Infertility, Embryonic Mortality and Nest-Site Selection In Leatherback and Green Sea Turtles in Suriname

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ABSTRACT

Nest-site selection and causes of non-viability in eggs of leatherbacks Dermochelys coriacea *and green turtles* Chelonia mydas *were investigated for two consecutive seasons on a beach used for nesting by both species in Suriname. Examination of nests and artificially incubated clutches after hatching showed that the main cause of an interspecies difference in hatching success was higher embryonic mortality in leatherbacks. Rupturing of eggs, used as an index of predation, was also greater in leatherback nests. Although infertility was slightly higher in leatherbacks, it was relatively low in both species.*

An interspecies difference in nest-site selection was found, with leatherbacks laying predominantly in open sand and green turtles in vegetated areas. Hatching success in the different areas was similar for green turtles, but only 12 % of green turtle nests were occasionally washed over by sea swell compared to 40 % of leatherback nests. Washover caused embryonic mortality in both species and is one of the causes of the increased embryonic mortality in leatherbacks. However, embryonic mortality was also higher in leatherback than in green turtle nests that were not washed over. Approximately half of the embryonic mortality occurred before days 22–24 of incubation in both species.

Artificial incubation produced hatching successes similar to those in nests laid above spring high tide level. Predation was eliminated in styrofoam boxes and reduced in reburied clutches. Increased embryonic mortality during late development was found in the boxes. The implications for conservation of sea turtles are discussed.

INTRODUCTION

The Suriname beaches provide a major nesting area for leatherback *Dermochelys coriacea* and green *Chelonia mydas* sea turtles (Hirth, 1971; Pritchard, 1971; Sternberg, 1981). Both species are considered endangered (Groombridge, 1982; Pritchard, 1982) or threatened (Mrosovsky, 1983a) and conservation efforts to increase the hatching success of nests have been implemented in Suriname since 1964 (Schulz, 1975). The hatching success of leatherback natural nests in Suriname (50%) is lower than that of green turtles (83%) nesting on the same beaches (Schulz, 1975) and lower than that of leatherbacks nesting in other countries: Hughes *et al.* (1967) reported hatching success of 76·1% in leatherback nests in Tongaland; Siow (in Hirth, 1980) reported 63% in Malaysia and Pritchard (1971) 70% in Mexico.

This paper aims to investigate four possible causes of the lower hatching success of Suriname leatherbacks.

(1) Interspecies differences in nest-site selection

A major difference in nest-site selection of green turtles and leatherbacks in Suriname is the latter's tendency to nest nearer to the sea. Leatherbacks nest below high tide level more often than do green turtles (Schulz, 1975; Dutton & Whitmore, 1983; Mrosovsky, 1983b). Nests laid below spring high tide level (SHTL) in Suriname are routinely relocated to a safer site to save them from complete destruction by high tides, and therefore are neither included in previous calculations of hatching success (Schulz, 1975) nor in this study.

Occasional inundation by extreme high tides or storms might cause mortality in nests laid just above SHTL (Bustard & Greenham, 1968; Schulz, 1975; Small, 1982). If more leatherback than green turtle nests are subjected to the waterlogging and high salinity of occasional surf washover, this may account for the interspecies differences in hatching success.

(2) Infertility, and (3) embryonic mortality

Infertility has not previously been quantified in Suriname for either species, though it has been suggested as a possible reason for the low hatch rate of leatherbacks (Pritchard, in Schulz, 1975).

Infertility has previously been judged by the absence of a visible embryo (Hughes *et al.*, 1967; Fowler, 1979). Here we further distinguish between infertility and embryonic mortality by the presence of a white circle on the outside of the eggshell. This circle indicates the adherence of the shell membranes to the shell that occurs during early incubation of fertile eggs (Blanck & Sawyer, 1981).

