affect fitness by reducing the cohort generation time (Cole, 1954). Alternatively, growth rates can influence size at first reproduction, thereby affecting the size and number of offspring a female can produce. Because growth rates can affect fitness, identification of factors that influence growth rates are critical to understanding life history evolution (Bernardo, 1993). One factor that can produce variation in offspring quality and subsequent growth is maternal investment in offspring.

Numerous studies have found egg size to be correlated with hatchling size in turtles (reviewed in Packard and Packard, 1988; Brooks et al., 1991; Janzen, 1993; Bobyn and Brooks, 1994; Spotila et al., 1994). Additionally, growth rates of turtles are affected by variation in food resources (Avery et al., 1993), temperature (Avery et al., 1993), climate (Frazer et al., 1993), the presence and age of conspecifics (McKnight and Gutzke, 1993), and incubation environment (Brooks et al., 1991; McKnight and Gutzke, 1993; Bobyn and Brooks, 1994; Spotila et al., 1994). Furthermore, egg size affects size at 10 months for *Chelydra serpentina* (Bobyn and Brooks, 1994).

Studies of lizards with comparatively short life cycles have demonstrated that egg size directly affects hatchling size, performance, survivorship, and thus fitness of offspring (Sinervo, 1990; Sinervo and Huey, 1990; Sinervo and Licht, 1991a, b; Sinervo et al., 1992). Because turtles are slow growing, late maturing organisms, similar studies of the importance of egg size in ontogeny beyond one year have not been conducted.

Many species of turtles are sexually dimorphic (Berry and Shine, 1980; Gibbons and Lovich, 1990). Sexual size dimorphism can result from differences in growth rate or age at maturity between males and females (Dunham and Gibbons, 1990). One interesting possibility is that factors influencing growth may have different consequences for males and females. For example, if males mature at smaller body sizes than females, factors affecting growth may produce greater variation in age or size at maturity in females because differences in growth have more time to diverge.

In this study, we investigated how incubation temperature influences sex and how egg size and sex affect juvenile growth in the diamond-back terrapin, *Malaclemys terrapin*. We asked the following questions: (1) Does incubation temperature have a permanent effect on sexual development? (2) Does egg size affect hatchling size? (3) Does incubation temperature and/or egg size have long term effects on the growth trajectories of terrapins? Terrapins, and turtles in general, are well suited to studies of egg size effects on life history traits because the total energetic requirement for both development

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and post-hatchling parental care is provided in the egg. In turtles, no additional parental care typically occurs after oviposition (Congdon and Gibbons, 1990; but see Iverson, 1990).

MATERIALS AND METHODS

Diamondback terrapins are estuarine emydid turtles that range from Cape Cod, Massachusetts to the Gulf Coast of Texas, USA. Terrapins are sexually dimorphic with mature females weighing 2–4 times more than males. Sexes also differ in age at maturity: depending on the population, males mature 2 to 4 years earlier than females (Hildebrand, 1933; Cagle, 1952; Lovich and Gibbons, 1990; Roosenburg, 1991; Seigel, 1984).

Forty-eight *M. terrapin* eggs from four natural nests were collected from the shores of the Patuxent River, a tributary of the Chesapeake Bay in Maryland. Eggs were obtained from a population that exhibits marked sexual dimorphism: adult females are 3–4 times heavier than males (Roosenburg, 1991). Clutches were collected within six hours of oviposition and transported to the laboratory. The eggs were cleaned of sand, weighed (± 0.01 g), measured (length and width ± 0.1 mm) and placed in compartmentalized plastic boxes with autoclaved vermiculite within 12 h of oviposition. Eggs from each clutch were randomly assigned to two temperature treatments, 26 C and 32 C, and maintained at those temperatures until hatching. Soil moisture was not monitored during incubation, although the vermiculite was kept near saturation. All eggs in the 26 C treatment hatched, and 21 of the 24 in the 32 C treatment hatched. Upon hatching, individuals were removed from the containers, weighed (± 0.1 g), measured (± 0.1 mm), individually marked, and then reared in growth tanks (described below).

