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Reproductive Biology of the Green Turtle (*Chelonia mydas*) at Tern Island, French Frigate Shoals, Hawai'i[1]

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ABSTRACT: We monitored nesting of the green turtle (*Chelonia mydas* Linnaeus) on Tern Island, French Frigate Shoals, in the Northwestern Hawaiian Islands from 1986 through 1991. Egg oviposition occurred between 26 April and 20 October. Nesting peaked between mid-June and early August. Hatchlings emerged between 8 July and 27 December. Hatchling emergence peaked between mid-August and early October. Mean incubation period was 66.0 (range 53–97) days. Mean clutch size was 92.4 (range 33–150) eggs. Mean hatching success was 78.6% when averaged over success of individual nests and 81.1% when calculated as percentage of total number of eggs. Natural hatchling emergence was 71.1%, based on percentage of total number of eggs. Live and dead hatchlings were found when nests were excavated and accounted for 10.0% of the eggs. Incubation periods tended to be longer in early and late portions of the season than in midseason, and incubation periods tended to decrease the farther inland the nest was situated from the high tide line. Maximum hatching success occurred at an incubation length of 66.7 days. Other trends indicated that nesting peaked near 5 July when conditions produced a near optimal incubation period for yielding maximum hatching success.

FRENCH FRIGATE SHOALS is the location of more than 90% of all breeding by the Hawaiian green turtle (*Chelonia mydas* Linnaeus) (Balazs 1976, 1980). Adult green turtles migrate from throughout the Hawaiian Archipelago to the small sandy islets of the atoll to nest (Balazs 1976). In 1978, the Hawaiian green turtle was protected under provisions of the U.S. Endangered Species Act. In response to listing, a recovery plan for Hawaiian sea turtles (Balazs et al. 1992) was prepared. Monitoring nesting of the green turtle at French Frigate Shoals was an integral portion of the recovery plan.

Survival of the Hawaiian green turtle depends heavily on successful nesting at French Frigate Shoals. Proper management and protection of the atoll's nesting beaches is essential for continued successful nesting. Tern Island, the northernmost islet in the atoll, was modified and used as an airstrip in World War II and then as a U.S. Coast Guard LORAN station. Currently, Tern Island is the site of a Hawaiian Islands National Wildlife Refuge field station that is staffed year-round by U.S. Fish and Wildlife Service personnel. Since decommissioning of the LORAN station in 1978, the use of Tern Island by green turtles has increased (Sheekey 1982). Increased nesting on Tern Island provided an opportunity to monitor green turtle nesting through entire seasons. Our objective was to document nesting and hatchling emergence phenologies, clutch size, incubation period, and hatching success on Tern Island and to examine data for trends or factors that may be used to ensure proper management of the nesting beaches.

Study Area

French Frigate Shoals is a crescent-shaped atoll, 16 km in diameter, near the midpoint of

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the Hawaiian Archipelago. The atoll is part of the Hawaiian Islands National Wildlife Refuge and consists of 11 sandy islets and one volcanic pinnacle (Amerson 1971). Tern Island (lat. 23° 52′ N, long. 166° 17′ W) is on the northwestern rim of the atoll. During World War II, the island was modified from a 4.5-ha islet into a 23.1-ha island that accommodated aircraft. The current island was constructed by installation of metal seawalls that were filled with dredge spoil. It now resembles a small aircraft carrier and is about 914.5 m long and 36.6 m wide.

Since modification of the island, a sand beach has accumulated along the south-facing seawall. Nesting on Tern Island is confined to the beach fringe because of a hard-packed landing strip that covers most of the interior of the island. Tern Island's south-facing shoreline provides easy access and coral sand substrate for nesting green turtles. The upper beach zone is vegetated by sporadic shrubby vegetation and grasses. A more comprehensive description of the vegetation on Tern Island was provided by Amerson (1971). Most of the remaining shoreline consists of exposed steel seawall that prevents access to the island by nesting turtles.

MATERIALS AND METHODS

We documented seasonal ambient temperature variation by recording daily high and low temperature and calculating mean monthly temperatures. Morning patrols of Tern Island's beaches were conducted to locate nests and monitor hatchling emergence from initial nesting until the emergence of the last hatchling. We determined nest locations either by observing the turtle laying eggs or by observing the physical characteristics of the turtle's diggings. A successful nesting attempt usually was differentiated from an unsuccessful attempt by the evidence of backfilling or covering of the nest and by tracks that returned directly to the ocean. We marked all potential sites to prevent nests from being missed. We marked nest locations by placing a numbered stake about 150 cm inland of the nest and by recording the location on a 4-m grid map. The coordinates from the grid maps enabled us to find a nest even if the stake was knocked over and lost because of movements of other nesting turtles or Hawaiian monk seals (*Monachus schauinslandi* Matschie). We also recorded the distance from the high tide line to the nest.

We detected hatchling emergences through pre- and postemergent pit formation and by observing tracks of hatchlings. If hatchlings emerged from a nest on more than one night, we recorded the first night hatchlings emerged as the date of emergence for that nest. Incubation period was recorded as the time (in days) from when eggs were laid until the first hatchlings emerged from the nest. If either the oviposition or hatchling emergence date of any nest was unknown, the mean incubation length for all nests of that year was used to estimate the missing parameter. This estimated parameter was not used in any analyses except for the phenology diagrams.

We determined clutch size and hatching success by excavating the nests after the hatchlings emerged. If hatchling emergence was not detected at a marked nest site, the area was excavated to verify if a nest was present.

