NOAA Technical Report NMFS 56

Some Aspects of the Ecology of the Leatherback Turtle *Dermochelys coriacea* at Laguna Jalova, Costa Rica

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July 1987

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ABSTRACT

The ecology and reproductive biology of the leatherback turtle (*Dermochelys coriacea*) was studied on a high-energy nesting beach near Laguna Jalova, Costa Rica, between 28 March and 8 June 1985. The peak of nesting was between 15 April and 21 May. Leatherbacks here measured an average 146.6 cm straight-line standard carapace length and laid an average 81.57 eggs. The eggs measured a mean 52.12 mm diameter and weighed an average of 85.01 g. Significant positive relationships were found between the carapace lengths of nesters and their clutch sizes and average diameter and weight of eggs. The total clutch weighed between 4.02 and 13.39 kg, and yolkless eggs accounted for an average 12.4% of this weight. The majority of nesters dug shallow (<24 cm) body pits and spent an average 81 minutes at the nest site. A significant number of clutches were laid below the berm crest. In a hatchery 42.2% of the eggs hatched, while in natural nests 70.2% hatched. The average hatchling carapace length was 59.8 mm and weight was 44.6 g. The longevity of leatherback tracks and nests on the beach was affected by weather. One nester was recaptured about one year later off the coast of Mississippi, U.S.A. Egg poaching was intense on some sections of the Costa Rican coast. Four aerial surveys in four different months provided the basis for comparing density of nesting on seven sectors of the Caribbean coast of Costa Rica. The beach at Jalova is heavily used by green turtles (*Chelonia mydas*) after the leatherback nesting season. The role of the Parque Nacional Tortuguero in conserving the leatherback and green turtle is discussed.

INTRODUCTION

The leatherback turtle, *Dermochelys coriacea*, is the only living member of the family Dermochelyidae. It has a leathery carapace that lacks scutes but possesses seven longitudinal keels and has relatively long front flippers. This animal, the largest living turtle, can never be mistaken for anything else.

The species suffers mortality from a variety of sources. Leatherback eggs are widely harvested and in some places nesting females are killed for their meat and oil. The rising human population and man's development schemes are encroaching on some of the important nesting beaches. Leatherbacks are subject to incidental drowning in fishing gear; they may be harmed by swallowing plastic material; and they are poor candidates for captive breeding. For these and other reasons, the leatherback is classified as an endangered species by the International Union for the Conservation of Nature and is on the U.S. Endangered Species List. Some recent accounts of its general biology, distribution, and conservation status are provided by Pritchard (1980), Bjorndal (1982), Groombridge (1982), and Bacon et al. (1984).

For many years it has been widely known that leatherbacks nest in the early part of the year on the eastern coast of Costa Rica and that the poaching of eggs may be intense. Carr and Ogren (1959) spent a short time observing the nesting behavior of leatherbacks and the depredation of eggs on the beach near Matina, and they concluded that the turtles in this area were in need of further study.

The main purposes of the present study were to document some aspects of the ecology and the reproductive biology of a nesting population of leatherbacks near Laguna Jalova on the Caribbean coast of Costa Rica. Emphasis was placed on studying the morphometrics of eggs, hatchlings, and mature females; nesting behavior; hatching success; and some aspects of human ecology as related to the leatherback turtle.

MATERIALS AND METHODS

Two types of tags (style 4-1005, No. 49 and No. 19 from the National Band and Tag Co., Newport, Kentucky, U.S.A.) were placed on turtles after oviposition. Number 49 was a monel metal tag clamped on the trailing edge of the left front flipper. Number 19, also monel metal, was clamped to the skin between the tail and left rear flipper. Tags were applied with their respective applicators. A number was inscribed on one side of the tag and a return address on the obverse.

Six carapace measurements were taken on nesting turtles. The straight-line total carapace length (or tip to tip) was measured by extending calipers from the anteriormost to posteriormost projections of the carapace. The straight-line standard carapace length (or notch to tip) was measured by extending calipers along the midline from the anterior notch to the posteriormost projection of the shell. Straight-line carapace width was measured with calipers spread between the widest points of the carapace, perpendicular to the longitudinal body axis. Overcurvature total carapace length was measured with a flexible tape lying in the groove between the anteriormost and posteriormost projections of the carapace. Overcurvature standard carapace length was measured with the flexible tape lying alongside the median dorsal ridge and extending from the anterior notch to the posteriormost extension of the shell. The overcurvature carapace width was measured with the tape extended between the shell's widest points, at right angles to the long axis of the body.

Table 1

Four aerial surveys in 1985 of leatherback halfmoons and nests on seven beach sectors between Boca del Río Tortuguero and Puerto Limón, Costa Rica. Order of notation (left to right) is number of halfmoons, number of nests (index of relative importance).

Sector	27 March[a]	8 April[b]	15 May[b]	9 June[b]
Boca del Río Tortuguero to Tortuguero	0, 9 (0.67)	?	1, 5 (0.50)	0, 2 (0.17)
Tortuguero to Laguna Jalova	29, 166 (2.24)	3, 31 (1.86)	19, 79 (1.59)	16, 88 (1.72)
Laguna Jalova to Boca del Río Parismina	0, 16 (0.75)	0, 2 (0.50)	14, 16 (1.13)	4, 12 (0.88)
Boca del Río Parismina to Boca del Río Pacuare	2, 15 (0.43)	0, 8 (1.00)	9, 33 (1.36)	1, 20 (0.79)
Boca del Río Pacuare to Laguna Urpiano	0, 38 (1.00)	1, 9 (1.07)	1, 15 (0.60)	3, 12 (0.47)
Laguna Urpiano to Boca del Río Matina	0, 11 (0.67)	0, 4 (1.17)	0, 11 (1.00)	8, 18 (1.67)
Boca del Río Matina to Puerto Limón	0, 1 (0.02)	0, 3 (0.23)	5, 11 (0.27)	6, 24 (0.64)
Totals	31, 256	4, 57	49, 170	38, 176

[a]All nests and all halfmoons were counted because it was early in the nesting season.
[b]Fresh nests and fresh halfmoons only.
?A hard rain squall just prior to take-off prohibited an accurate census.

Most eggs and hatchlings were weighed and measured immediately after deposition and emergence and all were processed within 7 hours. Eggs and hatchlings were weighed on an electronic-digital balance accurate to ±0.05 g. Vernier calipers were used to measure the diameter of eggs and the carapace and plastron of hatchlings. Loose sand was carefully wiped from eggs and hatchlings before processing.

Statistical analyses were performed on a computer using the 1981 version of the BMDP package. Statistical significance was at the 5% level.

Aerial surveys

In order to determine the distribution of nesting effort along the coast between Puerto Limón and Boca del Río Tortugero, four aerial surveys were made during the course of the study. All flights were made between 0715 and 0850 hours in a Cessna 206 single-engine high-wing aircraft, flying at a speed between 80 and 100 knots at an altitude of about 50 m. In order to ensure consistency in identifying the fresh (<24 hours) crawls and nests, Ogren counted the halfmoons and nests on each flight and Hirth (or another observer) coordinated landmarks with the pilot and recorded pertinent information. The index of relative importance (IRI) was determined following the methodology of Hopkins-Murphy and Murphy (1982). The greater the IRI value above 1, the more important that sector of beach relative to other sectors in the survey area.

