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VARIATION IN CLUTCH SIZE AND EGG SIZE IN THE GREEN TURTLE NESTING POPULATION AT TORTUGUERO, COSTA RICA

KAREN A. BJORNDAL AND ARCHIE CARR

Center for Sea Turtle Research, Department of Zoology, University of Florida, Gainesville, FL 32611, USA

ABSTRACT: Data on clutch size for green turtles, *Chelonia mydas*, nesting at Tortuguero, Costa Rica, for a period spanning over 30 yr, and data on egg size from one nesting season are analyzed to determine sources of variation in clutch parameters. Mean clutch size is 112.2 (SD = 24.2, n = 2544) with a range from 3–219 eggs. Female body size is significantly correlated with clutch size but accounts for only a small proportion of the variation in clutch size. At the population level, clutch size increases significantly throughout a nesting season, but at the individual level, the increase in clutch size is not significant. Annual variation in mean clutch size was significant only between the years with the highest and lowest mean values. Clutch size increases significantly with age of the female; increase in body size with age is not significant. Number of days between clutches within a nesting season, number of years between nesting seasons, and egg size are not significantly related to clutch size. Egg size, which is significantly correlated with female body size, is less variable than clutch size. Apparently clutch size is not under strong environmental control.

Key words: *Chelonia mydas*; Clutch size; Egg size; Green turtle; Reproduction; Reptilia

REPRODUCTIVE output in the green turtle, *Chelonia mydas*, is a function of clutch size, number of clutches per nesting season, interval between nesting seasons, and length of reproductive life (survivorship and senescence). The first three parameters vary widely within and among individual green turtles nesting at Tortuguero, Costa Rica, the largest green turtle colony in the Atlantic (Carr et al., 1978). Almost certainly the fourth parameter has similar variation. Data collected from 1956–1987 for green turtles nesting at Tortuguero are used to assess possible sources of variation in one of these parameters—clutch size. The number of eggs deposited by a female green turtle when she ventures onto the beach varies considerably. Identifying the sources of this variation is important for determining what factors control reproductive output in green turtles and for understanding their life history patterns.

The potential sources of variation in clutch size investigated in this paper are female body size, female relative age, egg size, number of years between nesting seasons, and number of days between successive nests. Annual variation and seasonal variation in clutch size are analyzed at both individual and population levels.

In addition to clutch size, we also examined variation in egg size. The relationship between female body size and egg size is determined, and seasonal variation in egg size, at both the individual and the population level, is analyzed. Variability of egg size and clutch size is compared.

Methods

At Tortuguero, female green turtles are tagged, after they have completed nesting, by tagging teams that patrol the northernmost 8 km of the 35 km beach at hourly intervals every night from early July to mid-September. The tags bear identification numbers and identify recruits (turtles that arrive without tags or tag scars), renesters (turtles that return to nest again within the same season), and remigrants (turtles that return in later breeding seasons). The tagging program was initiated in 1955 and continues to the present. In early years, carapace length, carapace width, and plastron length were recorded for every turtle. In recent years, carapace length, carapace width, and body mass have been recorded for a sample of turtles from throughout the season. Carapace length and width are both straight-line measurements of maximum distance. Plastron length is straight-line distance at the mid-line. Clutch size (number of eggs) has been recorded sporadically over the more than 30 yr of work on the beach. Clutch size data represent random counts throughout the season including, at times, successive nests of individuals.

Data on clutch size were gathered in 1977 by counting all clutches laid by turtles of known size and mass throughout the season. Also, mean egg size was recorded for 97 clutches by measuring minimum egg diameter for 30 eggs taken at random from throughout the clutch on the morning after the eggs were deposited. Egg measurements were taken with calipers to the nearest 0.1 mm.

Clutches were excluded from the data set if the female depositing the clutch appeared to have stopped egg deposition prematurely or if she returned to nest again within six days. Six days is used as the minimum internesting interval between two normal clutches (Carr et al., 1978). Clutches laid within six days of each other are usually split clutches. After these clutches have been deleted, many small clutches remain in the data set (Fig. 1). To avoid including abnormal clutches—interrupted or split clutches—clutches with 35 or fewer eggs were not included in the analyses (see next section).

Parametric statistics were only used for those data sets that met the assumptions of equal variances and normal distributions. For both nonparametric statistics (Ryan et al., 1985; Siegel, 1956) and parametric statistics (SAS, 1982; Sokal and Rohlf, 1969), $\alpha = 0.05$.