(4) Predation

The main predator of turtle eggs on the Suriname beaches, the ghost crab *Ocypode quadrata* (Schulz 1975), destroys about 12 % of green turtle eggs per nest (Hill & Green, 1971). No previous quantitative data are available on predation in Suriname leatherback nests by ghost crabs, or by any other predator.

The hatching success, predation, infertility and embryonic mortality were quantified for green turtle and leatherback clutches laid on the same beach, by excavating nest chambers after hatchling emergence. Beach plant zonation was identified and compared to nest distributions in these zones. Eggs incubated artificially were also compared with natural nests for embryonic mortality and infertility.

METHODS

Study area

The study was conducted during two consecutive nesting seasons in 1981 and 1982, on Krofajapasi beach on the Wia-Wia Nature Reserve in Suriname. The beach is a sparsely vegetated sand spit extending approximately 12 km along the coast and separated from the mainland by a brackish lagoon. The North Equatorial Current constantly erodes the beach at the east end and deposits sand at the west end, so that the beach moves westwards at a rate of approximately 2 km year^{-1} (Schulz, 1975; H. Reichart, pers. comm.).

Topographical zones and nest-site selection

The vegetation on Krofajapasi beach consisted of mainly beach creepers *Ipomea-pes-caprae* and *Canavalia maritima*. By using continuous

quadrat sampling along a series of transects three distinct vegetation zones were identified:

(1) A zone of open sand with between 0 and 5% vegetation cover, called the sand zone.
(2) An intermediate zone with 5–45% vegetation cover, the border zone.
(3) A zone with 45–100% vegetation cover, the vegetation zone.

The entire beach was patrolled in the morning at least once a week throughout the nesting season from March to August 1982 and from April to August 1981, and the number of nests laid by both species in each of the sand, border and vegetation zones were counted. Only freshly laid nests from the previous night were included.

Sampling

Eggs incubated in three different ways were studied: (1) those in natural nests, and (2) eggs relocated from below SHTL which were either reburied in a central sand plot, or (3) incubated above ground in styrofoam boxes.

Natural nests

Nests were located and labelled either as they were laid at night or with a probing stick the following morning, taking care not to pierce any eggs. From May to September 1982 notes were kept on those nests above SHTL that were observed to be washed over by extreme high tides. Washover ranged from wetting by tides during a single high tide or storm, to complete inundation for up to *ca.* 1 h during high tides for 1–3 consecutive days.

Nests were excavated and the remains examined about 2–5 days after the first hatchlings had emerged. In 1981, 41 green turtle and 9 leatherback nests were examined in this way, and in 1982, 39 green turtle and 28 leatherback nests. In 1982 an additional 7 leatherback nests were examined that were not marked at laying but located after the hatchlings had emerged, leaving a visible depression and some tracks in the sand. All these unmarked nests were from a section of beach which was not washed over.

Relocated clutches

Clutches were dug up the morning after they were laid and transferred to

either hand-dug holes in the sand, or styrofoam boxes. Prolonged exposure to the heat of direct sunlight was avoided.

Clutches reburied in the sand
Thirteen leatherback clutches laid in July 1982 were moved to a central area of beach free of vegetation and with few signs of ghost crab activity. Artificial nests 1 m apart were dug by hand and consisted of a 60 cm deep tunnel with a chamber to one side of the base. Fifty eggs from each clutch were reburied in each chamber as described in Balasingam (1967). The nests were excavated one day after emergence of the hatchlings.

Clutches incubated in styrofoam boxes
Eleven leatherback clutches (6 laid in May and 5 laid in June 1982) were taken to a central hatchery where they were incubated above ground in nineteen styrofoam boxes, using methods described in Schulz (1975). Each box contained 45 eggs from the same clutch. For green turtles, 8 clutches laid in March 1982 were relocated to styrofoam boxes, *ca.* 88 eggs per box. Eggs and eggshells were examined after hatching.