The results of the aerial surveys indicated that IRI values for the nesting beach between Tortuguero and Laguna Jalova were consistently greater than for other sectors throughout the nesting season, and that the beach between Laguna Urpiano and Boca del Río Matina was average or above-average in three of the four aerial surveys (Table 1, Fig. 1). It is interesting to note that more halfmoons were recorded on the last two flights (during the peak and near the end of the nesting season). Halfmoons are non-nesting emergences in which the track takes the form of a parabolic curve. The significance of these crawls is unknown, but they may be related to reproductive readiness or to the nest-site selection process.

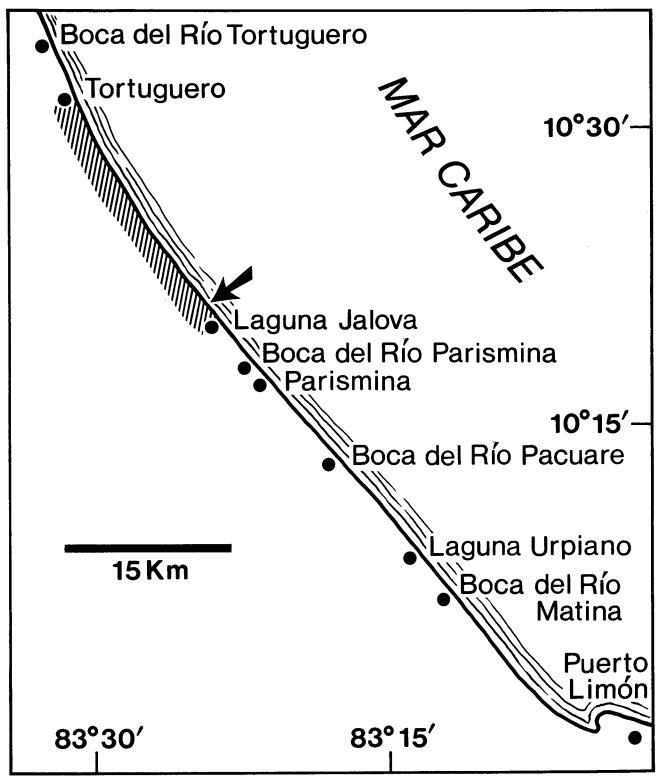

Figure 1

A portion of the Caribbean coast of Costa Rica showing localities mentioned in the text. Hatching indicates extent of the coast lying within the Parque Nacional Tortuguero. Arrow indicates the leatherback turtle study site just inside the Parque.

The study site

A 4.8-km section of beach bordering Laguna Jalova was selected as the study site and was intensively monitored between 28 March and 8 June 1985. The site was also examined several times in July and August 1985. The study site, inside the Parque Nacional Tortuguero (Tortuguero National Park) at its southern boundary, is located at lat. 10°21.5′N and long. 83°23.5′W (Fig. 1). This site was selected because our aerial reconnaissance of the coast between Puerto Limón and Tortugero on 27 March 1985 indicated this was one of the better areas of leatherback activity and because poaching would be minimal inside a National Park. The Parque Nacional Tortuguero extends along the coast from Laguna Jalova to the village of Tortuguero and includes 18,946 hectares of largely tropical wet forest. Laguna Jalova is separated from the sea by a well-developed berm most of the year.

The nearest village to the study beach is Parismina, 7.5 km to the south, a community of about 300 residents. The next village, Tortuguero, is 21.5 km to the north and has a total population of about 150 people. Both villages are growing in population. There is a large amount of boat traffic of tourists, traders, and fishermen in the canal (Caño Negro) about 1 to 1.5 km inland from the study site, and this traffic will, no doubt, increase in the coming years.

The Jalova study site is a typical high-energy beach with a medium-to-steep slope and with a crenate-to-dentate shoreline. The width of the nesting beach platform, or berm, varies from 0 to 40 m (Fig. 2). The configuration of some parts of the berm and the height of the beach scarp changed over the course of the nesting and hatching seasons in response to longshore currents, storm waves, and high spring tides (Fig. 3). For example, between 7 June and 6 August a second berm, about 30 m in length and 10 m wide, formed on the north end of the study area where there was only a single berm from April through 6 June. Also during the same June-August interval, a 60-m-long section of beach at the middle of the study area had almost completely washed away. In some places the roots of the edaphic hedgerow at the rear of the beach were exposed.

The dominant plants on the nesting beach are railroad vine (*Ipomoea Pes-Caprae*), sea-purslane (*Sesuvium portulacastrum*), and rush grass (*Sporobolus virginicus*). There are also scattered clumps of a beach grass (*Uniola pittieri*) and a sedge (*Remirea maritima*). The berm is bordered by a hedgerow of cocoplum (*Chrysobalanus icaco*) and seagrape (*Coccolobis uvifera*), and this is backed by a mixture of coconut palms (*Cocos nucifera*) and various tropical hardwoods.

The beach is littered with a variety of debris including logs, coconut husks, tar balls, and a wide variety and amount of plastic articles. Water hyacinth (*Eichhornia crassipes*) and sargassum (*Sargassum* sp.) are frequently washed up on the strand during storms.

Precipitation and air temperature were measured at the nearby Jalova Ranger Station. Total precipitation during the 5-month nesting and hatching season was similar in 1984 and 1985 (Table 2). Noon air temperatures from 1 April through 6 June ranged between 25.5 and 31.1°C.

Soil samples were obtained from the beach surface (0-5 cm) and at a depth of a typical clutch of eggs (70 cm, to the middle of the egg mass). The sand analyzed was a composite of five samples taken five meters apart on a transect through the middle of the berm (Table 3). The color of the sand was olive-gray when dry and dark-olive-gray when moistened to field capacity. The sand on the nesting beach was predominantly fine-to-medium grain. The size of the sand particles along with moisture content can affect embryonic development by limiting diffusion of gases (Ackerman 1980).

Figure 2
A typical segment of the nesting beach at the Jalova study site, Costa Rica, in April 1985. Turtles nested on all parts of the beach.

Figure 3
Erosional processes frequently change the configuration of the berm at the Jalova study site, Costa Rica. A significant number of leatherback turtle clutches were laid below the berm crest.

Table 2
Rainfall (mm) at the Jalova Ranger Station (2.4 km inland from the leatherback study site), Costa Rica measured at 0700 daily. Data available for only 5 months in 1985.

Month	J	F	M	A	M	J	J	A	S	O	N	D
1984	484	426	108	115	397	426	304	654	151	478	629	409
1985			111	71	294	619	291					

Table 3
Analysis of sand on the Jalova nesting beach, Costa Rica. Color determined with Munsell Soil Color Charts, 1975 Edition; pH measured by Hellige-Truog colorimetric method; particle size determined by standard soil sieves.