Nests were excavated at different intervals after hatchling emergence to determine the optimum time for excavation. Nests were excavated the day after hatchling emergence in 1986, 1987, and 1991, 2–3 days after emergence in 1988, 4 days after emergence in 1990, and 5 days after emergence in 1989.

We determined the number of emerged hatchlings by counting empty eggshells. We categorized the remainder of the nest's contents as follows: live hatchlings remaining in the nest, dead hatchlings, unhatched eggs with embryos (3/4, 1/2, and 1/4 developed), and eggs showing no embryonic development (undeveloped eggs). After analysis, we returned all nest materials to the excavated pit. Live hatchlings were released the following night.

We calculated annual and total hatching successes by two different methods: (1) the mean of individual nest successes (individual nest success was expressed as percentage of eggs that hatched within the nest), or (2) the percentage of the total number of eggs. The first type of summary is useful because statistical tests are valid (such values are independent of one another). The latter values are useful for comparison with the results reported in other studies.

Analysis of variance (ANOVA) was used to test for differences in mean hatching success, incubation period, clutch size, distance from high tide mark to nest, and Julian oviposition date among years. A *P*-value of 0.05 or less was used to infer statistical significance. When significant differences were found among years, Tukey's multiple comparison procedure (Sokal and Rohlf 1981) was used to separate means ($\alpha = 0.05$). To investigate trends or relationships among hatching success, incubation period, clutch size, distance from high tide mark to nest, and Julian oviposition date, stepwise analyses of covariance (ANCOVA) were performed. Analysis of covariance fits a separate multiple regression for each level of the class variable (in this case, the 6 yr 1986 through 1991). Hatching success was regressed on incubation period, clutch size, distance to beach, Julian oviposition date, and the square of each of these independent variables to test for possible quadratic effects. Incubation period was regressed on clutch size, distance from high tide mark to nest, Julian oviposition date, and the appropriate quadratic terms. Clutch size was regressed on distance from high tide mark to nest, Julian oviposition date, and their quadratic terms, and distance from high tide line to nest was regressed on Julian oviposition date and the square of Julian oviposition date.

Initially, the full model for each ANCOVA was fit into separate regressions for each of the 6 yr of data. A likelihood ratio *F*-test (Scheffe 1959) was used to test whether the intercepts and slopes were equal among years. If there was no significant year effect ($P > 0.05$), years were pooled and a multiple regression and *F*-tests were used. A stepwise approach was followed, dropping out nonsignificant terms until a model was obtained for each dependent variable consisting only of significant independent variables.

RESULTS

Temperatures at Tern Island for the 6-yr period of this study ranged from 16 to 34°C. Mean monthly temperatures ranged from a low of about 22°C in January through March to a high of about 27°C in September (Table 1). Annual precipitation ranged from a low of 43.0 cm in 1987 to 91.5 cm in 1989 with an annual average of 73.9 cm. During the green turtle nesting season, monthly precipitation was highly variable, ranging from a low of 1.1 cm in July 1991 to 20.5 cm in August 1986.

During the 6-yr study, we located 432 green turtle nests on Tern Island. The number ranged from 23 nests in 1986 to 103 nests in 1989. We recorded the oviposition date for 407 of the 432 nests located. Oviposition occurred between 26 April and 20 October (Table 2). Oviposition phenology, by 2-week intervals, for each year is presented in Table 3. Oviposition peaked between 15 June and 1 August, with 53.1% of the nesting occurring during that period (Figure 1). Yearly mean Julian oviposition dates ranged from 176.8 (26 June) in 1991 to 214.7 (3 August)

TABLE 1

MEAN MONTHLY TEMPERATURES (°C) AT TERN ISLAND, FRENCH FRIGATE SHOALS, HAWAI'I, 1986–1991

	YEAR						COMBINED MEAN
MONTH	1986	1987	1988	1989	1990	1991	1986–1991
Jan.	22.3	21.4	21.9	23.6	21.7	21.9	22.1
Feb.	21.3	21.0	22.4	21.9	20.5	21.9	21.5
Mar.	21.8	21.5	22.7	23.1	21.1	22.0	22.0
Apr.	23.1	22.1	23.0	22.1	21.8	23.8	22.6
May	24.4	22.1	24.3	23.8	22.3	24.6	23.6
June	25.3	24.4	26.2	25.7	23.9	25.3	25.2
July	25.8	26.1	26.3	25.6	24.3	26.7	25.8
Aug.	26.3	27.0	27.1	26.7	26.3	26.9	26.7
Sept.	27.4	26.7	27.1	26.6	27.3	27.4	27.1
Oct.	26.2	25.6	26.6	25.5	25.9	25.7	25.9
Nov.	24.1	24.2	25.7	23.3	23.3	25.3	24.3
Dec.	23.1	23.4	23.9	22.1	22.7	23.3	23.1

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TABLE 2

DATES FOR FIRST AND LAST NESTS AND HATCHLING EMERGENCES FOR GREEN TURTLES ON TERN ISLAND, FRENCH FRIGATE SHOALS, HAWAI'I, 1986–1991

	OVIPOSITION DATES		HATCHLING EMERGENCES	
YEAR	FIRST	LAST	FIRST	LAST
1986	6 June	22 Sept.	15 Aug.	16 Nov.
1987	25 May	20 Oct.	29 July	26 Dec.
1988	26 Apr.	1 Oct.	8 July	9 Dec.
1989	28 Apr.	28 Sept.	19 July	27 Dec.
1990	9 May	25 Sept.	13 July	17 Dec.
1991	29 Apr.	3 Sept.	11 July	5 Nov.

in 1987 (Table 4). The combined 6-yr average Julian oviposition date was 188.6 (8 July) (SD = 32.4; range, 116–293; median = 187). Among years, differences ($P < 0.0001$) between Julian oviposition dates were significant; in 1991, eggs were laid significantly earlier in the season and in 1987 significantly later than in most of the other years (Table 4).