Hatching success

Hatching success was ascertained by counting hatched egg shells. When eggshells were fragmented, pieces were grouped together to represent one egg. Using this method to estimate clutch size for green turtles Fowler (1979) found errors of no more than $\pm$ 8 eggs. We checked this method against hatchling counts for those nests where data were available. For 32 of the total number of nests sampled for both species, only eggshell counts were available. For the remaining 92 nests sampled, hatchlings were also collected on emergence in a trap placed above each nest. These hatchling counts were identical to the eggshell counts in 16 of the nests. In 42 of the nests, the number of eggshells exceeded hatchlings by an average of 19. This was because hatchlings had either been eaten by vultures or had emerged outside the trap. Hatchling count was therefore ignored in these cases. In styrofoam boxes where hatchlings were confined and protected, and in reburied clutches where hatchling emergence was closely observed and protected from crabs or vultures, eggshell counts were all accurate. In 34 of the natural nests, hatchling count exceeded eggshell count by an average of 6, indicating an error in the latter. Hatchling count was used in preference to eggshell count in these cases.

Infertility

In 1981, unhatched eggs without visible embryos or blood formation were classed as infertile. In 1982 stricter criteria were adopted following those used by Blanck & Sawyer (1981) for loggerhead turtles, *Caretta caretta*: unhatched eggs were first examined for signs of a white circle or patch on the outside of the shell. This mark appears on the shell at the site of adherence between the vitelline membrane and the shell membrane within approximately 24 h of oviposition in fertile eggs and enlarges as incubation progresses, whereas infertile eggs generally remain a creamy beige colour (Blanck & Sawyer, 1981). Where no signs of embryonic development were found upon examination of the egg contents the presence of a clear white circle on the eggshell was taken as an indication of fertility.

Embryonic mortality

Fertile unhatched eggs were classed into three categories, based on the extent of embryonic development.

Early embryonic development
In 1981 this consisted of eggs showing signs of blood formation or a small embryo without any pigmentation (approx. < 10 mm long). In 1982 eggs showing very early signs of development such as a white circle on the outside of the shell indicating adherence of membranes were also included in this category.

Mid embryonic development
Eggs containing a small embryo with a pigmented eye, but unpigmented body measuring approximately 10–30 mm from head to tail.

Late embryonic development
Eggs containing a pigmented embryo (usually > 30 mm long). All embryos were examined for visible deformities.

Predation

The number of unhatched eggs that were ruptured or intact were recorded for each clutch. Possible causes of rupturing were noted and contents were examined for signs of embryonic development.

Unidentified eggs

Where egg contents had decomposed and eggshell coloration was obscured by fungus, moulds or mats of roots, the egg was classified as unidentifiable.

RESULTS

Nest-site selection and hatching success

The distribution of nests laid above SHTL by leatherbacks differed from that of green turtles (Table 1). Leatherbacks laid predominantly in the sand zone, and green turtles nested more frequently in the border zone than in the sand zone (Chi^2, $P < 0.01$, 2 df).

No difference in the mean hatching success for the two years was found in green turtle nests laid in the sand, border and vegetation zones of the beach using a Kruskal-Wallis one way analysis of variance (Table 2). The hatching success in nests which were washed over by extreme high tides was found to be significantly lower than in nests which were not washed over for both species, using a Mann Whitney two-tailed test ($P < 0.05$ for green turtles and $P < 0.005$ for leatherbacks, Table 2). Since a greater proportion of leatherback than green turtle nests were washed over

TABLE 1

Nest-site Selection of Leatherback and Green Turtles Laying Above Spring High Tide Mark (% of Observed Nests) and Percentage of Nests which were Subsequently Washed Over by Sea Swell (% of Marked Nests).

