

Journal of Herpetology, Vol. 30, No. 3, pp. 407-410, 1996
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Reproductive Ecology of the Florida Green Turtle: Clutch Frequency

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Clutch frequency can have a profound influence on annual reproductive output and has been considered one of the most important parameters of turtle reproduction (Gibbons, 1982). Clutch frequency is defined as the number of egg clutches produced by an individual over the course of a single nesting season. Evaluation of this parameter is particularly important for sea turtles because these data are necessary to estimate female population size from annual nest counts (Meylan, 1982). Demographic models may reveal valuable insights into conservation strategies for marine turtles and clutch frequency values are used in the construction of these models (Crouse et al., 1987).

Although the number of times a female nests within a season has been determined at numerous *Chelonia mydas* rookeries (Hendrickson, 1958; Schulz, 1975; Carr et al., 1978; Mortimer and Carr, 1987), no such data were previously available for green turtles nesting in Florida. This population is listed as Endangered at the federal and state levels (National Marine Fisheries Service and U.S. Fish and Wildlife Service, 1991; Ehrhart and Witherington, 1992). Prior to our study, encounters with green turtles on Florida beaches had only been made incidental to tagging efforts that focused on *Caretta caretta* (Bjorndal et al., 1983; Witherington, 1986). This was due to the small size of the Florida colony, recently estimated to number fewer than 900 reproductively active females (Johnson, unpubl. data). The objective of this study was to determine clutch frequency for Florida green turtles.

Study Area.—The study was conducted on the Atlantic coast of east-central Florida along the southernmost 21 km of Brevard County, U.S.A. The southern terminus of the study site (80°27.25'W, 27°52.43'N) was the northern boundary of Sebastian Inlet State Recreational Area and the northern terminus

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(80°30.34'W, 28°02.33'N) was approximately 2 km south of the town of Melbourne Beach. This area is commonly referred to as "Melbourne Beach." Green turtles nest along Melbourne Beach from late May or early June, through mid- to late September. This beach annually supports approximately 35% of all nesting activity of *Chelonia* in Florida (Meylan et al., 1995).

Nightly Surveys.—In an attempt to encounter all nesting green turtles, nightly surveys were conducted from the last week in May through the second week of September during 1991 and 1992. Surveys were conducted from 2200 to 0500 hrs and were usually confined to the southernmost 12 km of the study site. An investigator driving a small all terrain vehicle equipped with a dim, red, headlight traversed the study area four times each night. In 1991, surveys were conducted on 86 nights, whereas in 1992 they were conducted on 90 nights. In 1991, we identified the individuals responsible for 73 of 99 green turtle nests recorded along the southernmost 12 km of the study area (74% coverage). In 1992, we identified the individuals responsible for 281 of 403 nests within the same area (70% coverage).

Each turtle encountered was checked for tags. If previously tagged, tag identification numbers were recorded. If untagged, two monel metal tags (National Band and Tag Co.), each bearing a unique identification number, were attached after the turtle had completed oviposition. Tags were placed on the trailing edge of each front flipper just distal to the shoulder joint. Straight and curved carapace lengths (notch to tip) were taken with a forester's caliper and a flexible fiberglass tape measure. Shell and flipper damage, morphological abnormalities, as well as nesting success (clutch deposited or not) were noted. Clutch size was determined for some nests from direct counts made as turtles deposited eggs, or by excavating clutches by hand within ten hours of oviposition. If clutch size was known for more than one nest for any turtle, the mean size of all available clutches for that individual was used in statistical analysis of the influence of clutch size on clutch frequency.

Clutch Frequency.—Observed clutch frequency (OCF) and estimated clutch frequency (ECF) values were calculated for each turtle encountered nesting at least once within the southernmost 12 km of the study area. OCF is the number of times a turtle was encountered during a confirmed nesting emergence. Direct observation of oviposition, as well as evaluation of the crawl and site, were used to determine nesting success. In some cases, the site was excavated the following morning to confirm the presence of eggs. Because OCF may underestimate true clutch frequency for some individuals, an estimated clutch frequency (ECF) value was calculated for each turtle. ECF is the number of clutches that a turtle was believed to have deposited. ECF values were based on confirmed nesting events, the number of days between encounters (re-nesting intervals), and each turtle's record of nesting and non-nesting emergences throughout the season. If an interval of 20 days or longer occurred between known nesting events of a turtle, it was assumed that she nested undetected during the interim and additional nests were added to her OCF to derive an ECF. The mean re-nesting interval for green turtles at Melbourne Beach was 12.9 d ($N = 165$; $SD = 1.59$),