Hatchlings emerged between 8 July and 27 December (Table 2). Hatchling emergence phenology, by 2-week intervals, for each year is presented in Table 5. Emergence activity peaked between 15 August and 1 October, with 55.6% of the emergences occurring during that period (Figure 1).

We recorded the incubation period for 375 of 432 nests (Figure 2). The average incubation period for these nests was 66.0 days (SD = 7.4; range, 53–97; median = 65). Yearly mean incubation periods ranged from 62.5 days in 1987 to 70.5 days in 1989 (Table 4). Incubation period was significantly different among years, with 1989 having a significantly longer incubation period than most of the other years (ANOVA, $P < 0.0001$, Table 4). In 1988, we documented incubation periods of 56, 61, 63, 66, and 76 days for five nests from the same female (identified by tag number).

Clutch sizes ranged from 33 to 150 eggs (Figure 3). The combined 6-yr average clutch size was 92.4 eggs (SD = 19.2; median = 93). Yearly mean clutch sizes ranged from 85.6 eggs in 1986 to 98.5 eggs in 1991 (Table 4). Clutch size was significantly different among years (ANOVA, $P = 0.0003$, Table 4).

We found no significant differences among years for distance from the high tide line to the nest (Table 4). The 6-yr average was 8.0 m from the high tide line to the nest ($n = 298$; SD = 5.0; range, 1–25 m; median = 7 m).

We measured nest hatching success for 428 nests during the study. We found no significant differences among years for mean percentage nest hatching success (Table 4). The 6-yr average hatching success was 78.6% (SD = 22.8%; range, 0–100% median = 87%).

The percentage of the total number eggs that hatched for a given year ranged from 77.5% in 1987 to 85.1% in 1986, with a 6-yr egg hatching success of 81.1% (Table 6). The percentage of eggs that resulted in live hatchlings remaining in the nest upon excavation ("trapped") was inversely related to the number of days after initial hatchling emergence that the nest was excavated. An average of 12.0% of the eggs resulted in "trapped" hatchlings from nests that were excavated the day after initial hatchling

TABLE 3

NESTING PHENOLOGIES, PERCENTAGE OF NESTS BY "2-WEEK" INTERVALS, FOR GREEN TURTLES AT TERN ISLAND, FRENCH FRIGATE SHOALS, HAWAI'I, 1986–1991

		APR.	MAY		JUNE		JULY		AUG.		SEPT.		OCT.	
YEAR	n	16–30	1–15	16–31	1–15	16–30	1–15	16–31	1–15	16–31	1–15	16–30	1–15	16–31
1986	23				13.0	21.7	17.4	13.0	21.7	4.4	4.4	4.4		
1987	50			2.0	4.0	12.0	10.0	26.0	12.0	18.0	12.0		2.0	2.0
1988	88	2.3	4.5	6.8	12.5	15.9	21.6	18.2	10.2	4.5	2.3		1.1	
1989	103	1.0	3.9	10.7	16.5	15.5	20.4	13.6	11.7	2.9	1.0	2.9		
1990	90		1.1	6.7	10.0	18.9	16.7	22.2	13.3	6.7	2.2	2.2		
1991	78	1.3	6.4	11.5	17.9	21.8	15.4	15.4	6.4	2.6	1.3			
Total	432	0.9	3.2	7.6	13.0	17.4	17.6	18.1	11.3	5.8	3.0	1.4	0.5	0.2