	Color			% particle size (mm)				
	Dry	Wet	pH	>1.0	1.0-0.5	0.5-0.25	0.25-0.125	<0.125
Surface (0-5 cm)	5.0Y 4/2	5.0Y 3/2	7.0	0.5	7.3	48.7	41.4	2.1
70 cm	5.0Y 4/2	5.0Y 3/2	7.0	0	5.7	41.3	50.5	2.5

RESULTS

Nesting season and number of nests

By direct observation it was estimated that 224 clutches were laid on the 4.8-km study beach between 28 March and 8 June 1985. Although 82 turtles were tagged here, we do not know the actual number of females which accounted for these clutches because more turtles need to be tagged and more information is needed on the nest site fidelity of this deme. The peak of nesting was between 15 April and 21 May when 78% of the clutches were laid. Based upon the aerial survey of 27 March, on-site inspection, discussion with park rangers, and the emergence of hatchlings in mid-May, we estimated that nesting at Jalova began in the middle of March. The park rangers informed us that very little nesting took place after the middle of June. The last confirmed nesting on the study site was on 2 August. For comparison, 31 clutches were laid between 17 April and 6 May on 4.8 km of beach between Boca del Río

Tortuguero and the village of Tortuguero. Knowledgeable villagers there considered 1985 a good year for leatherbacks.

Twenty-four halfmoons, which represented about 10% of the nesting emergences, were recorded on the study site between 28 March and 8 June. Nine and 15 halfmoons were made in the first and second half of the nesting season, respectively.

Periodic surveys were made to record the number of clutches laid below the beach scarp and to observe the number of orientation circles made by adults (Tables 4 and 5). Eggs laid below the berm crest are certainly subject to saltwater seepage at high tide as long as the beach topography remains the same. Work on other sea turtle beaches has demonstrated that embryonic development is adversely affected by high concentrations of chloride, restricted gas exchange, and excessive moisture (Bustard and Greenham 1968; Ackerman 1980; Kraemer and Bell 1980; Whitmore and Dutton 1985). Poor siting of nests on other leatherback beaches ranges from less than 2.5% to about 50% and appears to be related to beach topography (Mrosovsky 1983a). Orientation circles (Fig. 4) were made in ascending and descending crawls (the circling performed by some individuals on the nest site itself was not included in these records). Their significance is probably related to phototaxis (Bacon 1973).

Measurements of tagged turtles

During the study a total of 93 sea turtles were tagged (Fig. 5). Of these, 89 were leatherbacks with tagging sites as follows: 82 on the Jalova study beach, 6 at Parismina, and 1 at Tortuguero. It was not possible to tag every leatherback which nested on the study site. Four green turtles (*Chelonia mydas*) were tagged at Jalova. Six carapace measurements are provided in Table 6. The carapace widths varied less than the lengths.

Table 4

Number of leatherback turtle clutches laid below the beach scarp at the Jalova study site, Costa Rica, at various intervals.

	Number nests	
Interval	Total	Below berm
22-28 April	44	10 (23%)
29 April-8 May	16	2 (13%)
14-21 May	44	13 (30%)
22-30 May	20	8 (40%)
1-8 June	6	1 (17%)

Table 5

Number of orientation circles made by adult leatherback turtles on their ascending and descending crawls at various times of the nesting season at the Jalova study site, Costa Rica.

		No. orientation circles	
Interval	No. nests	Ascending	Descending
15-21 April	39	0	10
9-13 May	31	2	5
22-30 May	20	4	3
1-8 June	6	1	0

Figure 4

Orientation circle of a leatherback turtle at Jalova Beach, Costa Rica. Some crawls had two or, on a rare occasion, three loops.

Figure 5
Leatherback turtle starting to construct a body pit. Dorsally the turtle is predominately black with white spots scattered on the head, neck, carapace, and flippers.

Table 6
Carapace measurements (cm) of female leatherback turtles nesting at Jalova (*N*=82) and Parismina (*N*=6), Costa Rica, in 1985. Abbreviations: SL = straight line; OC = overcurvature. Other terms defined in the text.

	N	Mean	SD	Range
SL total	76	152.1	8.55	134.6 - 172.7
SL standard	76	146.6	8.25	128.3 - 165.1
SL width	79	82.8	5.51	69.9 - 96.5
OC total	84	159.7	8.56	142.2 - 180.3
OC standard	84	152.8	8.12	134.6 - 171.5
OC width	88	112.4	5.90	100.3 - 132.1

Relationships of carapace lengths and eggs

The scaling of reproductive traits to body size can illuminate some important aspects of autecology. In the following regressions and correlation, eggs or clutch refer to normal, yolked eggs. The carapace length is the straight-line standard measurement.

The clutch sizes of 47 nesters at Jalova were regressed on the carapace lengths and the result was a strong positive relationship (Fig. 6). It would be informative to determine if this relationship is maintained with the total number of eggs laid by an iteroparous individual over the nesting season. The average number of eggs laid by the 47 nesters was 81.57 (SD 18.10).

Twenty eggs selected at random from the clutches of 20 nesters were measured. Mean egg diameters were used as data points and regressed on the carapace lengths of the nesters (Fig. 7). There was a strong positive relationship between size of nester and the sample mean size of eggs. The average egg diameter of the 400 eggs was 52.12 mm (SD 1.08). Mean egg diameters at some of the well-known leatherback colonies range between 50 and 55 mm with those in the East Pacific rookeries being smaller than most others (Hirth 1980; Fretey 1980; Benabib-Nisenbaum 1983; Eckert and Eckert 1983; Limpus et al. 1984; Tucker and Hall 1984).

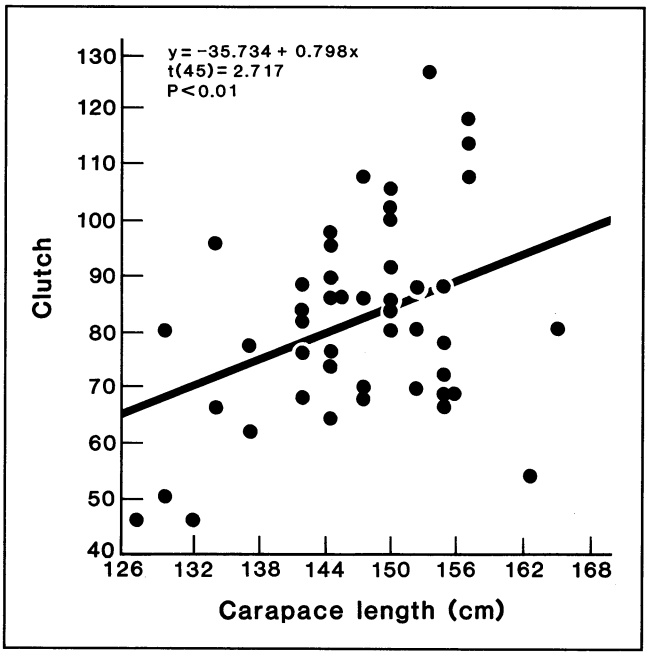

Figure 6
Relationship between clutch sizes and carapace lengths of nesting leatherback turtles at the Jalova study site, Costa Rica.

Twenty eggs selected at random from the clutches of 19 nesters were weighed. Logarithms of the mean egg weights were used as data points and regressed on the carapace lengths of the nesters and a positive relationship was revealed (Fig. 8). Average weight of the 380 eggs was 85.01 g (SD 2.61).