After five months, 10 animals from each temperature treatment were randomly chosen and killed to determine sex using both gross morphological and histological techniques. Morphological identification of females was based on the presence of Mullerian ducts, accompanied by a thin translucent ovarian structure. Males were identified by the absence of a Mullerian duct and the presence of small opaque white testes (Ynetma, 1981). Histological samples were embedded in paraffin, sectioned, and stained with an eosin acid bath procedure (Spotila, unpubl.). Females were distinguished histologically by primary oocytes within the ovaries, and males were identified by the presence of seminiferous tubules (voucher slides available from WMR). At five months of age no secondary sexual characters were evident.

The remaining turtles were raised under conditions that permitted year-round growth. For

the first two years they were kept in three 1 m diameter plastic pools. The turtles were randomly moved among the tanks to reduce tank effects. During the final year, turtles were moved to a single 1.22 m \times 2.44 m tank. Between September and May the tanks were housed in a growth chamber and illuminated with fluorescent and incandescent lights (12 h light, 12 h dark), producing near constant water temperature (approximately 24 C). During the remaining months, the tanks were placed outside in a location with partial sun, thus the temperature of the tanks varied during the day. Terrapins were fed meal worms, midge larvae, soft shell clams, and fish ad libitum (a minimum of 3 times per week). There was always an excess amount of food available after each feeding. In the natural environment, growth rates may be affected by spatial and temporal variation in resources and microclimatology; however our goal was to limit these potential sources of variation in growth.

All turtles were measured (mass [± 1 g], plastron length and carapace length [± 1 mm]) 13 times during the three year period. The sex of these remaining animals was determined at the conclusion of the experiment by the presence of two secondary sexual characteristics that enable accurate and consistent identification of sex in the Patuxent population: (i) the size of the tail between the base and the cloaca and (ii) the position of the cloaca in relation to the posterior edge of the carapace. Males had a tail enlarged at the base and their cloaca positioned posterior to the carapace edge. Females had a tail thin at the base and their cloaca positioned anterior to or at the carapace edge.

Hatchling growth was analyzed with a repeated measures analysis of variance (Keppel, 1982) on (1) the log-transformed mass of hatchlings at different age classes and (2) the residuals of a regression of log-transformed initial hatchling mass and log-transformed mass at the different age classes. Because repeated measures analysis treats time as a discrete variable, we grouped the 13 measurement periods into age classes so that actual age between members of the two treatments never differed more than 35 d. The first analysis tested for clutch and incubation temperature effects on growth. The second analysis investigated the effect of the incubation temperature independent of the variation in hatchling size attributable to egg size. The small number of clutches included in the experiment increased the probability of a Type II error in testing for clutch effects; therefore the interpretation of clutch effects in these analyses was limited. Additionally, because only two incubation temperatures were used, we were not able to determine whether the differences

TABLE 1. Means, (standard deviation) and range for egg mass, egg width, and egg length among the four clutches.

	Egg mass (g)	Egg width (mm)	Egg length (mm)
Clutch 1	6.6 (0.97) 5.0-8.0	19.6 (0.81) 18.8-20.6	29.5 (2.01) 25.9-32.3
Clutch 2	10.4 (1.23) 8.2-12.1	22.4 (0.99) 20.7-23.6	25.1 (1.75) 31.8-37.3
Clutch 3	10.4 (1.10) 7.9-11.9	22.7 (0.98) 20.7-24.3	33.7 (1.59) 30.5-35.9
Clutch 4	8.7 (0.73) 7.8-10.3	21.6 (0.48) 20.9-22.7	31.5 (1.24) 29.9-33.9
\bar{x}	9.1 (1.81)	21.6 (1.46)	32.4 (2.64)

in growth were a result of incubation temperature or sex. Data were analyzed using PC-SAS (SAS Institute, 1988).

RESULTS

Incubation temperature determined the sex of the developing embryos. The 26 C treatment produced 100% males ($N = 24$), while the 32 C treatment produced 100% females ($N = 21$).

Clutch of origin contributed significantly to overall variation in egg mass, length, and width (MANOVA, Wilk's Lambda = 0.1810, $F_{(9,95)} = 10.7552$, $P < 0.0001$), but overall egg size varied little within clutches (Table 1). Eggs assigned to the two incubation treatments were not biased in overall size (MANOVA, Wilk's Lambda = 0.9224, $F_{(3,41)} = 1.1491$, $P = 0.34$).