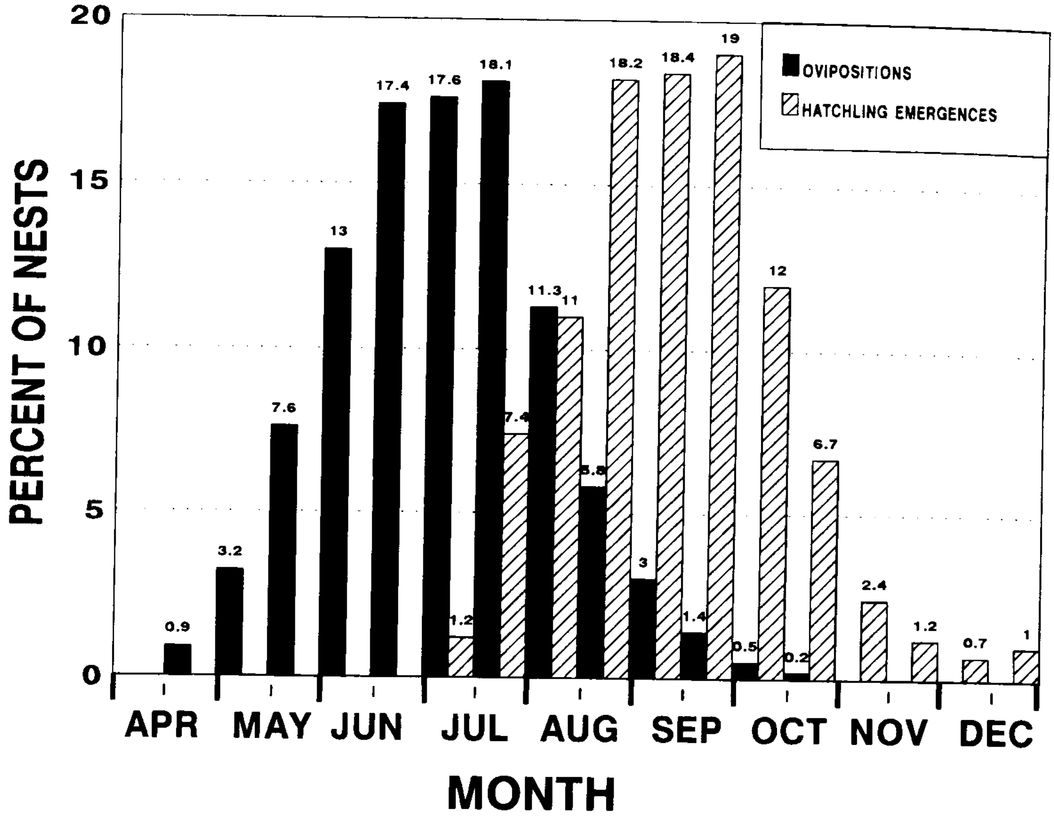

FIGURE 1. Green turtle nesting and hatching phenologies at Tern Island, French Frigate Shoals, Hawai'i, 1986–1991 combined. Nesting and hatching activity are shown by 2-week intervals.

emergence (1986, 1987, and 1991), 6.8% for excavation 2–4 days after initial emergence (1988 and 1990), and 2.4% when nests were excavated 5 days after initial hatchling emergence. Of the 39,249 eggs monitored during the study, 31,321 (79.8%) produced hatchlings that made it to the ocean either on their own (71.1%) or released by researchers after being found in the nest (8.7%). We found 510 (1.3%) dead hatchlings and 7418 (18.9%) eggs that failed to hatch. Of the eggs that failed to hatch, 13.5% showed no signs of development and 5.4% were embryos that died before reaching term (Table 6).

For the ANCOVA, a total of 297 nests had measurements for all of the variables: percentage hatching success (*H*), incubation period (*I*), clutch size (*C*), distance from the high tide mark to nest (*D*), and Julian oviposition date (*J*). All results and conclusions pertaining to the ANCOVA are based on this subset of 297 nests.

Hatching success did not differ significantly among years ($P = 0.09$); therefore, data were pooled. The final model, determined by the stepwise procedure, is given by

$$H = -1.2253 + 0.0620(I) - 0.0005(I^2)$$

with $P < 0.0001$ for testing the significance of the slope coefficients for the I and I^2 terms. Although each of these terms was very significant, the r^2 for this model was 0.07, indicating that much of the variability in hatching success remains unexplained. Figure 4 shows a graph of the relationship between hatching success and incubation period, along with the 297 data points used to estimate it. The maximum hatching success occurred at an incubation length of 66.7 days.

TABLE 4

SUMMARY STATISTICS FOR HATCHING SUCCESS, INCUBATION PERIOD, CLUTCH SIZE, DISTANCE FROM NEST TO BEACH, AND JULIAN OVIPOSITION DATE FOR THE 6 YR OF THE STUDY, WITH RESULTS OF ONE-WAY ANOVA, TESTING FOR DIFFERENCES AMONG YEARS IN EACH VARIABLE

	1986			1987			1988			1989			1990			1991		
PARAMETER	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
Hatching success (%)[a]	23	84.0	19.0	48	73.8	25.2	88	79.4	24.9	103	81.2	19.5	89	76.9	25.9	77	77.7	19.9
Incubation period (days)[b]	19	66.7 ab	6.2	34	62.5 b	6.6	79	63.8 b	6.2	99	70.5 a	6.8	73	66.3 b	7.8	71	63.3 b	6.4
Clutch size[c]	23	85.6 ab	16.5	48	86.7 a	18.2	88	96.7 bc	18.3	103	89.0 ab	17.5	89	91.4 abc	18.9	77	98.5 c	21.7
Distance to nest (m)[d]	10	7.8	5.5	27	7.7	4.9	67	8.0	5.2	80	7.5	4.7	55	7.6	4.9	59	9.0	5.0
Julian oviposition date (days)[e]	20	197.6 abc	31.6	42	214.7 a	33.2	85	185.7 bc	31.8	103	183.3 bc	31.9	82	193.4 b	29.6	75	176.8 c	27.9

NOTE: Tukey's multiple comparison procedure (Sokal and Rohlf 1981) was used to separate year means when a significant difference occurred for a variable. Year means with the same letter (under the mean) within a row are not significantly different for that variable using Tukey's procedure ($\alpha = 0.05$).

[a] $F = 1.10$, $P = 0.36$ for one-way ANOVA, implying no significant differences in mean hatching success among years.

[b] $F = 14.84$, $P = 0.0001$ for one-way ANOVA, implying significant differences in mean incubation period among years. As used here, incubation period is the time (in days) from when eggs are laid until the first hatchlings emerge from the nest.

[c] $F = 4.73$, $P = 0.0003$ for one-way ANOVA, implying significant differences in mean clutch size among years.

[d] $F = 0.68$, $P = 0.64$ for one-way ANOVA, implying no significant differences in mean distance from high tide mark to nest among years.

[e] $F = 9.70$, $P > 0.0001$ for one-way ANOVA, implying significant differences in mean Julian oviposition dates among years.