Zone	Leatherback nests (%)			Green nests (%)		
	1981 $n = 152$	*1982* $n = 134$	$\bar{x}$	*1981* $n = 654$	*1982* $n = 161$	$\bar{x}$
Sand	84·0	89·5	86·75	28·0	46·5	37·25
Border	16·0	10·5	13·25	53·5	46·5	50·0
Vegetation	0	0	0	18·5	7·0	12·75
% marked nests subsequently washed over (1982)	39·7 n = 78			11·9 n = 143		

TABLE 2

Hatching Success (Mean Percent Hatch ± Standard Error) of Green and Leatherback Turtle Clutches Incubated in Natural Nests, Styrofoam Boxes and Reburied Clutches on Krofajapasi Beach

	Leatherbacks			Greens		
	1981	*1982*	*Both years*	*1981*	*1982*	*Both years*
Nests in sand zone[a]	55·2 ± 11·6 n = 9	52·4 ± 5·7 n = 25[c]	53·2 ± 5·1 n = 34	80·9 ± 3·8 n = 10	80·2 ± 3·8 n = 17	80·5 ± 2·7 n = 27
Nests in border zone[a]	61·6 ± 10·4 n = 2	24·4 ± 6·2 n = 3[d]	39·3 ± 10·2 n = 5	76·1 ± 2·8 n = 18	81·5 ± 3·5 n = 15	78·5 ± 2·2 n = 33
Nests in vegetation zone	— n = 0	— n = 0	— n = 0	85·7 ± 3·4 n = 8	68·2 ± 3·3 n = 2	82·2 ± 3·6 n = 10
Nests in all 3 zones[b]	56·4 ± 9·5 n = 11	51·1 ± 4·5 n = 35[c]	52·4 ± 4·0 n = 46	80·5 ± 1·8 n = 41	80·3 ± 2·9 n = 39	80·4 ± 1·5 n = 80
Nests washed over by sea swell		32·7 ± 6·6 n = 12			66·8 ± 7·5 n = 5	
Nests NOT washed over by sea swell		61·9 ± 6·4 n = 16			82·3 ± 2·4 n = 29	
Styrofoam boxes		59·9 ± 7·0 n = 11			72·9 ± 3·4 n = 8	
Reburied clutches		68·7 ± 4·9 n = 13				

[a] Includes nests which were washed over.
[b] Includes some nests without zone data.
[c] Includes 7 nests not marked at laying.
[d] These nests were washed over.

(Chi^2 = 18·1, 1 df, $P < 0.001$, Table 1) it can be concluded that the interspecies difference in mean hatching success (Table 2) was related to the leatherback's more frequent selection of nest sites close to SHTL.

Infertility

Mean infertility was higher in leatherback clutches than in green turtle clutches in both years (Mann Whitney $P < 0.0001$, Tables 3 and 6). In 1982 the majority (61 %) of leatherback clutches had between 1 and 10 % infertility while the majority (74 %) of green turtle clutches had 1 % or less.

No seasonal variation was found in green turtle clutches, but in leatherbacks the mean infertility of clutches laid in 1982 in March–June (n = 40, $\bar{x} = 6.3$ %) was higher than in later clutches laid in July–August (n = 15, $\bar{x} = 2.4$ %, Mann Whitney $P < 0.05$).

For both green turtles and leatherbacks infertility rates recorded in the styrofoam boxes were similar to those in natural nests (Table 3). This suggests that infertility was not obscured by ruptured eggs in our analysis of the nests.

Our estimate of infertility was lower in 1982 than in 1981 because stricter criteria were used in 1982. The 1982 data may still be an overestimate of infertility. It is possible that the white circle on the outside of the eggshell was not clearly visible in some fertile eggs which ceased to

TABLE 3

Infertility (Mean Percent Infertile Eggs ± Standard Error) in Leatherback and Green Turtle Clutches in Natural Nests, Styrofoam Boxes and Reburied Clutches in 1982. (Index of infertility: no visible embryo + no white circle on eggshell.)

	Leatherbacks	Greens
Nests	6·1 ± 2·3 n = 30	1·6 ± 0·6 n = 35
Styrofoam boxes	7·0 ± 2·5 n = 11	0·9 ± 0·5 n = 8
Reburied clutches	2·5 ± 1·4 n = 13	
Total clutches	5·4 ± 0·2 n = 54	1·4 ± 0·5 n = 43

develop very early in incubation. In these instances very early embryonic mortality would have been mistakenly classed as infertility.