Twenty eggs selected at random from 26 clutches were measured and weighed and the means were used as data points. The range of average egg weights was 72.6-103.5 g, and the range of mean

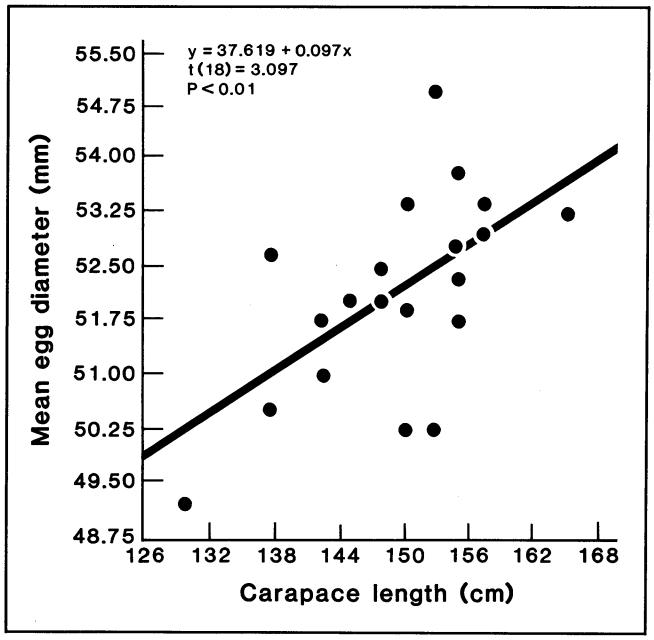

Figure 7
Relationship between sample mean egg diameters and carapace lengths of leatherback turtles at the Jalova study site, Costa Rica.

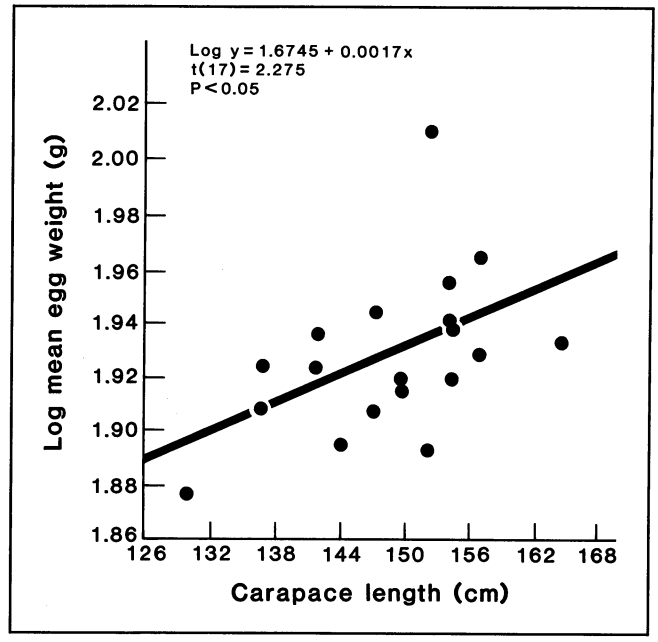

Figure 8
Relationship between sample mean egg weights and carapace lengths of leatherback turtles at the Jalova study site, Costa Rica.

egg diameters was 49.2-54.9 mm. As expected, we found a strong correlation between the log of the average egg weight in grams (Y_1) and the mean egg diameter in millimeters (Y_2) (principal axis: $\log Y_1 = 0.9121 + 0.0194\ Y_2$: $r = 0.83$; $P < 0.01$).

Yolkless eggs

Leatherback turtles everywhere and some hawksbill turtles (*Eretmochelys imbricata*) lay a number of smaller, yolkless eggs along with normal-sized, yolked eggs (Fig. 9). At Jalova, as elsewhere, most of the yolkless eggs were laid last. In a few instances some of these eggs were deposited first or along with normal eggs.

In a sample of 46 clutches, the number of yolkless eggs averaged 29.8% (SD 13.30, range 9.4-77.7) of the total clutch. In a sample of 19 clutches, the diameters of the yolkless eggs ranged from 1 to 47 mm and the mode varied between 29 and 37 mm. In the same sample of 19, the weight of the yolkless eggs represented from 3 to 23% ($\bar{x}$ 12.4%, SD 4.90) of the weight of the

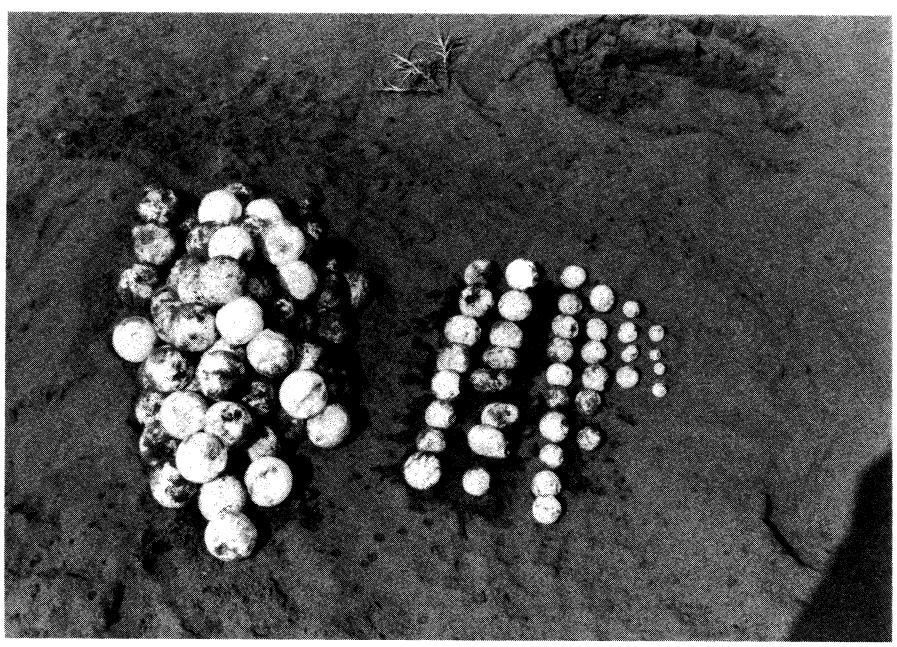

Figure 9
A typical leatherback turtle clutch showing normal eggs and variety of yolkless eggs at the Jalova study site, Costa Rica.

entire clutch. The weight of the entire clutch ranged from 4.02 to 13.39 kg ($\bar{x}$ 7.4 kg, SD 2.00). Fretey (1980) found that the weight of the total clutch in French Guiana ranged from 3.83 to 11.6 kg ($\bar{x}$ 8.07, SD 1.77).

Nesting sites on the berm

Nesting sites of 74 of the tagged leatherbacks that nested between 30 March and 31 May were examined. Nineteen laid eggs on the forward one-third of the nesting beach, 27 deposited eggs in the middle third, and 28 nested on the rear third of the berm. The spatial distribution of clutch sites was not statistically different from an equal distribution. When the nesting season was divided into halves, the distribution of nest sites was again not statistically significant from an equal distribution.