with a range of 10 to 17 (Johnson, 1994). The number of nests added to each turtle's record was calculated by dividing the number of days at large (if longer than 25 d) by 12.9. For turtles exhibiting intervals from 20 to 24 d between observed nestings, it was assumed that one clutch was deposited during the interim. Additionally, if a turtle was encountered during a non-nesting emergence at least 10 d prior to or after an observed nesting event, it was assumed that she nested undetected later the same night or during the next few nights. For six turtles, the OCF value is one while ECF is greater than one. In these instances, turtles were encountered during non-nesting emergences at least 10 d prior to or after the single observed nesting event. For these few turtles, ECF was calculated as stated above, based on the number of days between the nesting and non-nesting emergences. Our method of estimating clutch frequency is similar to that described by Frazer and Richardson (1985).

The frequency distribution of the data did not approximate a normal distribution. Therefore, nonparametric statistical tests (Siegel and Castellan, 1988) were used to analyze the data. The level of statistical significance was set at $\alpha = 0.05$.

During the two years of the study, ECF and OCF values were determined for 145 turtles (Fig. 1). Mean OCF for these individuals was 2.4 and mean ECF was 3.0 (Table 1). Because most Florida green turtles observed nesting during more than one breeding season adhered to a biennial remigration pattern (Johnson, 1994), turtles encountered each year represented distinct cohorts. Mean clutch frequency of the 1991 cohort differed from that of the 1992 cohort (Table 1). OCF was not significantly different between years (Mann-Whitney test, $P = 0.24$), but ECF was significantly greater in 1991 (Mann-Whitney test, $P = 0.03$).

To determine whether female body size or clutch size influenced ECF, we conducted Spearman rank correlation tests. There was no correlation between either straight carapace length or curved carapace length and ECF (SCL: $r_s = 0.14$, $P = 0.21$, $N = 80$; CCL: $r_s = 0.09$, $P = 0.42$, $N = 85$). Clutch size also was not correlated with ECF ($r_s = -0.16$, $P = 0.14$, $N = 91$).

Whether a green turtle is an experienced nester (remigrant) or is reproducing for the first time (neophyte or recruit) may have an influence on the num-

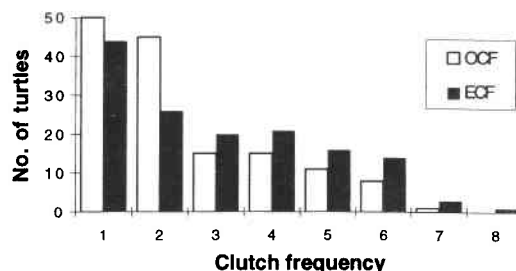


FIG. 1. Observed clutch frequency (OCF) and estimated clutch frequency (ECF) values for green turtles nesting at Melbourne Beach, FL, during 1991 and 1992.

TABLE 1. Summary statistics for observed clutch frequency (OCF) and estimated clutch frequency (ECF) values for green turtles nesting at Melbourne Beach, FL, during 1991 and 1992.

	N	Mean	Median	SD	Mini- mum	Maxi- mum
1991						
OCF	26	2.7	2.0	1.64	1	6
ECF	26	3.7	3.5	1.89	1	7
1992						
OCF	119	2.4	2.0	1.54	1	7
ECF	119	2.8	2.0	1.80	1	8
Combined						
OCF	145	2.4	2.0	1.55	1	7
ECF	145	3.0	3.0	1.84	1	8

ber of clutches she will lay. At some rookeries, remigrants exhibit significantly greater clutch frequencies than do recruits (Schulz, 1975; Carr et al., 1978; Mortimer and Carr, 1987). Few green turtles had been tagged at Melbourne Beach prior to this study. Therefore, there was no way to confidently separate neophytes from all experienced nesters. The small number of remigrants encountered, plus our inability to recognize neophytes, precludes any evaluation of the relationship between female age and clutch frequency for the Florida green turtle at this time.