Embryonic mortality

Embryonic mortality in natural nests was higher in leatherbacks than in green turtles (Fig. 1). Even when we excluded from the sample those nests which had been washed over, leatherback embryonic mortality exceeded that of green turtles (Mann Whitney $P < 0.002$, Fig. 1).

Washover by extreme high tides greatly increased embryonic mortality in both leatherback and green turtle nests ($P < 0.002$, $P < 0.01$ respectively).

Embryonic mortality in styrofoam boxes was higher than in the nests. The increased mortality in the boxes was significant, ($P < 0.005$ green
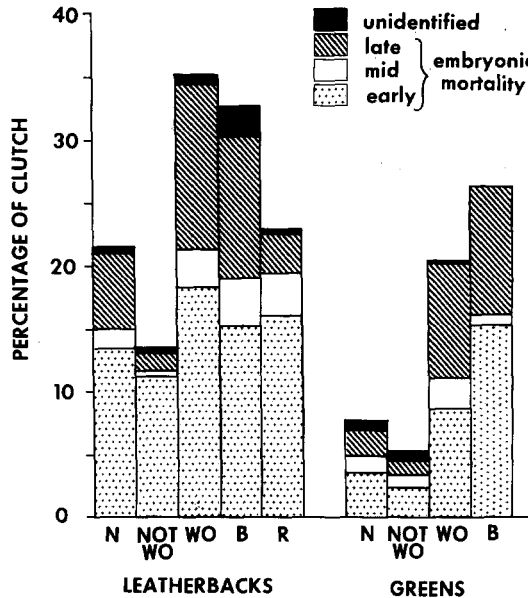

Fig. 1. Early, mid and late embryonic mortality (mean % of clutch) in intact eggs from leatherback and green turtle clutches laid on Krofajapasi 1982 and incubated: N, in nests sited above SHTL (n = 30 leatherback clutches, 35 greens); NOT WO, nests that were not washed over during incubation (n = 13 and 26, respectively); WO, nests which were occasionally washed over by sea swell (n = 10 and 5, respectively); B, styrofoam boxes (n = 11 and 8, respectively); R, clutches reburied into artificial nests (n = 13 leatherbacks). Unidentified eggs may have contained early or mid embryonic mortality or have been infertile.

TABLE 4

Embryonic Deformities in Leatherback and Green Turtles in Natural Nests, Styrofoam Boxes and Reburied Clutches, 1982.
(All deformities were observed in dead or unhatched embryos.)

Incubation treatment (number of clutches)	% clutches with deformed embryos	Deformities (total number observed)						Mean % deformed embryos in a clutch ($\bar{x} \pm SE$)
		Shortened Deformed/ jaws/ no eyes no egg tooth		Albino	Deformed pastron	Eggs with twins	Total	
Leatherbacks								
Nests (n = 30)	10·0	2[a]	0	0	18[a]	1	21	0·78 ± 0·6
Styrofoam boxes (n = 6) (laid in June)	50·0	5(1m)[b]	2[a]	3[a]	0	0	10	1·72 ± 0·9
Reburied clutches (n = 13)	38·5	2	4(1m)[b]	0	0	1(m)[b]	7	1·08 ± 0·4
Greens								
Nests (n = 35)	20·0	5[a]	1	3	1	2(m)[b]	12	0·29 ± 0·2
Styrofoam boxes (n = 8)	87·5	2	4	1	1	0	8	1·14 ± 0·2

[a] This number of embryos from one clutch
[b] m, mid-development embryo

TABLE 5

Predation (Mean Percent Ruptured Eggs ± Standard Error) of Green and Leatherback Turtle Clutches in Natural Nests, Styrofoam Boxes and Reburied Clutches on Krofajapasi Beach