Results and Discussion

Clutch Size

Of 2544 clutches counted at Tortuguero, the mean and standard deviation (SD) were 112.2 ± 24.2 with a range of 3–219 eggs (Fig. 1). The smooth distribution of clutch sizes (Fig. 1) makes it difficult to place limits on "normal" clutch sizes. Although a three-egg clutch has little reproductive value and is probably not a normal clutch, a 210-egg clutch is also abnormal. Eggs in the latter clutch probably have a lower chance of survival because top eggs in large clutches are usually broken and the clutch destroyed from bacterial attack (see below). However, many of the very small clutches doubtless represent split clutches for which the other half was not recorded by our patrol teams. Because clutch sizes of 36–40 eggs are the smallest clutch sizes repeatedly recorded for individual females, we designated 36 as the smallest "normal" clutch size for this study. When clutches with 35 or fewer eggs are deleted from the data set, the values change to 2519 clutches with a mean and SD of 113.1 ± 22.6 and a range of 36–219.

Relationship of Clutch Size to Body Size

Mean clutch size of a female within a nesting season was correlated with three linear body size parameters (cm): carapace length ($\bar{x} \pm SD = 100.2 \pm 5.0$, $n = 2107$), carapace width ($\bar{x} \pm SD = 76.6 \pm 4.1$, $n = 2108$), and plastron length ($\bar{x} \pm SD =$

79.8 ± 4.1, n = 1982) (Table 1). All correlations were significant (P < 0.0001) but accounted for only a small proportion of the variation in clutch size, from 8–9.5%. Body mass values ($\bar{x}$ ± SD = 128.1 ± 16.7 kg) are available for a small subset (n = 74) of these turtles. Correlations were repeated for the linear measures of this subset to allow comparisons among the linear and mass parameters (Table 1). All body size parameters yielded significant correlations (P < 0.0001), and all accounted for a similar amount of variation, from 29–32.5%. Thus, all measures of body size related equally well to clutch size.

There is a great difference in the amount of variation accounted for by body size between the two data sets. This difference illustrates the importance of comparing the amount of variation accounted for by various factors using the same data set. If the contribution of body mass had been compared with that of carapace length and width using the small data set for mass and the larger ones for length and width, it would have been concluded that body mass accounted for a much greater percentage of the variation than linear measurements (32.5 vs. 8–9.5%). By comparing all measures within one data set, it is clear that they all account for a similar amount of variation.

A significant, positive relationship between clutch size and body size has been reported for marine turtles (Ehrhart, 1982; Hirth, 1980) and many species of freshwater turtles (Congdon and Gibbons, 1985; Gibbons et al., 1982; Moll, 1979). Variation in carapace length accounted for 30% (n = 77) of the variation in clutch size in loggerheads, *Caretta caretta*, nesting on Little Cumberland Island, Georgia (Frazer and Richardson, 1986). Carapace length also accounted for 30% (n = 135) of the

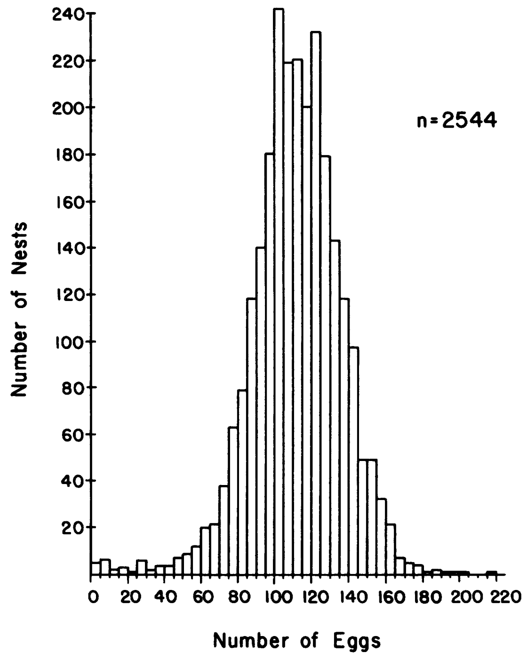

FIG. 1.—Distribution of clutch size (number of eggs) for the Tortuguero green turtle colony.

TABLE 1.—Relationship of female body size to clutch size and egg size, Spearman rank correlations and regression equations. Correlations are repeated for carapace length and carapace width against clutch size on the smaller (n = 74) data set to allow comparison between body mass and the linear measures.