Incubation period varied significantly among years ($P < 0.0001$). To facilitate interpretation, a multiple regression was fit by pooling the data, even though the results of the ANCOVA imply that years are significantly different. This multiple regression can be interpreted as the average relationship over all of the years 1986–1991, with an $r^2 = 0.36$. It is given by the equation

$$I = 151.9852 - 0.6466(D) - 0.8243(J) + 0.0020(J^2)$$

Each of the slope coefficients was very significant for this model ($P < 0.0001$), as was the intercept ($P < 0.0001$). Figure 5 shows the 297 data points and the relationship between incubation period and Julian oviposition date, with the distance from high tide mark to nest fixed at its median level, 7 m. Figure 6 shows the same data set and the relationship between incubation period and distance from the high tide mark to nest, with Julian oviposition date data fixed at its median value, day 186.

We detected no significant difference among years for clutch size ($P = 0.29$), so data were pooled. The final model had a significant J term ($P = 0.008$) and a significant J^2 term ($P = 0.005$). The equation for this model, which had a very low $r^2 = 0.03$, is

$$C = 21.0325 + 0.8114(J) - 0.0022(J^2)$$

Figure 7 shows a graph of the relationship between clutch size and oviposition date, with the 297 data points used to estimate it. The maximum clutch size occurred at an oviposition date of day 182.7 (2 July).

An ANCOVA was also run for distance from high tide mark to nest versus Julian oviposition date. There were no significant year terms and none of the slope coefficients was significant. Distance to nest does not appear to vary with oviposition date.

DISCUSSION

Protection and proper management of the nesting beaches at French Frigate Shoals is of paramount importance in ensuring survival of

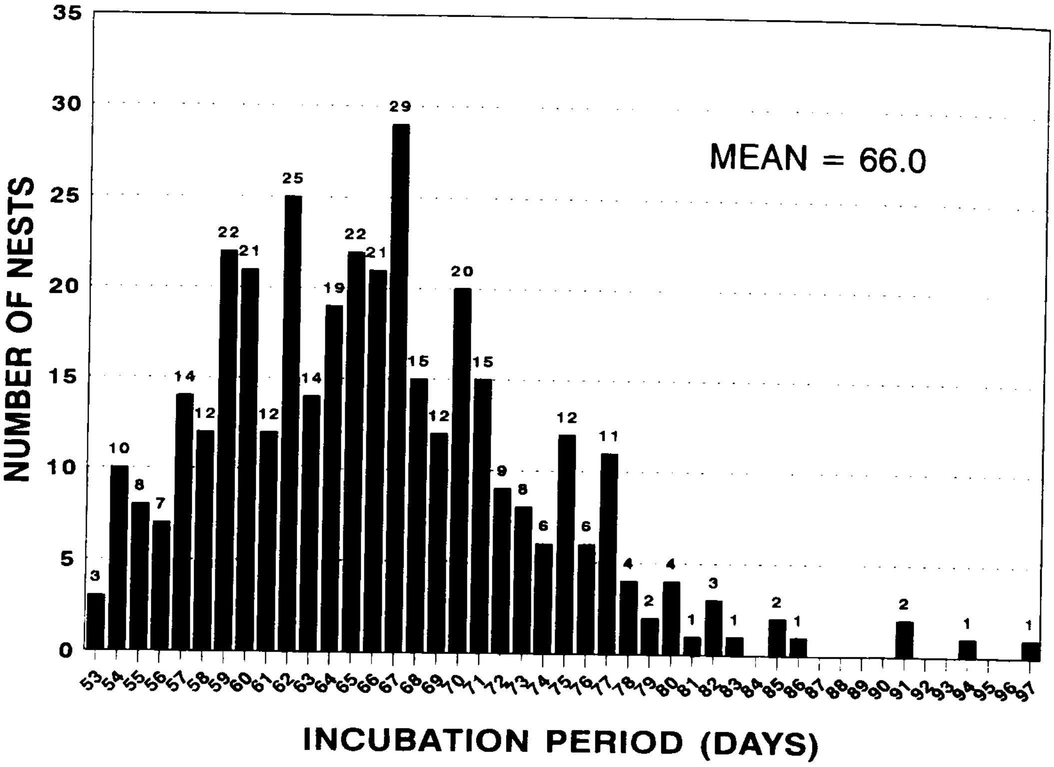

FIGURE 2. Frequency distribution of incubation periods for 375 green turtle nests from Tern Island, French Frigate Shoals, Hawai'i, 1986–1991.

TABLE 5

HATCHLING EMERGENCE PHENOLOGIES, PERCENTAGE OF NESTS BY "2-WEEK" INTERVALS, FOR GREEN TURTLES AT TERN ISLAND, FRENCH FRIGATE SHOALS, HAWAI'I, 1986–1991

		JULY		AUG.		SEPT.		OCT.		NOV.		DEC.	
YEAR	*n*	1–15	16–31	1–15	16–30	1–15	16–31	1–15	16–31	1–15	16–31	1–15	16–31
1986	23			4.4	21.7	21.7	17.4	13.0	13.0	4.4	4.4		
1987	48		2.1	2.1	14.6	12.5	22.9	14.6	14.6	10.4	2.1		4.2
1988	85	3.5	11.8	10.6	17.6	18.8	22.4	7.1	5.9	1.2		1.2	
1989	101		8.9	12.9	17.8	15.8	16.8	15.8	7.9		1.0	2.0	1.0
1990	84	1.2		8.3	20.2	23.8	21.4	16.7	3.6	1.2	2.4		1.2
1991	77	1.3	14.3	19.5	18.2	18.2	18.2	5.2	2.6	2.6			
Total	418	1.2	7.4	11.0	18.2	18.4	19.9	12.0	6.7	2.4	1.2	0.7	1.0

the Hawaiian green turtle population. French Frigate Shoals is one of the most northern green turtle nesting colonies (Hirth 1971). Because this nesting colony is on the northern extreme of the green turtle breeding range, small changes in beach conditions, which can affect the microhabitat of nests, may have dramatic consequences on nesting.