Similarly, clutch of origin contributed significantly to overall variation in hatchling mass and plastron length (MANOVA, Wilk's Lambda = 0.4050, $F_{(6,80)} = 7.6156$, $P < 0.0001$), although there were no differences in overall size be-

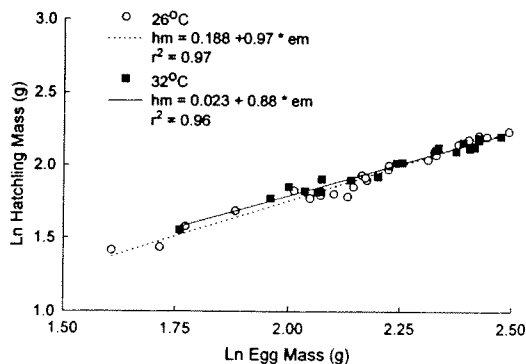


FIG. 1. The relationship between log-transformed egg mass and log-transformed hatchling mass for the two treatment groups. The regression equations are presented for the two treatments.

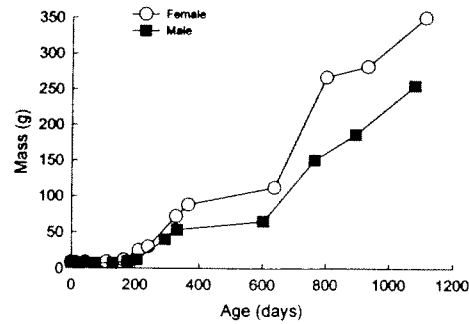


FIG. 2. The growth rates of two individuals from the same clutch incubated at different temperatures. The difference in age, 34 days, between these two individuals is due to the difference in the incubation period.

tween hatchlings from the two incubation treatments (MANOVA, Wilk's Lambda = 0.9665, $F_{(2,42)} = 0.7264$, $P = 0.48$). Egg mass accounted for a high percentage of the variation in hatchling mass in both incubation treatments (least squares regression, $r^2 = 0.97$ at 26 C, $P < 0.001$; $r^2 = 0.96$ at 32 C, $P < 0.001$ Fig. 1). No significant differences in log-transformed hatchling mass between the two incubation treatments were observed when egg mass was used as a covariate (ANCOVA, $F_{(1,42)} = 2.26$, $P = 0.14$), following an analysis to insure that the homogeneity of slopes assumption of ANCOVA was met (ANCOVA, $F_{(1,42)} = 2.80$, $P = 0.10$).

There was a 34 d difference in average incubation time between the two incubation temperatures: 81 d (26 C) and 47 d (32 C) (ANOVA, $F_{(1,43)} = 4855.04$, $P < 0.0001$). Terrapins grew, as indicated by a significant age-class effect ($P < 0.0001$, Table 2), although perceptible growth occurred only after the first 180 d (age class 6, Fig. 2). Incubation temperature (or sex) affected the growth of terrapins ($P < 0.01$, $P < 0.025$, Table 3a and b, Fig. 3): individuals incubated at 32 C grew faster than individuals incubated at 26 C. The age class by temperature interaction also supports a difference in growth between warm and cool incubation conditions ($P < 0.0001$, Table 2, Fig. 3).

The clutch effect detected in terrapins was attributable to differences in egg size. Clutch was significant when log-transformed hatchling mass was the dependent variable ($P < 0.01$, Table 3a), yet when variation in juvenile size due to egg size was removed by regression, the clutch effect disappeared ($P = 0.45$, Table 3b). No significant clutch interactions were detected (Tables 2 and 3).