Parameter	n	Spearman rank r	Spearman rank P	Regression equation
Clutch size				
Carapace length	2107	0.294	0.0001	Y = −16.5 + 1.29X
Carapace width	2108	0.309	0.0001	Y = −10.1 + 1.61X
Plastron length	1892	0.285	0.0001	Y = −4.89 + 1.47X
Body mass	74	0.574	0.0001	Y = 2.16 + 0.87X
Carapace length	74	0.569	0.0001	Y = −147 + 2.63X
Carapace width	74	0.552	0.0001	Y = −124 + 3.10X
Egg size				
Carapace length	74	0.336	0.001	Y = 33.1 + 0.111X
Body mass	52	0.159	0.259	—

TABLE 2.—Mean ($\bar{x}$), standard deviation (SD), and sample size (n) of clutch size for nests laid during six 2-wk intervals, all years combined. Means with the same superscripts (a or b) are not significantly different (ANOVA, LSD test, $P < 0.05$).

Interval: Initial date:	1 24 June	2 8 July	3 22 July	4 5 Aug	5 19 Aug	6 2 Sept
$\bar{x}$	111.0[a]	110.7[a]	113.5[ab]	114.7[ab]	113.6[ab]	116.7[b]
SD	21.9	23.0	21.9	22.1	22.5	26.4
n	143	597	747	578	337	103

variation in clutch size in loggerheads nesting on Merritt Island, Florida (Ehrhart, 1980). These values are similar to those reported here for the smaller sample of green turtles (Table 1). However, carapace length accounted for 16% ($n = 17$) of the variation in clutch size of green turtles and 50% ($n = 97$) of the variation in clutch size for loggerheads nesting on Melbourne Beach, Florida (Ehrhart and Witherington, 1987).

Ehrhart (1980) found that body mass accounted for 56% ($n = 99$) of the variation in clutch size in Merritt Island loggerheads, a much greater percentage than we found for green turtles. Differences in the amount of variation that can be accounted for by female body size from population to population, and from sample to sample within a population, indicate that, while it is clear that there is a significant positive relationship between female body size and clutch size, it is difficult to be confident in our estimates of the amount of variation in clutch size that can be accounted for by female body size.

Seasonal Variation in Clutch Size

As Frazer and Richardson (1985*a*) noted, trends in clutch size throughout a nesting season have been assessed at both the population and the individual level. At the population level, trends are determined for all clutches laid during succeeding intervals of a nesting season. The nesting season at Tortuguero was divided into six 2-wk intervals from 24 June–15 September, because a 2-wk interval both approximates the internesting interval and allows comparison with loggerhead data (Frazer and Richardson, 1985*a*). Data from all years were combined, because clutch size does not vary significantly from year to year (see next section). Clutches laid in the first two intervals were significantly smaller than those laid in the last interval (ANOVA, $P < 0.01$, $F = 2.84$, $n = 2505$; LSD test, $P < 0.05$; Table 2). Body size of females laying eggs in each of the intervals does not account for the increasing trend, because the carapace lengths of turtles for which clutch counts were recorded were not significantly different among the six intervals (ANOVA). However, the number of clutches counted for remigrants is lower in the first season interval and higher in the last season interval relative to the number of clutches counted for recruits (Chi-square two-sample test, $\chi^2 = 20.25$, $n = 2505$, df $= 5$). Because remigrants have larger clutch sizes than do recruits (see below), the increase in clutch size across season could be a result of the differential distribution of recruits and remigrants.

This pattern of significantly smaller clutches in the first two periods and significantly larger clutches in the last period contrasts with that reported for loggerheads nesting on Little Cumberland Island, Georgia, and for green turtles and loggerheads nesting in Florida. In Georgia, clutches laid in the last two 15-day periods were significantly smaller than those laid in the four earlier periods (Frazer and Richardson, 1985*a*). On Melbourne Beach, Florida, there was a significant, negative correlation between clutch size and the date on which the clutch was deposited—that is, smaller clutches were laid as the season progressed—for loggerheads and no significant relationship for green turtles (Ehrhart and Witherington, 1987). However, Ehrhart (1980) found no significant seasonal trend in clutch size for loggerheads nesting on Merritt Island, Florida. Gibbons et al. (1982) reported that clutch sizes of three species of freshwater turtles decrease as the nesting season progresses. None of these authors discussed relative distributions of recruits and remigrants throughout the season.