	Leatherbacks			Greens		
	1981	*1982*	*Both years*	*1981*	*1982*	*Both years*
Nests in sand zone[a]	12·5 ± 5·3 n = 6	18·8 ± 3·8 n = 23[c]	17·5 ± 3·2 n = 29	9·4 ± 2·2 n = 10	9·9 ± 2·4 n = 17	9·7 ± 1·3 n = 27
Nests in border zone[a]	24·1 ± 0·3 n = 2	43·6 ± 0·4 n = 2[d]	33·9 ± 5·7 n = 4	16·5 ± 2·9 n = 12	13·1 ± 3·2 n = 15	14·6 ± 2·2 n = 27
Nests in vegetation zone	— n = 0	— n = 0	— n = 0	11·6 ± 3·3 n = 5	20·2 ± 3·0 n = 2	14·1 ± 2·8 n = 7
Nests in all three zones[b]	15·4 ± 4·3 n = 8	20·3 ± 3·1 n = 32[c]	19·3 ± 2·6 n = 40	12·0 ± 1·6 n = 31	11·1 ± 1·5 n = 39	11·5 ± 1·1 n = 70
Nests washed over by sea swell		27·2 ± 6·2 n = 10			10·9 ± 3·5 n = 5	
Nests NOT washed over		16·5 ± 4·6 n = 15			12·0 ± 1·9 n = 29	
Styrofoam boxes		0 n = 19			0 n = 8	
Reburied clutches		6·3 ± 2·8 n = 14				

[a] Includes nests which were washed over.
[b] Includes some nests without zone data.
[c] Includes 7 nests not marked at laying.
[d] These nests were washed over.

turtles, $P < 0.02$ leatherbacks) even when the late embryonic mortality in ruptured eggs from the nests was included in the sample.

A higher percentage of dead, deformed embryos was found in the styrofoam boxes than in natural nests of both species ($P < 0.0001$ for both species, Table 4). However, this accounted for only a small part of the total increase in embryonic mortality in the boxes.

Predation

We estimated predation from percentage of ruptured eggs in each clutch (Table 5).

Rupturing of eggs was mainly attributed to attacks by ghost crabs which burrowed into the nest and left characteristic snip marks in the eggshells. Eggs were also found with small holes (< 5 mm diameter). Ants, larvae of the fly *Megaselia scalaris* and larvae of the locust, family *Acrididae*, were often observed in these clutches. Dense mats of roots that had pierced several eggs were observed in at least 4 leatherback and 4 green turtle nests sited in the border and vegetation zones.

On average there were more ruptured eggs in leatherback than green turtle nests ($P < 0.001$, Table 5). 2·8 % of leatherback and 2·7 % of green turtle eggs in the nests were ruptured during late development. We were unable to distinguish eggs which had been ruptured during early and mid stages of development.

We can conclude that part of the interspecies difference in hatching success may be related to more rupturing of eggs in leatherback nests, but we cannot be certain that this was due to differential predation by ghost crabs.

Unidentified eggs

Approximately 90 % of unidentified eggs (Fig. 1) were ruptured eggs which had rotted. The remaining 10 % were rotten intact eggs which were covered by roots or fungi. Since the pigmented remains of late development embryos were detected in very rotten eggs both ruptured and intact, we suggest that the unidentified eggs were unlikely to include any late embryonic mortality, but may include some infertile eggs and early or mid embryonic mortality if these eggs had ceased to develop prior to rupturing.

DISCUSSION

The lower hatching success found in our leatherback sample (Table 2) is consistent with previous findings for Suriname. The two main causes of non-viability in leatherback and green turtle nests were embryonic mortality in intact eggs and predation (ruptured eggs) (Fig. 2).

Infertility

Infertility in both species accounted for a relatively small proportion of non-viability and, although a contributing factor, was not responsible for the large disparity in hatching success between the two species, as has been previously speculated (Pritchard in Schulz, 1975; Owens, 1982).