Egg mass accounted for a considerable portion of the variation in female juvenile size, but

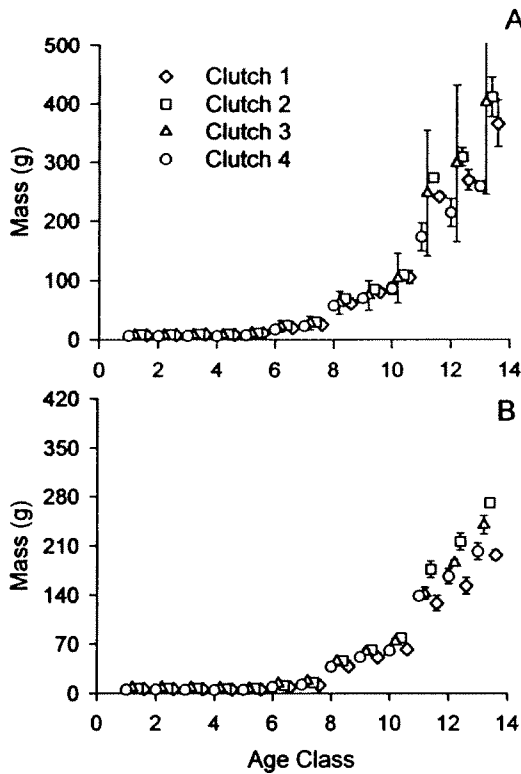


FIG. 3. Growth rates females (3A) and males (3B) for each clutch incubated in the two temperature treatments. Bars represent one standard error.

not male juvenile size, at the termination of the experiment (least squares regression: $P < 0.01$, $r^2 = 0.59$ for females; $P = 0.12$ for males; Fig. 4). Because of the small sample size, we conducted a jackknife procedure that removed each datum, one at a time, and reran the regression analyses. Our previous findings were upheld; significance values ranged from 0.06–0.23 for males and from 0.006–0.03 for females, suggesting that the original regression result was robust. Thus, egg size had a greater influence on growth of individuals incubated at warm temperatures than at cool incubation tempera-

tures. The egg size effect persisted to at least three years of age.

DISCUSSION

Incubation temperature had a permanent effect on the sexual development of the diamondback terrapin, *Malaclemys terrapin*. Terrapins exhibit pattern Ia temperature-dependent sex determination (Ewert and Nelson, 1991; Ewert et al., 1994): lower temperatures produced females and higher temperatures produced males (reviewed in Bull, 1980, 1983; Packard and Packard, 1988; Ewert and Nelson, 1991; Janzen and Paukstis, 1991). ESD has been previously reported in the Patuxent terrapin population (Jeyasuria et al., 1994); this study confirms those findings and demonstrates the persistence of temperature effects on sex (i.e., no sex reversals were noted). Sachsse (1984), Auger (1989), and Ewert and Nelson (1991) also reported biased sex ratios as evidence for ESD in diamondback terrapins.

Egg mass was the major factor contributing to variation in initial hatchling mass at both incubation temperatures. Thus, initial hatchling size was determined primarily by the resources provided to the egg by the mother, or possibly by the size of the egg. At the termination of the experiment, there remained a strong relationship between egg mass and body mass for females (Fig. 4), although a similar relationship was not found for males. In similar experiments, egg size effects were still detectable at 10 months of age in snapping turtles (Bobyne and Brooks, 1994) and at 40 d in desert tortoises (Spotila et al., 1994).

The observed differences in body size among the females (due to egg size) may result in a two to three year difference at age of first reproduction if maturity is size-dependent, or in larger adult body size if maturity is age-dependent, based on a comparison with growth trajectories for Patuxent (Roosenburg, 1996) and South Carolina terrapins (Lovich and Gibbons, 1990). In contrast, the differences in egg size appear to have had little effect on age or size at maturity of males. By year three all males

TABLE 2. Results of the univariate repeated measures analysis of variance for the within subject effects. The dependent variable is the residual of natural log-transformed hatchling mass and juvenile mass (see text).

Source	df	Type III SS	Mean square	F value	P value
Age Class (AC)	12	542.550	45.212	3291.67	0.0001
AC•Temperature	12	1.833	0.153	11.12	0.0001
AC•Clutch	36	0.554	0.015	1.12	0.3069
AC•Temperature•Clutch	36	0.353	0.010	0.71	0.8840
Error	180	2.472	0.014		

TABLE 3. Results of repeated measures analysis of variance for the between subject effects. A) The dependent variable is the log-transformed hatchling mass. B) The dependent variable is the residual of natural log-transformed hatchling mass and juvenile mass (see text). This is a mixed-model design with clutch as a random variable.