There was no significant seasonal trend in clutch size on the individual level. At Tortuguero, three clutches within a given season have been counted for 55 turtles. The means and standard deviations of the three clutches (113.8 ± 27.9, 119.5 ± 24.4, and 123.3 ± 28.4, respectively) are not significantly different (Kruskal-Wallis test, $H = 3.032$). In contrast, for green turtles nesting at Ascension Island, the second clutch was significantly smaller when pairs of clutches were compared (Mortimer and Carr, 1987). Frazer and Richardson (1985*a*) found a significant trend of decreasing clutch size for loggerheads that laid three clutches at Little Cumberland Island. However, loggerheads at Little Cumberland Island that laid four or five clutches showed no significant trend, whereas turtles that laid six clutches had a significantly smaller last clutch (Frazer and Richardson, 1985*a*). Gibbons et al. (1982) reported a decreasing trend in clutch size in individual freshwater turtles.

Annual Variation in Clutch Size

Annual variation in clutch size can also be studied at both the population and the individual level. Annual variation for the Tortuguero population was determined by comparing clutch sizes for the 13 yr in which 30 or more clutches had been counted during season intervals 3–5 (Table 3). Comparisons were limited to within intervals 3–5 to avoid any seasonal bias; in some years, most of the clutches counted were in the early intervals, which have significantly smaller clutches (see previous section). Only the year with the smallest mean clutch size (1976) was significantly different from the 3 yr (1958, 1960, 1975) with the largest mean clutch size (ANOVA, $P < 0.0001$, $F = 4.47$, $n = 1633$; LSD test, $P < 0.05$). However, the carapace lengths of turtles for which clutch counts were recorded in 1976 were significantly shorter than in all other years (ANOVA, $P < 0.0001$, $F = 4.65$, $n = 1265$; LSD test, $P < 0.05$); there was no significant difference in carapace lengths among the other years. Because clutch size is related to body size, the smaller clutch size in 1976 may have resulted from the smaller size of the turtles for which clutches were recorded.

TABLE 3.—Mean ($\bar{x}$), standard deviation (SD), and sample size (n) for size of clutches laid during season intervals 3–5 in different years. Means with different superscripts are significantly different (LSD test, $P < 0.05$).

Year	$\bar{x}$	SD	n
1956	116.8^{ab}	21.2	81
1957	114.1^{ab}	22.5	71
1958	119.6^{a}	19.9	120
1959	106.7^{ab}	20.7	158
1960	119.2^{a}	27.1	50
1961	110.2^{ab}	22.1	299
1962	115.6^{ab}	21.8	280
1963	112.8^{ab}	22.6	92
1964	116.1^{ab}	20.7	227
1975	119.3^{a}	23.8	43
1976	103.9^{b}	26.5	30
1977	113.7^{ab}	23.6	126
1984	115.5^{ab}	26.7	48

Frazer and Richardson (1985*b*) also found the only significant annual variation in clutch size in loggerheads at Little Cumberland Island to be that between the 2 yr with the largest and smallest clutch sizes. No annual variation in clutch size was found in five species of freshwater turtles (Gibbons et al., 1982).

Lack of annual variation in clutch size indicates that clutch size is probably not affected by environmental conditions such as temperature, salinity, and forage availability. For demographic models or management plans, mean clutch size for a population of green turtles can be assumed to be constant over time, unless mean female body size changes significantly.

Change in Clutch Size with Age

Assessing annual variation in clutch size at the individual level is the same as asking whether clutch size changes with age. At Tortuguero, at least one clutch has been counted in two different nesting seasons for 100 green turtles. These pairs do not necessarily represent comparisons between the first breeding season and a later breeding season or between successive breeding seasons (that is, the female may have nested in one or more breeding seasons between the two breeding seasons being compared). Because there is no significant seasonal effect on clutch size of individuals over a nesting season (see above), single clutches can be compared between years; if more than one clutch was counted for an individual in 1 yr, the mean value was used for the comparison. Clutch size increased significantly for individual green turtles between successive breeding years (paired *t*-test, $P < 0.02$, $t = 2.427$). This increase in clutch size with age cannot be attributed to increased female body size with age. Carapace length of the 100 green turtles did not increase significantly (paired *t*-test, $t = 1.959$).