Infertility in the Suriname leatherbacks and green turtles was similar to that reported in other populations (Table 6). In Suriname, infertility in leatherback eggs was 4–5 % higher than in green turtle eggs. As the same
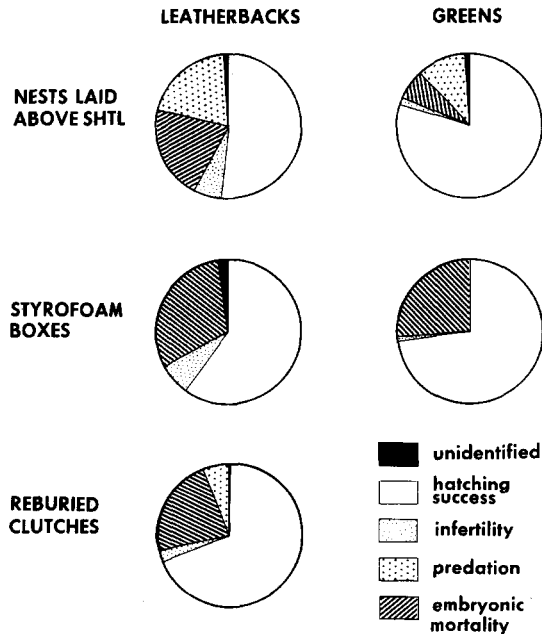

Fig. 2. Hatching success and fates of unhatched eggs (mean % of clutch) of leatherback and green turtle clutches incubated in nests laid above SHTL (n = 30 leatherbacks, 35 greens); styrofoam boxes (n = 11 and 8, respectively); and reburied clutches (n = 13 leatherbacks) on Krofajapasi 1982.

TABLE 6
Infertility in Green and Leatherback Turtles from Different Localities.

Index of infertility	Infertility % of clutch	Locality	Reference
Chelonia mydas			
No visible embryo	8·81	Tortuguero	Fowler (1979)
(Infertile eggs + undeveloped embryos)	(n = 134)	Costa Rica	
Unhatched eggs	< 8·0	Heron Island	Limpus *et al.* (1983)
(Infertile eggs + all embryonic mortality)	(n = 60)	Australia	
No visible embryo	6·3	Krofajapasi	1981 result, this paper
	(n = 43)	Suriname	
Dermochelys coriacea			
No visible embryo	13·4	Tongaland	Hughes *et al.* (1967)
	(n = 4)	South Africa	
No visible embryo	11·3	Krofajapasi	1981 result, this paper
	(n = 9)		

difference has been found between Tongaland leatherbacks and Costa Rican green turtles we might suggest that the difference is due to species specific characteristics rather than particular to the Suriname populations.

Embryonic mortality

The greater embryonic mortality in leatherback nests when compared with green turtle nests (Fig. 1) was partly due to nest-site selection by the leatherbacks which resulted in more of their nests being washed over by extreme high tides (Table 1). The most significant effects of washover by sea water on turtle nests would be the suffocation of the developing embryos and disruption of egg metabolism as a result of exposure to higher salinities. Dead loggerhead *Caretta caretta* and hawksbill *Eretmochelys imbricata* eggs and hatchlings have been reported from nests inundated by rainfall and sea swells, and the mortality attributed to lack of respiratory oxygen (Kraemer & Bell, 1980; Small, 1982). Increasing the time eggs are submerged decreases survivorship of eggs of the freshwater turtle *Trionyx muticus* (Plummer, 1976). Incubation in sand moistened by water with salinities equal to 75 % and 100 % sea water

prevented normal metabolism and caused subsequent failure in green turtle eggs (Bustard & Greenham, 1968).

Increased embryonic mortality occurred in all three stages of development in washover nests. Many of these nests were only washed over towards the end of incubation. This would explain the relatively high late embryonic mortality as compared with early or mid embryonic mortality in the washover nests. Kraemer & Bell (1980) found all embryonic stages of development in loggerheads were sensitive to inundation.