Throughout the green turtle's nesting range, nesting phenology varies from about a month to year-round and changes seasonally according to latitude (Hirth 1971). During our study, oviposition at Tern Island began in late April or early May and ended in September or early October. This coincides with the warmer months of the year at French Frigate Shoals. Oviposition phe-

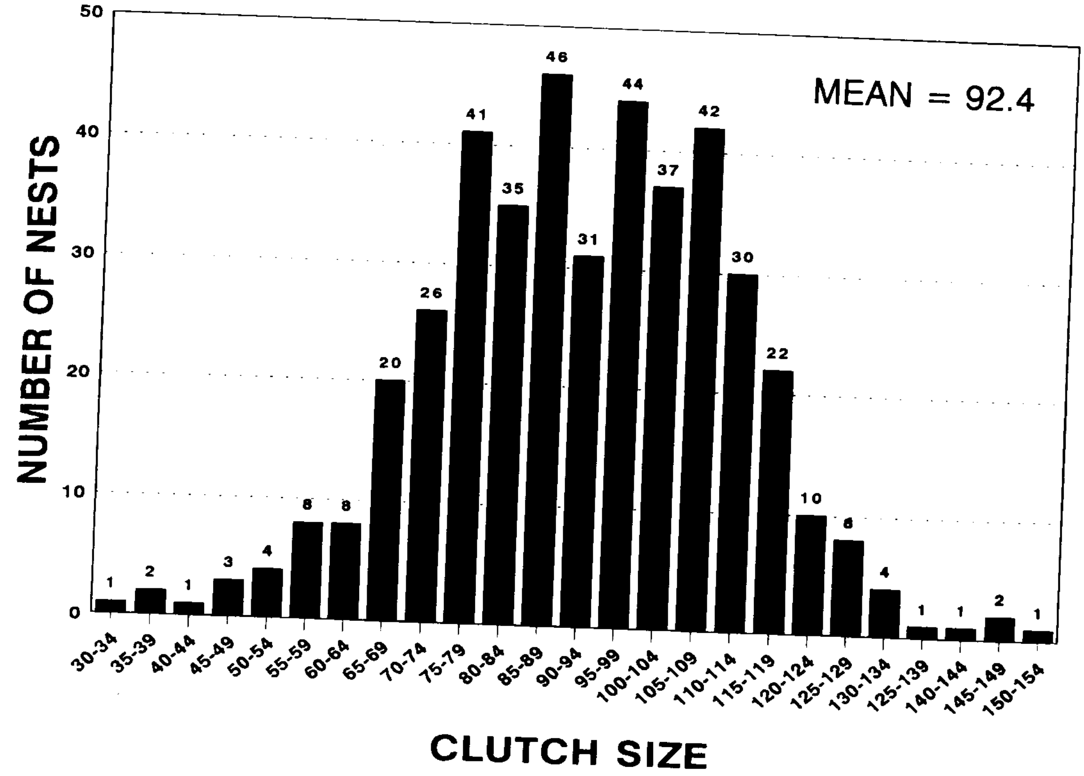

FIGURE 3. Frequency distribution of clutch sizes for 428 green turtle nests from Tern Island, French Frigate Shoals, Hawai'i, 1986–1991.

TABLE 6

HATCHING SUCCESS OF GREEN TURTLE NESTS AT TERN ISLAND, FRENCH FRIGATE SHOALS, HAWAI'I, 1986–1991, CALCULATED AS A PERCENTAGE OF TOTAL NUMBER OF EGGS

CATEGORY	1986	1987	1988	1989	1990	1991	1986–91 COMBINED
No. of nests	23	48	85	103	89	77	425
No. of eggs	1,969	4,161	8,232	9,170	8,135	7,582	39,249
Hatched							
Emerged	73.9	63.8	73.7	79.5	71.0	64.9	71.1
Live: left in nest	10.9	11.6	6.5	2.4	7.2	13.5	8.7
Dead: left in nest	0.3	2.1	1.0	0.7	1.8	1.6	1.3
Total	85.1	77.5	81.2	82.6	80.0	80.0	81.1
Unhatched							
3/4 developed	2.7[a]	2.9	2.2	2.8	2.0	4.1	2.8
1/2 developed		2.6	1.7	1.4	1.7	2.5	2.0
1/4 developed		1.8	1.2	0.6	0.5	2.1	1.2
Undeveloped	12.2	15.2	13.8	12.5	15.8	11.4	13.5
Total	14.9	22.5	18.9	17.3	20.0	20.1	18.9

[a] All partially developed hatchlings were lumped together in 1986.

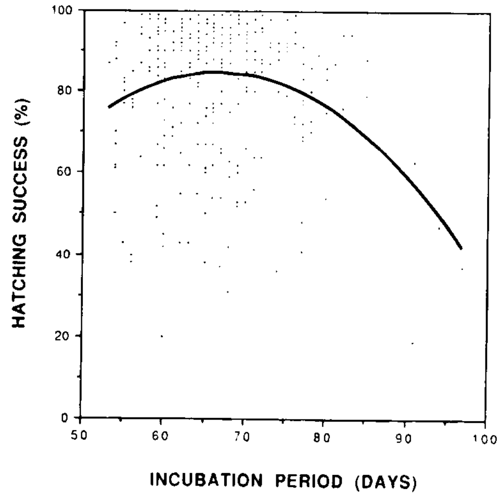

FIGURE 4. Relationship between percentage hatching success and incubation period ($n = 297$).