Reproductive output increases with age in Tortuguero green turtles (Bjorndal, 1980). However, this increase results more from an increase in the number of clutches laid in a nesting season than from an increase in clutch size. Frazer (1984) reported that reproductive output increased with age in loggerheads nesting on Little Cumberland Island, but he did not reveal the relative contributions of clutch frequency and clutch size to the increase. No relationship between clutch size and age was found in several species of freshwater turtles (Gibbons, 1982; Gibbons et al., 1982).

Other Factors that May Affect Clutch Size

The relationship of clutch size to the length of the remigration interval (the number of years between nesting seasons) and to the internesting interval (the number of days between successive clutches in one nesting season) has not been investigated in sea turtles. The most common remigration intervals for Tortuguero green turtles are 2 and 3 yr (Carr et al., 1978). There was no significant difference between the size of clutches laid by turtles following a 2-yr remigration interval (120.4 ± 18.0, $n = 31$) and the size of those laid by turtles following a 3-yr remigration interval (116.7 ± 21.7, $n = 43$) (Mann-Whitney test, $W = 1839.0$). Thus, a longer preparation time prior to a nesting season does not increase clutch size.

At Tortuguero, internesting intervals range from 8–19 days (Carr et al., 1978). The internesting interval before a clutch was laid (pre-nest interval) was known for 290 clutches and the internesting interval following a clutch (post-nest interval) was known for 374 clutches. No significant relationship was found between clutch size and either pre-nest or post-nest intervals (Spearman rank correlation, $r = 0.012$ and -0.096, respectively).

The relationship of minimum egg diameter (= egg size) to clutch size is not significant (Spearman rank correlation, $r = 0.185$, $n = 95$). Congdon and Gibbons (1985) also found no significant relationship between egg size and clutch size in six species of freshwater turtles, although earlier reports (Allard, 1935; Legler, 1960; Moll and Legler, 1971; Risley, 1933) had suggested that clutch size and egg size were inversely related in freshwater turtles.

Of the clutches counted in 1977, 29 clutches have corresponding data on female carapace length and body mass, pre-nest interval, season interval, and egg size. Forward stepwise regression (SAS, Stepwise Regression, Stepwise procedure) was performed on this data set. The factors were added to the model in the following order: carapace length and pre-nest interval. The final two-factor model accounted for 41% of the variation in clutch size. Although pre-nest interval was not significantly correlated with clutch size in the larger data set discussed above, it increased the r^2 value from 0.283 to 0.413 when added to carapace length.

Optimal Clutch Size

The determinants of clutch size in sea turtles are many and complex, and our understanding of the factors involved has not improved since Carr (1967) enumerated the factors that would act to either increase or decrease clutch size over evolutionary time. Maximum clutch size may be limited by the capacity of the body cavity of the female or by the volume of the nest cavity, which in turn is determined by the size of the female's rear flippers. Large clutches that overfill the nest cavity suffer high mortality because the top eggs are broken during nest-covering (Bjorndal, personal observations), which results in further—often complete—loss of the clutch due to microbial invasion (Hill, 1971) or discovery by predators. At Tortuguero, the upper limit is approximately 180 eggs (Bjorndal, personal observations).

Minimum clutch size may well be set by the number of hatchlings required for successful escape from the nest (Carr and Hirth, 1961). Carr and Hirth (1961) estimated that this minimum number was eight hatchlings. Between the minimum (eight eggs) and maximum (approximately 180 eggs), there is a wide range in which other selective factors operate.

Although production of a greater number of small clutches would increase the probability of at least one clutch surviving the many sources of mortality (e.g., predation, inundation, destruction by other nesting females), each nesting emergence is costly to the female, both in energy (Bjorndal, 1982) and risk of predation (Stancyk, 1982). If egg production is energy-limited, the energy saved from nesting excursions could be channeled into an overall increase in the number of eggs produced by a female that produces larger and fewer clutches. One might predict a trade-off between the number of clutches that a female lays in a season and clutch size. Data are not available for the Tortuguero population to test this prediction.

If there is an optimal clutch size for a sea turtle population or species, we are far from determining the relative importance of the many factors that have exerted selective pressure in forging this optimal size. However, given the variation in clutch size of Tortuguero green turtles, selective pressure for precise adherence to one optimal size seems to have been weak.