Nesting behavior

Carr and Ogren (1959) photographed and described the important nesting stages of the leatherbacks at Matina, and the following accounts amplify their basic descriptions.

All the turtles at Jalova nested at night (Fig. 10). The time it takes for a leatherback to crawl from the surf to the nest site and return to the sea after nesting varies with such things as the stage of the tide, height of the beach scarp, position of the nest on the berm, obstacles (e.g., logs), whether or not she makes an orientation circle, and perhaps whether she is a neophyte or experienced nester. Considering all things, we estimate that it takes the average leatherback at Jalova about 10 minutes to reach the nest site from the surf and a little less time to return to the sea after nesting.

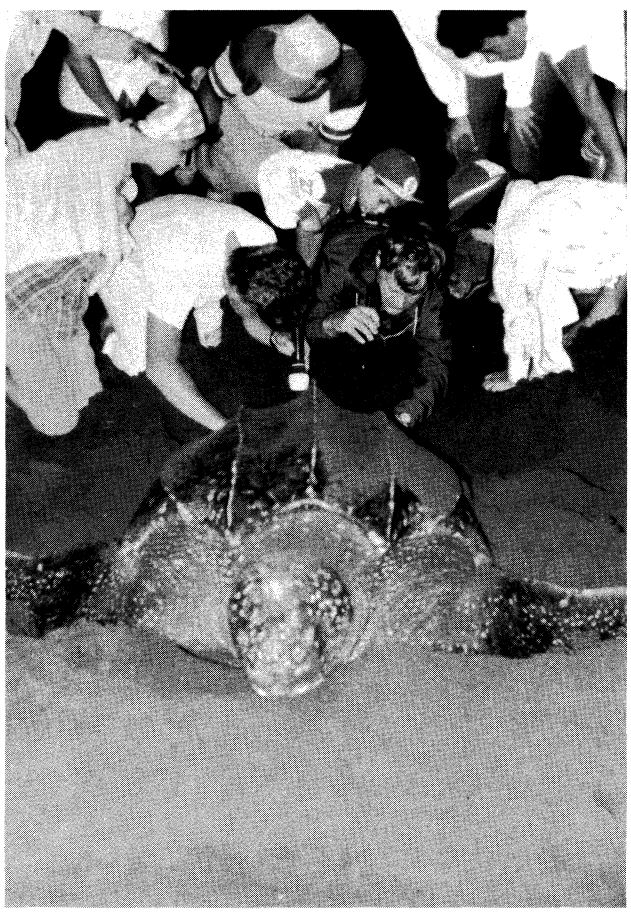

Figure 10
Tourists watching egg-laying at Jalova Beach, Costa Rica. The local name for the leatherback turtle is tortuga baula (less frequently tortuga canal).

The behavior of 10 females at the nest site was examined (Table 7). These individuals nested between 10 April and 30 May, i.e., somewhat evenly spread throughout the nesting season, and thus probably included some first nestings and some late nestings of the season. Seven nested at the unvegetated front of the berm, two nested in the middle of the berm where plant cover was about 40%, and one laid eggs at the edge of the cocoplum hedge. Seven females dug shallow body pits (i.e., <24 cm below the sand surface at the head end) and three constructed deep pits (>24 cm). Of 50 turtles observed throughout the nesting season, 62% dug shallow body pits and 38% dug deep ones. Jalova leatherbacks typically spend 81 minutes at the nest site. They spend more than twice as much time in filling the body pit and camouflaging the nest as they do in digging a body pit. The total time spent by leatherbacks in these five stages of nesting is remarkably similar at other nesting locales (Carr and Ogren 1959; Pritchard 1971; Fretey 1981; Benabib-Nisenbaum 1983; Eckert and Eckert 1983) but there is some variation in the time spent in each stage.

Upon reaching the vicinity of the nest site, many leatherbacks at Jalova made a few tentative sweeps with the front flippers and then would turn around on the site or would crawl a meter or two further before settling down on the final site that would become the body pit. Much sand was thrown around in this process.

Only three turtles were observed to make false or trial body pits on the chelonery. One dug a body pit in 10.5 minutes, moved 4 m, and then dug another one in 10 minutes. She then continued normal egg laying. The other two females returned to the sea after abandoning their body pits.

Two turtles dug nests below the beach scarp and struck water while digging the egg chamber. One laid her eggs in the chamber (about one-fifth filled with saltwater) and the other abandoned the nest, crawled over the scarp, and laid her eggs on the berm after going through a normal nesting sequence.

The position of the hind flippers during oviposition varied a little. Of 20 individuals observed, 9 positioned both rear flippers flat on the sand surface but with one flipper extending over the egg chamber more than the other. The eggs were not visible. Nine individuals exhibited a similar pattern except that the edge of one rear flipper was extended into the egg chamber, and again the eggs were not visible. Two turtles exhibited slight variations of these two patterns and their eggs were visible.

The action of the hind flippers, immediately after filling the egg chamber and before the filling of the body pit begins, can best be described as a "pressing" or "packing" action. In a few cases a "kneading" pattern was noted.

Table 7
Length of time (minutes) spent by ten leatherback turtles in five nesting stages, Jalova nesting site, Costa Rica.

Stage	Mean	SD	Range
Dig body pit	11.7	1.85	10 - 15
Dig egg chamber	19.7	5.54	15 - 29
Oviposition	10.7	1.31	9 - 13
Fill egg chamber	10.4	2.01	8 - 14
Fill body pit and camouflage	28.4	7.86	17 - 41

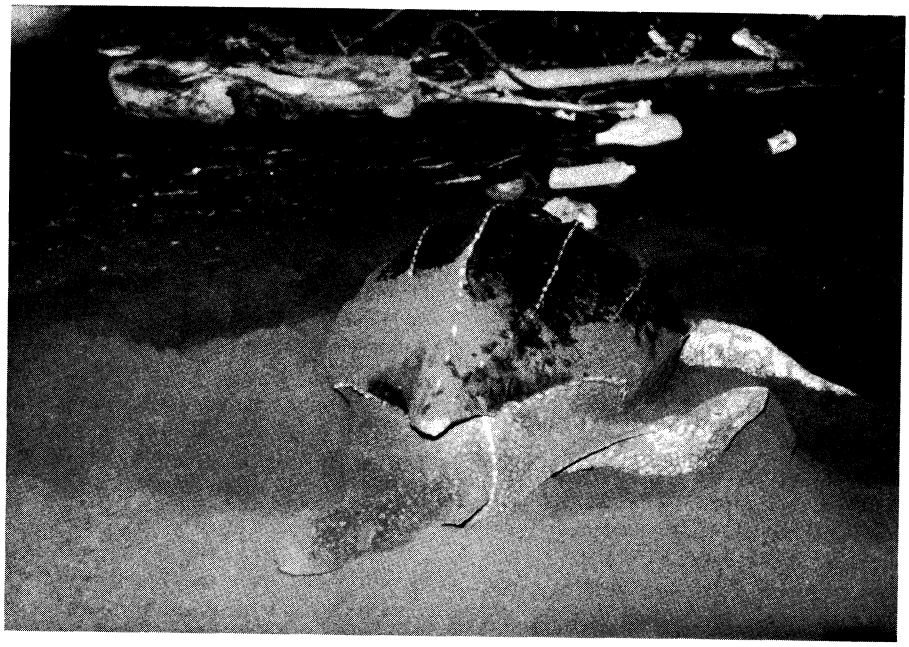

Figure 11
Rear flippers of a leatherback turtle are swinging side-to-side as it finishes digging the body pit. The same movements will be made in the early stages of concealing the nest site.