Moll (1979) predicted that clutch frequency should increase with body size in most species of turtles. Few studies have addressed this issue with respect to reproductive patterns in sea turtles (but see Van Buskirk and Crowder, 1994). No significant correlation between either straight or curved carapace length and clutch frequency was found for Florida green turtles.

Within a season, it might be expected that turtles exhibiting high clutch frequencies would have smaller clutch sizes than turtles exhibiting low clutch frequencies. There was no influence of clutch size on ECF for the Florida green turtles we studied. Additionally, based on data compiled from eight different rookeries, there was no significant correlation between clutch frequency and clutch size for *Chelonia mydas* at the species level (Van Buskirk and Crowder, 1994).

Few investigators have analyzed annual variation in green turtle clutch frequency. Bustard (1974) claimed that clutch frequency varied over three consecutive nesting seasons for *Chelonia* at Heron Island, Australia, but conducted no statistical analysis. OCF values were not significantly different between 1991 and 1992 for Florida green turtles, however, ECF values were significantly different between years. The difference in ECF values can be attributed to the percentage of "one-time-nesters" encountered in 1991 versus those encountered in 1992. In 1991, only 15% of all turtles observed nesting were estimated to have oviposited only once. In 1992, the percentage of "one-time-nesters" was 34%. Disparity in sample sizes between years (26 in 1991, 119 in 1992) may be a factor contributing to the difference. With the smaller sam-

TABLE 2. Mean clutch frequencies reported for green turtles at various rookeries.

Rookery location	Clutch frequency	Reference
Sarawak	4.1	Hendrickson, 1958
Ascension Island	3.0	Mortimer and Carr, 1987
Florida	3.0	This Study
Surinam	2.9	Schulz, 1975
Costa Rica	2.8	Carr et al., 1978

ple size in 1991, each turtle contributes a greater percentage to the overall ECF mean value for that year. When data for turtles estimated to have nested only once were removed from the comparison, there was no significant difference found between years (Mann-Whitney test, $P = 0.27$).

Mean clutch frequency of the Florida population is similar to values reported for other green turtle rookeries (Table 2). Hendrickson (1958) did not provide a calculated mean value but he presented a histogram depicting the number of successful nests recorded for 447 females. Using those data, we calculated a mean of 4.1 nests per turtle. One outstanding finding of Hendrickson (1958) was the observation of a single female that deposited eleven clutches in one season, the largest number recorded for *Chelonia mydas*. A striking feature common to each study in Table 2 was the relatively large percentage (ranging from approximately 25–50%) of turtles estimated to have deposited only one clutch. For Florida turtles, 30% were estimated to have nested only once. It seems that at most green turtle rookeries, a fairly large percentage of females (possibly comprised mostly of neophytes) that make the reproductive migration can be expected to nest only one time that season. Schulz (1975) suggested that some females may actually make the migration to the rookery but not lay eggs.

Differences in clutch frequencies reported for various rookeries may represent actual variation in intraseasonal clutch production among sites. On the other hand, reported differences may be artefacts, due in part, to variation in tagging and survey effort, tag loss, and possibly nest-site fixity of turtles among beaches. Differences are probably due to a combination of biological and methodological disparities. It should be stressed though, that the consequences of biasing factors result in underestimation, rather than overestimation, of true clutch frequencies. Although the mean ECF reported herein for the Florida population is 3.0 (Table 1), the true average number of clutches deposited per turtle may be larger. Despite drawbacks, studies utilizing intense monitoring effort provide the best estimates of clutch frequency currently available for marine turtles.

Acknowledgments.—We thank the U.S. Fish and Wildlife Service and the Florida Department of Environmental Protection (FDEP) for financial support to L. M. Ehrhart. This research was conducted under permit from FDEP. We are also indebted to the Brevard County Natural Resources Management Division for permission to operate our ATVs on Mel-

bourne Beach. Our deepest appreciation is extended to all student members of the University of Central Florida Marine Turtle Research Group during 1991 and 1992. Lastly, we would like to thank C. K. Dodd Jr., J. A. Mortimer, and two anonymous reviewers for comments on the manuscript.

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Accepted: 14 April 1996.