Egg Size

Mean minimum egg diameter (= egg size) of 97 clutches at Tortuguero in 1977 was 44.4 mm (SD = 1.7, range = 39.1–48.4 mm). Green turtle eggs are nearly spherical; mean minimum egg diameter was only 1.5 mm less than mean maximum diameter for eggs from 30 nests. Thus, egg diameter would be closely correlated with egg volume and mass. Minimum egg diameter was chosen as the measure of egg size, because the difference between maximum and minimum diameter was often a result of surface granulations that increased the diameter.

Egg size is significantly and positively correlated with carapace length of the female (Table 1), but only 13% of the variation in egg size is accounted for by variation in carapace length. There is a nonsignificant relationship between egg size and the body mass of the female (Table 1). As indicated above, the correlation of egg size and clutch size is not significant (Spearman rank correlation, $r = 0.185$, $n = 95$).

Fewer data are available for egg size than for clutch size in sea turtles. Bustard (1972) reported that egg size did not change with size of the female in the population of green turtles nesting at Heron Island, Australia, but he presented no data to support his statement. For loggerheads nesting on Merritt Island, Florida, there is a weak but positive relationship ($r = 0.29$, significance not indicated) between egg size and female body size (Ehrhart, 1982). Significant positive correlations between egg size and female body size have been found in several freshwater turtle and tortoise species (see review in Congdon and Gibbons, 1985).

Egg size did not exhibit significant seasonal variation in 1977 at either the population (Kruskal-Wallis test, $H = 7.22$, $n = 96$, df $= 3$) or the individual (paired sign rank test, $n = 20$ pairs) level. Ehrhart (1980) found no significant seasonal trend in egg size (minimum egg diameter or mass) for loggerheads nesting on Merritt Island, Florida. Because minimum egg diameter was measured only in 1977 at Tortuguero, we cannot examine annual variation in egg size.

Egg size is less variable than clutch size in Tortuguero green turtles. Coefficients of variation for egg size and clutch size for the 74 clutches for which both parameters were known were 3.7 and 18.7, respectively.

Optimal Egg Size

Theories on optimal size of propagules assert that, for any population, there is an optimal size at which selective pressure to increase the size of the propagule is balanced by selective pressure to increase the number of propagules. Variation in propagule size should therefore be low, and any variation in reproductive output should be in the number, rather than the size, of propagules (Brockelman, 1975; Smith and Fretwell, 1974). Our intention here is not to debate the validity of the theory but to determine whether our data conform to the theory's predictions. In discussing optimality theories, Congdon and Gibbons (1985, 1987) concluded that many species of turtles and tortoises appear to be exceptions to these theories because of the significant variation in egg size within a population, because egg size increases significantly with female body size and because a trade-off between egg size and clutch size does not exist. The same conclusions can be made for green turtles nesting at Tortuguero.

However, green turtles fit some predictions of the optimal egg size model. As expected from optimality theory, clutch size varies more than egg size in Tortuguero green turtles. Also, the amount of variation in egg size accounted for by female carapace length (13%) is only half of that for clutch size (26%) when compared with data from 74 clutches. [As discussed above, comparisons of the amount of variation accounted for by various factors must be made using the same data set. Therefore, the appropriate value to use in this comparison for the variation in clutch size accounted for by body size is that of the 74 clutches for which we also have data on egg size. It would be inappropriate to use either of the values presented in Table 1.]

In addition, clutch size varies much more among populations of green turtles than does egg size (Hirth, 1980). Hirth (1980) concluded from his comparisons of green turtle populations that "there is selection for a green turtle egg with a diameter of about 45 mm." Our data from Tortuguero support this conclusion.

Conclusions

Clutch size in green turtles is apparently not influenced by environmental factors. Improved nutrition increases reproductive output in green turtles by increasing the number of clutches produced in a nesting season and by shortening the interval between nesting seasons, but clutch size is not affected (Bjorndal, 1985; Wood and Wood, 1980). Mean clutch size does not vary among years, indicating that environmental factors, which would vary among years, do not affect clutch size.

Female body size does have a significant effect on clutch size, but the amount of variation in clutch size accounted for by female body size is relatively small. Egg size, the number of days between nests within a nesting season, and the number of years between nesting seasons do not significantly affect clutch size.

Egg size varies less than clutch size in green turtles. Female body size has a significant effect on egg size, but it accounts for only 13% of the variation in egg size.

The majority of the variation in both clutch size and egg size measured in Tortuguero green turtles cannot be accounted for by the factors examined. The primary control of clutch size may be female genotype.

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