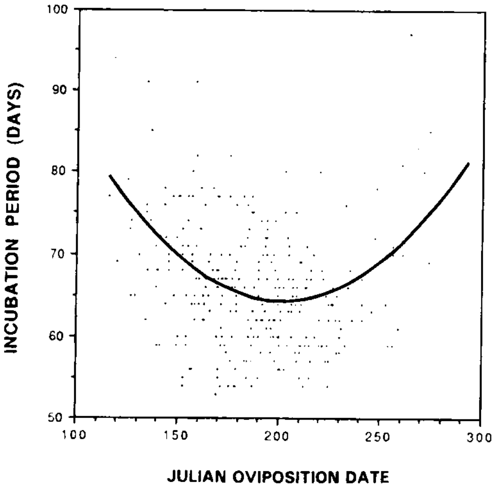

FIGURE 5. Relationship between incubation period and Julian oviposition date ($n = 297$).

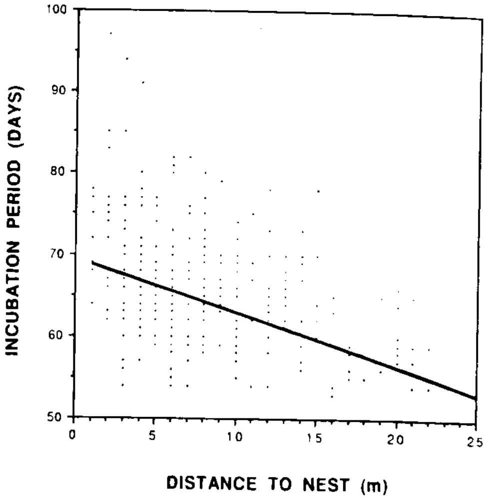

FIGURE 6. Relationship between incubation period and distance from high tide mark to nest ($n = 297$).

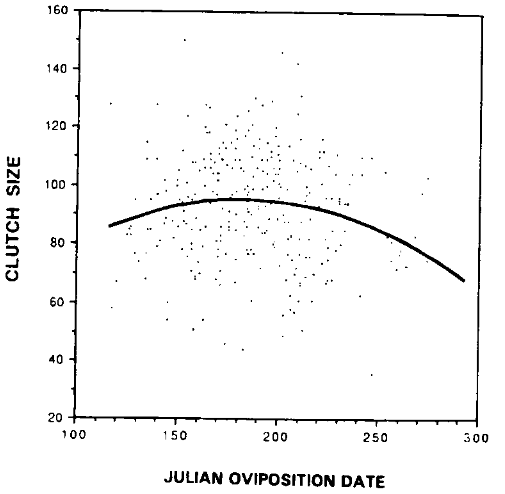

FIGURE 7. Relationship between clutch size and Julian oviposition date ($n = 297$).

nology varied somewhat between years. These differences indicated that environmental conditions may alter nesting phenology by several weeks. Because green turtles migrate to French Frigate Shoals to nest from throughout the Hawaiian Archipelago, it was beyond the scope of this paper to correlate changes in the green turtle nesting phenology with oceanic temperatures, current movements, etc.

Generally, female green turtles oviposit between three and seven clutches within a season at about 10- to 15-day intervals with 2- to 4-yr reproductive cycles (Hirth 1971). The breeding characteristics of the population at French Frigate Shoals were similar to those reported by Hirth (1971). Balazs (1980), working on East Island, French Frigate Shoals (10 km from Tern Island), documented females laying one to six clutches with oviposition occurring at 11- to 18-day intervals. Balazs (1983) reported that 43.1% of 130 females had a 3-yr reproductive cycle, 36.2% a 2-yr cycle, 7.7% a 4-yr cycle, and 12.2% nested at intervals ranging from 5 to 8 yr. A single female nested after an interval of only 1 yr. These breeding characteristics result in different sets of females nesting each year. Individual females may lay clutches throughout a 3-month period, which complicates analyses of the data. Our intent was to present parameters as they pertain to the general Tern Island nesting population and to examine the data for any trends that may suggest future research and management needs.

Mean incubation periods from various green turtle studies range from 55.6 to 66.0 days (Table 7). Incubation was as short as 48 days (Carr and Hirth 1962) and as long as 97 days (this study). We documented incubation periods ranging from 56 to 76 days for the same female in the same season, indicating that genetic differences/similarities between clutches may not explain the wide range of incubation periods. The wide range of incubation periods was probably a function of environmental conditions that affected the temperature in the egg chamber. Bustard and Greenham (1968) found that a 3° increase in temperature reduced incubation length by 25 days. Chemical and physical characteristics of beach sand, weather, nest depth, clutch size, and degree of shading all may affect temperature within the nest, resulting in the wide range of incubation periods.