A turtle with only stumps, 20-23 cm in length, for rear flippers took one hour to construct a primitive, shallow egg chamber. She carried on as best she could through all the stages of nesting. The resulting clutch of eggs (normal number) was much closer to the sand surface than a normal clutch.

One behavioral pattern was particularly interesting in that it occurred both prior to and after oviposition and made it challenging for an observer to determine if eggs had been laid. We noted the hind flippers swinging in tandem left-right-left-right (repeated several times at irregular intervals) over the site of the egg chamber at the late stages of building a body pit. The same movements appeared at the early stages of filling the body pit (the front flippers are throwing sand backward between bursts of rear flipper movements). If she had thrown around a lot of sand in the site selection process, it was challenging to determine (looking at the swaying of the rear appendages alternating with the backward heaving of sand by the front appendages) whether or not she had oviposited (Fig. 11). Egg poachers were also temporarily thwarted when encountering a turtle exhibiting this behavior.

Of 55 nesters observed while ovipositing, 12 were facing toward the sea, 21 toward the hedgerow, and 22 in a position between these two viewpoints. The average straight-line distance between 78 nests and the sea was 29.3 m (SD 8.51, range 13-45). Distances were measured at the time of oviposition.

Recaptures

Nine leatherbacks were recorded nesting a second time (Table 8). One individual traveled 12.3 km between successive nestings while another moved only 0.8 km (assuming about a 10-day renesting interval for this species). More data are needed to determine the nest site fidelity of the leatherbacks in this population. Poachers believe the nesting turtles "shift" some distances north and south along the coast during the nesting season. The available data indicate that 2- or 3-year nesting cycles are the most common for leatherbacks and that annual nesting is rare (Groombridge 1982; Bacon et al. 1984).

Table 8
Days and distances between recaptures of nesting leatherback turtles. All individuals were tagged and recaptured in 1985, except No. 6 which was recaptured in 1986.

Individual	Date, place tagged	Date, place recaptured	Days	Km
1	30 March, Parismina	9 April, Jalova	10	12.3
2	4 April, Jalova	23 May, Jalova	49	2.4
3	5 April, Jalova	23 April, Jalova	18	0.8
4	5 April, Jalova	2 May, Jalova	27	0.4
5	6 April, Jalova	25 April, Jalova	19	0.4
6	10 April, Jalova	25 July, South of Pacuare	471	27.0
7	26 April, Jalova	End of May, Urpiano	~30	32.2
8	8 May, Jalova	16 May, Jalova	8	0.8
9	23 May, Jalova	26 June, Matina	34	44.0

One leatherback tagged after nesting at Jalova on 23 May 1985 was recaptured by a shrimp fisherman a few kilometers offshore of Gulfport, Mississippi, in the middle of June 1986. The shortest distance between the site of tagging and recapture is 2,300 km. A leatherback tagged at Tortuguero on 11 July 1979 was captured at sea off the south coast of Cuba on 23 August 1983 (Carr and Meylan 1984). Meylan (1982) has summarized some of the long-distance recoveries of tagged leatherbacks in other regions.

Injuries and an epibiont

Of 80 adult female leatherbacks examined, 16 had one or more recent or old injuries. Observations were made at night and some old scars may have been missed. The venters of the body and flippers were not checked. The most to least common injuries were: mutilations and cuts on rear flippers, lacerations on front flippers, mutilations of the carapace (mostly to the caudal peduncle) and

gashes on the shoulders and head. Both rear flippers of one individual were paralyzed and one female had a deformed tail. Fretey (1982) describes how leatherbacks in French Guiana are injured by encounters with mangroves and driftwood on the beach and with sharks and boat screws in the sea. The barnacle, *Platylepas hexastylos* was one of the more common epibionts on the carapaces.

Incubation period and hatching success

Ten clutches of eggs laid in the early part of the nesting season were reburied in an egg hatchery located on the rear third of the rookery. The eggs were carefully transplanted from one-half to 8 hours after being laid. The yolkless eggs were placed on top of the normal eggs. The clutches were excavated a few days after the majority of hatchlings emerged on the surface.

The average incubation period (from night of deposition to night that most hatchlings emerge on sand surface) of the hatchery eggs was 61.5 days (SD 2.41, range 58-66). Average hatching rate was 42.2% (Table 9). Of the hatchlings produced, 34% were dead, deformed, or weak. These hatchlings were found in the egg shell rubble, in the nest chimney, and on the sand surface. It is doubtful if many of the weak of deformed individuals would have had the strength to eventually reach the sea. Hatching success of transplanted leatherback eggs in the well-known Malaysian hatcheries has varied from 32 to 71.5% over a 19-year period (Siow and Moll 1982). Benabib-Nisenbaum (1983) recorded hatching rates of 51.03% and 10.11% in Mexico, and Eckert and Eckert (1983) found hatching rates of 64.4% and 50.5% in the U.S. Virgin Islands. Balasingam (1967) discovered that clutches of approximately 50 eggs in hatcheries have better hatching success than other size clutches. Whitmore and Dutton (1985) recorded a 68.7% hatch rate in reburied clutches of 50 eggs in Suriname.

Twenty-four natural clutches, located on all parts of the beach, were exhumed after the hatchlings emerged. These eggs were also laid in the early part of the nesting season. The number of hatchlings that successfully emerged was determined by correlating the number of tracks with the egg shells in the nest. The mean hatching success of the wild nests was 70.2%. Of the hatchlings produced, about 8.6% were dead, weak or deformed. In the Caribbean area, Eckert and Eckert (1983) found a 64.4% and 61.4% hatching success in natural nests in the U.S. Virgin Islands, Tucker and Hall (1984) noted a 72.2% hatching rate in Puerto Rico, and Whitmore and Dutton (1985) found a 32.7% and a 61.9% hatching rate, respectively, in wild nests in Suriname that were and were not washed-over by sea swells.

About 10% of eggs in both the hatchery and natural clutches at Jalova contained dead or moribund embryos. Most of these were in the middle-to-late stages of development. Non-developed eggs (no visible embryo) in both the transplanted and wild nests were largely intact and full of putrid fluid, and the yolkless eggs, though somewhat shriveled, usually contained some liquid.

Measurements of hatchlings

Hatchlings from four nests were measured and weighed within a few minutes after emergence and samples from two nests were processed 7 hours after emergence (Table 10, Fig. 12). The plastron length is the straight-line distance along the midline, and the head width is measured at the widest points. The mean carapace lengths of hatchlings at some of the better known colonies range between 55 and 63 mm, and the average weight registers between 39 and 47 g (Hirth 1980; Benabib-Nisenbaum 1983; Eckert and Eckert 1983; Limpus et al. 1984; Tucker and Hall 1984).