	Source	df	Type III SS	Mean square	F value	P value
A)	Temperature	1	8.650	8.650	48.38	0.010
	Clutch	3	4.355	1.452	4.96	0.0138
	Temperature*Clutch	3	0.536	0.179	0.61	0.6185
	Error	15	4.392	0.293		
B)	Temperature	1	3.751	3.751	27.68	0.025
	Clutch	3	0.420	0.140	0.93	0.4488
	Temperature*Clutch	3	0.407	0.1355	0.90	0.4633
	Error	15	2.254	0.1503		

showed signs of maturing in the same reproductive season, displayed secondary sexual characteristics, and had approached the size at maturity for the Patuxent population (± 300 g, Roosenburg, 1991), yet no significant influence of egg size on male size was evident. Differences in age or size of first reproduction attributable to egg size could have significant fitness consequences for terrapins, all other factors being equal (Cole, 1954); our study shows the affect is greatest for females.

We also detected a clutch effect (i.e., eggs produced by different mothers) on growth of terrapins; however, when the variation in hatchling body mass due to egg mass was removed, the clutch effect also was eliminated (Table 3). We interpret the clutch effect to be due primarily to differences in egg size among clutches, because of the influence egg size had on initial hatchling size and subsequent growth.

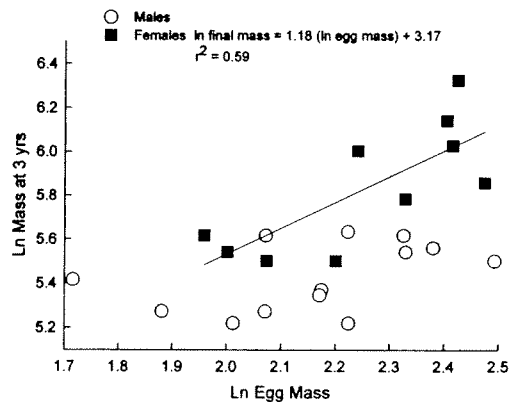


FIG. 4. Plot of log-transformed egg mass and log-transformed final mass for male (squares) and female (circles) terrapins. A significant effect of egg mass on final female mass is illustrated by the regression line. The regression is not significant for males.

These results suggest that egg size was a strong maternal effect.

An interesting pattern emerges from the available evidence concerning the interaction among sex determination, growth, and sexual dimorphism among different reptilian species with ESD: the larger sex at maturity grows the fastest, regardless of the relationship between sex and incubation temperature, i.e., the pattern of ESD. Three cases show that when males are larger at maturity, they grow faster than females; our study shows that when sexual dimorphism is reversed, females grow faster. First, in snapping turtles males are the larger of the two sexes (Gibbons and Lovich, 1990) and are produced at intermediate incubation temperatures (Yntema 1976). Individuals incubated at intermediate temperatures (i.e., males) had faster growth rates than those incubated at high and low temperatures (i.e., females) (Brooks et al., 1991; McKnight and Gutzke, 1993; Bobyn and Brooks, 1994). Second, males are the larger sex in desert tortoises also (Gibbons and Lovich, 1990), but males are produced at cool temperatures (Spotila et al., 1994). Male desert tortoises grew faster than females, even when more than one incubation temperature was employed to produce each sex (Spotila et al., 1994). Third, male American alligators are larger than females, also. When eggs were incubated at temperatures producing both sexes, the males grew faster or had growth indistinguishable from the females (Joanen et al., 1987). Finally, we have shown in terrapins that females, i.e., the sex that reaches the larger size at maturity and is produced at warmer temperatures, grew faster than males. While our experiment did not have the ability to distinguish between the effects of incubation temperature and sex on growth (Janzen and Paukstis, 1991), the results support the pattern between growth rate and sexual dimorphism: the larger sex grows faster, independent of the pattern of ESD. Additional ex-

periments that investigate growth rates of turtles and other reptiles with ESD by reversing sex with hormone treatments (e.g., Jeyasuria et al., 1994) will provide better insight into the interactions among incubation temperature, sex, and egg size and their effects on growth and sexual development.

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