TABLE 7

INCUBATION PERIODS (DAYS) AND CLUTCH SIZE FOR GREEN TURTLE NESTS AT TERN ISLAND, FRENCH FRIGATE SHOALS (FFS), AND OTHER LOCATIONS

LOCATION	INCUBATION PERIOD[a]	CLUTCH SIZE[a]	SOURCE
Tern Island, FFS	66.0 375 (53–97)	92.0 428 (33–150)	This study
East Island, FFS	64.5 38 (54–88)	104.0 50 (38–145)	Balazs (1980)
Costa Rica	61.9 125 (53–81)	104.0 188 (7–178)	Fowler (1979)
Costa Rica		112.0 2,544 (3–219)	Bjorndal and Carr (1989)
Ascension	59.5 10 (58–62)	115.5 140 (53–181)	Carr and Hirth (1962)
Tortuguero	55.6 217 (48–70)	110.0 406 (18–193)	Carr and Hirth (1962)

[a] Mean followed by sample size; range in parentheses.

In this study, incubation periods tended to be longer in the early and late portions of the season than in midseason. This relation may be explained by differences in ambient temperatures, because midseason clutches were incubated during the warmest months (July through September) of the year. Hendrickson (1958) also reported that incubation length varied in response to seasonal changes in environmental conditions. Incubation periods tended to decrease the farther inland the nest was located. Chemical and physical characteristics of the nest site probably produced the differences in incubation length as related to distance inland. However, our study did not examine enough nest-site parameters to adequately evaluate specific nest-site/incubation relations. Fowler (1979) also found that incubation period was influenced by nest position. Her data showed that low and midbeach nests had shorter incubation periods than nests found within a densely vegetated high beach zone. Vegetative shading of the nest site evidently cooled the area, increasing the incubation period. Most of the inland nests on Tern Island were in open, unshaded areas. Perhaps solar warming of the exposed inland sites on Tern Island produced the shorter incubation periods that we found at inland sites. However, other chemical and physical characteristics of the nest sites may be involved, such as the organic content, albedo, or moisture level of the nest site substrate.

Because incubating temperature determines the sex of green turtle hatchlings (males are produced at temperatures <28.5°C and females at temperatures >30.3°C [Spotila et al. 1987]), future management of green turtle nesting beaches at French Frigate Shoals requires a better understanding of the dynamics of incubation. For example, would increasing the shrub component of beach vegetation, to provide additional nesting habitat for seabirds, affect incubation periods and hatchling sex ratio of the green turtle?

The mean clutch size (92 eggs) in this study is slightly smaller than means reported from other studies (Table 7). Clutch size tended to be larger during midseason than during early and late season. Maximum clutch size occurred on about 2 July. During laboratory incubation, Bustard and Greenham (1968) documented an increase of about 6° in nest temperature from metabolic heating of the eggs. Clutch size may affect incubation temperature and incubation length, with larger clutches producing more metabolic heat and having shorter incubation periods. This relationship was reported by Fowler (1979) of nests at some beach locations. However, no correlation between clutch size and incubation period was found in our study. The influence of metabolic heating may have been masked by other nest-site factors.

Predation is not a factor in nest success at French Frigate Shoals. Ghost crabs (*Ocypode* spp.) are the only potential egg predators. Ghost crabs take turtle hatchlings as they emerge and head to the sea; however, egg predation by ghost crabs was not observed at French Frigate Shoals during this study or during earlier work (Balazs 1980). The mean natural emergence success of 71.1% was for all nests made during the 6-yr study. Additional hatchlings were found alive in the nests upon excavation and subsequently released. These hatchlings accounted for another 8.7% of the eggs. Some of the live hatchlings found in the excavated nests eventually may have succeeded in emerging if the nests had not been disturbed. This assumption is based on an inverse relationship between the number of live hatchlings and the number of days after initial hatchling emergence that the nest was excavated. Hatchlings have been observed emerging from a nest in small lots during a period of 24–72 hr (Hirth 1971). Hatchlings trapped within a nest chamber expend valuable energy struggling to free themselves. The loss of this energy, needed during their initial few days at sea, may determine whether they survive or not. The failure of some hatchlings to emerge from the nest may be a form of natural selection. However, many that we found in the nests were apparently healthy hatchlings trapped by physical barriers such as large pieces of coral or unhatched eggs. If nests are to be excavated, we recommend that they be excavated 3 days after initial hatchling emergence to maximize emergence and hatchling survival.

The natural emergence success could be slightly higher than documented because in some cases nests were excavated before all hatchlings had ample time to emerge on their own. Balazs (1980) reported a 70.8% natural emergence at East Island, French Frigate Shoals. Other investigators worldwide have reported natural nest emergence successes of 54% (Carr and Hirth 1962), 55% (Moorhouse 1933), 71% (Bustard 1973), 83.1% (Fowler 1979), and 85% (Schulz 1975).

Only one significant relationship was associated with hatching success. That relationship was that maximum hatching success occurred at an incubation period of 66.7 days, which is very close to the mean incubation period of 66.0 days. As discussed above, incubation period is influenced by several factors. For example, chemical and physical characteristics of the substrate encompassing the nest, which affect incubation time, also influence clutch survival (Mortimer 1990).

Beaches on different nesting islands at French Frigate Shoals differ in physical characteristics. Some, such as on Tern Island, consist of uniformly fine to medium coralline sands. Others (e.g., East and Whale-skate Islands at French Frigate Shoals) are characterized by very coarse fragments of corals, coralline algae, molluscs, and barnacles (Balazs 1980). These beaches have various amounts of humus from nesting seabird colonies. Understanding the composition of beaches and how it affects sea turtle nesting is essential for proper management (Mortimer 1990).

Our data indicate that nesting peaked near 5 July when conditions produced a near optimal incubation period for yielding maximum hatching success. Maximum clutch size also occurred about the same time. More nest-specific studies are needed to further define and understand nest location, nest substrate, incubation length, and hatching success relationships on the beaches at French Frigate Shoals.

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