Predators

Several predators or possible predators were noted. It was common to see coatis (*Nasua narica*, locally called pizote) tracks going from nest to nest at the rear of the nesting beach. We could confirm only two egg nests excavated by coatis. Both of these nests were at the cocoplum-seagrape hedgerow where, because of the difficulty of digging, the eggs may have been deposited nearer the surface than normal. Black vulture (*Coragyps atratus*) tracks around one of these nests suggested these birds fed on what was left. In two instances coatis ate some emerging hatchlings. A ghost crab (*Ocypode quadratus*) was seen eating a hatchling, but whether the crab caught this hatchling or found a weak or dead one is unknown. We observed that active hatchlings on their crawl to the sea were easily able to fend off ghost crabs. Park guards said that raccoons (*Procyon lotor*, locally called mapachín) are in the area and eat eggs of both the leatherback and green turtles. This needs to be investigated because raccoons are significant predators on beaches where they occur.

Other sea turtles

Four green turtles nested on the study site along with the leatherbacks. Three of the four laid eggs at the edge of the cocoplum-seagrape hedgerow and one oviposited 3 m in the hedgerow. All the eggs were normal (i.e., no deformed or yolkless eggs) (Table 11). The 4.8 km leatherback beach at Jalova, as well as the rest of the beach inside the Parque Nacional Tortuguero, is heavily utilized by green turtles after most of the leatherbacks have nested (Table 12, Fig. 13).

Table 9

Hatching success of 10 clutches of leatherback turtle eggs reburied in a hatchery and of 24 natural clutches at Jalova nesting site, Costa Rica.

	Egg hatchery			Natural nests		
	Mean	SD	Range	Mean	SD	Range
Hatch (%)	42.2[a]	23.78	18-72	70.2[b]	11.50	51-98
Dead embryos (%)	10.8	6.94	3-21	10.1	7.95	1-26
Non-developed eggs (%)	47.0	29.82	14-80	19.7	8.42	0-32

[a]~34% (SD 25.95) of which were dead, deformed, or weak hatchlings.
[b]~8.6% (SD 10.63) of which were dead, deformed, or weak hatchlings.

Table 10

Measurements and weights of 120 leatherback turtle hatchlings. Computations based on 20 hatchlings collected at random from 6 nests at Jalova nesting site, Costa Rica. All measurements are SL mm; weight in grams.

Trait	Mean	SD	Range
Total carapace length	61.9	2.43	56-66
Standard carapace length	59.8	2.13	54-63
Carapace width	40.0	1.23	38-44
Plastron length	51.6	2.41	43-55
Head width	17.7	0.55	16-19
Weight	44.6	2.37	40-50

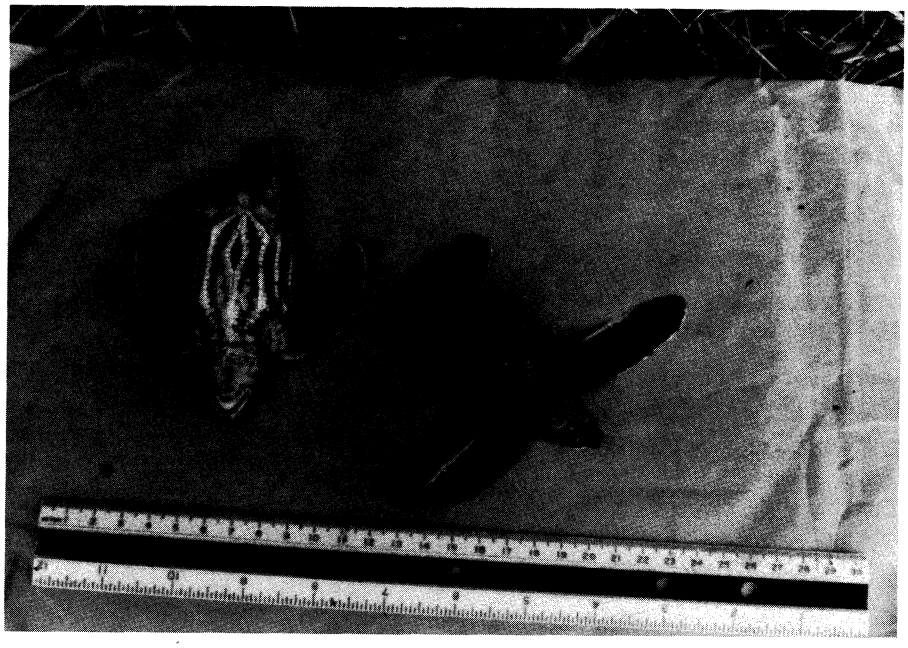

Figure 12

Typical leatherback turtle hatchlings showing relatively long front flippers characteristic of the species.

Table 11

Green turtles nesting on Jalova Beach, Costa Rica, with leatherback turtles, 1985.

Date	SL total carapace length (cm)	SL carapace width (cm)	No. eggs
9 April	102.9	74.9	121
16 April	102.1	78.7	139
3 May	102.9	76.2	113
25 May	106.7	74.9	—

Table 12

Number of clutches laid by green turtles on the Jalova leatherback turtle beach, Costa Rica, 1985. Only fresh (i.e., <24 h) nests and halfmoons were counted. Some nesting continues through September.

Date	No. nests	No. halfmoons
19 July	53	51
2 August	89	42
16 August	82	70
30 August	42	9

Figure 13

Aerial view of the nesting beach in the Parque Nacional Tortuguero, Costa Rica, on 15 May 1985 near the peak of the leatherback turtle season and at the beginning of the green turtle nesting season. The tracks from left to right are: a nesting green turtle, nesting leatherback, old leatherback crawl, and green turtle halfmoon.

There were two hawksbill turtle halfmoons on the study beach. One was made on 9 April and the other on 5 June. An immature loggerhead turtle (*Caretta caretta*) was caught in the Tortuguero River just north of the village of Tortuguero on 12 April. It had a straight-line total carapace length of 58 cm, a straight-line carapace width of 51.5 cm, and a weight of 32.7 kg.

Changes in track and nest appearance over time

At Jalova, weather and sea conditions affect the accurate aging of crawls and nests as the following seven summaries, taken from field notes, exemplify.

Nest 1—Laid in the middle of the berm on 11 April. Tracks to and from the nest clearly visible from the air (by an experienced observer under ideal flying conditions) through 27 April. Track unidentifiable to ground observer on 29 April. By 6 June there is 50/50 chance pit is recognizable from the air. On 2 August, shallow pit still identificable to ground observer (several *Ipomoea* vines growing in it).

Nest 2—Nested in shallow body pit without spreading much sand on front of berm on 11 April. Sharp, clear flipper marks in crawl still discernible from air through 14 April. Crawl unidentifiable by land or air on 23 April. Another turtle nested close on 28 April. Aerial observer would find it difficult to deduce if this was one or two successful nests. Ground observer would have same difficulty on 6 May.

Nest 3—Eggs laid just inside cocoplum hedge on 11 April. Much vegetation torn-up and scattered. Most of crawl still discernible on 13th, one-half crawl remains on 15th, and crawl invisible on 9 May. Pit recognizable by air or foot beyond 3 August because of ravaged appearance of hedge.

Nest 4—Eggs laid 11 April on berm crest. Turtle made a deep body pit and scattered much sand. Pit easily distinguishable from air or ground through 6 June because of furrow up the beach scarp. By 2 August the beach scarp was washed away and there was no evidence of nesting at all.

Nest 5—A half-moon, 40 m long, extending to the middle of the berm made on 11 April. Ascending and descending tracks visible to aerial observer through 15 April. Gradual weathering of crawl to complete disappearance on 9 May.

Nest 6—Nest made on 12 April on front of rookery. Turtle took long time to camouflage the nest site and "leaving-pit" was about 5 m from the clutch. Six hours later high waves obliterated the track and "aged" the "pit" several months.

Nest 7—On 8 May a large turtle nested under very windy conditions. About one hour after emerging, her tracks were almost invisible. The wind scattered the loose sand around the body pit and rounded off the sharp edges of the pit, giving the site an "aged" appearance in a couple of hours.

The fact that we observed only three false body pits would, however, facilitate the censusing of the nesting density here by counting body pits. Hopkins-Murphy and Murphy (1982) discuss the longevity of loggerhead tracks and body pits on the beaches of South Carolina, and they give techniques for conducting aerial surveys there.

Poaching

Based on discussions with park rangers, village guards, fishermen, merchants, and poachers, we estimate that the vast majority of eggs laid between Parismina and Pacuare during the peak of the nesting season in 1985 were taken by poachers. This degree of poaching may extend along the entire coast from Parismina to Puerto Limón and may be typical every year. Carr and Ogren (1959) described the high intensity of poaching near Matina in 1958. There was no evidence of adult turtles being taken in 1985. However, we did observe one dead leatherback stranded on the beach on 9 June, just north of Puerto Limón. We did not see or hear of any egg poaching at our Jalova study site nor on the southern half of the coast within the Parque Nacional Tortuguero.

Egg poachers (called hueveros) are men and young boys who usually work alone or in pairs. When an ovipositing turtle is encountered, they lay on their stomachs behind the turtle, partially fill in the egg chamber, and collect the eggs as they are dropped. Yolkless eggs are discarded. A metal rod, about 1 m long, is used to probe for eggs that have already been laid. They are adept at this. Sometimes a marker is placed on the nest and the clutch is probed after daybreak. Some poachers have horses to carry the sacks of eggs.

DISCUSSION

Recent studies in Panama have greatly extended our knowledge of the nesting range of leatherbacks in the western Caribbean (Meylan et al. 1985). Significant but discontinuous nesting is now known to occur from the northeast coast of Costa Rica south to the Golfo de Urabá region of Colombia. However, the relationships between these nesting aggregations are not known, and whether or not they represent a single widespread breeding assemblage or distinct demes remains to be determined. The leatherbacks nesting on the Pacific coast of Mexico represent a similar situation (Pritchard 1982).

Because some investigators have not stated precisely how carapace lengths were measured and because some measurements are not comparable, it is difficult to compare accurately the relationships between size of the average nester and average clutch size at different localities. The available data do suggest, however, that average nesting leatherbacks in the eastern Pacific Ocean are smaller and lay fewer eggs than their counterparts in the Caribbean (Hirth 1980; Brown and Brown 1982; Benabib-Nisenbaum 1983; Eckert and Eckert 1983; Tucker and Hall 1984). We recommend that researchers take several straight-line and overcurvature carapace measurements and provide measures of variance so that traits can accurately be compared. The available information also suggests that the eggs and hatchlings of leatherbacks on the eastern Pacific rookeries are smaller than most others.

In eastern Costa Rica the greatest threat to the survival of the leatherback turtle is excessive harvesting of its eggs. Some eggs are eaten locally and some are transported and sold in markets.

In Parismina, in 1985, the price of a dozen eggs was 25 colones (= $0.50 U.S.). The eggs are usually eaten raw, with a dash of tabasco sauce or lemon juice, by men in cantinas. The eggs are considered an aphrodisiac but they are also eaten for their nutritional contents by poorer families. Some villagers admitted that they preferred to eat the smaller green turtle eggs. Some leatherback eggs are taken by boat to Puerto Limón where the price of one fresh egg in 1985 was 10 colones (= $0.20 U.S.). The recently developed canal system on the Caribbean coast of Costa Rica makes transport of such commodities easy.

Leatherback populations have declined in India, Sri Lanka, and Thailand and the main reason appears to be the removal of eggs by people (Ross 1982). In 1978, Siow and Moll (1982) conducted a survey of West Malaysian beaches where eggs have been legally harvested for decades and found that leatherback egg production had decreased 66% from the 1956 level. There, however, adult mortality accounted for some of the decrease in egg production. In some places, a government-regulated egg harvest has been instituted or recommended to control poaching of sea turtle eggs (Schulz 1975; Mrosovsky 1983b).

The role of the Parque Nacional Tortuguero in the conservation of the leatherback turtle will become more important as human population, coastal development, and tourism increase on the Caribbean coast of Costa Rica. However, even within the Parque, knowledgeable guides will be needed to instruct and lead tourists on the nesting beach so that human behavior does not deter turtles from nesting. For example, we found that some leatherbacks at Jalova will return to the sea if they are subjected to lights or movements of people before reaching the stage of oviposition, and in some instances after laying commences. Poachers remain very quiet until a turtle starts to lay eggs. Lights also disorient hatchlings on their crawl to the sea. A sea turtle exhibit at the Jalova Ranger Station to acquaint campers (who must check-in at the station) with some of the sensitivities and natural history of leatherbacks and green turtles would be helpful in protecting these turtles.

ACKNOWLEDGMENTS

Herman Haug (Director) and Eduardo Chamorro (Associate Director) gave us permission to study the leatherbacks in the Parque Nacional Tortuguero and allowed us to use the ranger station at Jalova as our base of operations. To them we are very grateful. The following rangers at the Jalova Station were very helpful and cheeful companions: Melvin Betancourt Herrera, Jose Jesus Castro Costellano, Francisco Gutierrez Prenda, Pablo Martinez Castro, and Alberto MacFarlane. Ana Lorena Lopez Garcia cooked us some delicious food on an antique stove. Javier Mendez and Kirk Winemiller walked the beach several nights with us and helped tag turtles. Bob Carlson provided some basic amenities when we passed through "Casa Verde" in Tortuguero and he supplied the data on the loggerhead turtle. Durham Rankin recorded some of the green turtle nesting activity on the beach. The Caribbean Conservation Corporation loaned us a boat and outboard motor.

F. R. Fosberg and Lois Arnow aided in identification of plants; Ralph Hathaway identified the barnacle; and John Kircher helped with the statistical program. John Endler and Richard Van Norman provided constructive comments after reading a draft of the paper, and Maurine Vaughan cheerfully and efficiently typed several versions of the manuscript.

This research was financially supported by a grant to Hirth from Wildlife Conservation International of the New York Zoological Society.

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