The interspecies difference in embryonic mortality in nests was not completely accounted for by the higher percentage of leatherback nests washed over, since even in nests which were not washed over, leatherback embryonic mortality was 8·8 % higher than in green turtle nests. Further investigation would be needed to understand the cause of the higher embryonic mortality in the leatherbacks.

Rupturing of eggs while locating and marking leatherback nests reduced hatching success of the whole clutch (Hill, 1971). Therefore we tried to avoid rupturing eggs while marking nests of both species and, for leatherbacks, included a sub-sample of unmarked nests as a control. No difference in embryo mortality was found between marked and unmarked nests from the same zone on the beach.

Our results for both species show that embryonic mortality occurred predominantly during early development, before pigmentation of the eye (Fig. 1), and supports the belief that the first three weeks of incubation is a critical period in embryonic sea turtle development (Blanck & Sawyer, 1981). In leatherbacks incubated at 30–31 °C pigmentation of the eye occurs between days 20–24 of incubation (Deraniyagala, 1939; Raynaud *et al.*, 1980). This stage would occur earlier in green turtles, since incubation durations are shorter than in leatherbacks (Schulz, 1975).

Movement of loggerhead and green turtle eggs even a few hours after laying has been shown to reduce hatching success (Limpus *et al.*, 1979; Parmenter, 1980). This mortality has been attributed to disruption of the extra-embryonic membranes which begin to develop soon after oviposition (Blanck & Sawyer, 1981).

We suggest that the development of these membranes begins earlier in green turtle than in leatherback eggs. While relocating 'doomed' eggs we observed that the white circle indicating membrane attachment had already appeared within 24 h of laying on the eggshells of many of the green turtle, but none of the leatherback eggs. In loggerheads, the shell

membrane begins to adhere to the shell during the first 24 h of incubation (Blanck & Sawyer, 1981). Some of the green turtle eggs may therefore have already reached the stage at which they are vulnerable to movement before they were relocated to the styrofoam boxes, while disruption of membranes was avoided in the slower developing leatherback eggs. This would explain why early embryonic mortality of green turtles was greater in the boxes than in the nests, but similar in boxes and nests in leatherbacks.

The greater amount of late embryonic mortality and deformed embryos which occur in the boxes compared to nests for both species suggests some adverse incubation condition in the styrofoam boxes (Table 4). Daily temperature fluctuations are greater in styrofoam boxes than at 60 cm depth in the sand (Dutton *et al.*, 1985). Although the effect of large daily temperature fluctuations on embryonic development is unknown, prolonged exposure of reptilian eggs to below optimum temperatures can result in developmental abnormality and embryonic mortality (Packard *et al.*, 1977). Also, deformities of head structure and scutellation similar to those we observed (Table 4) have been experimentally induced in freshwater turtles by dehydrating eggs during days 30–50 of incubation (Lynn & Ullrich, 1950).

Predation

In the nests, ruptured eggs accounted for as large a proportion of non-viable eggs as did embryonic mortality (Fig. 2). Our data on the percentage of ruptured green turtle eggs (Table 5) correspond to those of Hill & Green (1971), who found 11·8 %. However, our results showed that ghost crabs were not the only cause of this rupturing. Roots, ants and maggots were observed in nests of both species. Roots had pierced some eggs and grown in mats around others. Roots have also been observed to pierce loggerhead eggs (Caldwell, 1959). Ants ruptured green turtle eggs in Tortuguero (Fowler, 1979). Maggots have previously been observed in green turtle and leatherback nests (Fretey, 1976; Fowler, 1979). In reburied leatherback clutches, 6·3 % of eggs were ruptured even though no ghost crabs, roots, ants or maggots were observed in these clutches. We suggest that the activity of the emerging hatchlings may have ruptured non-viable eggs. In the styrofoam boxes, where hatchlings were in a less confined space with the unhatched eggs, no eggs were ruptured.

It has been suggested that ghost crabs would attack leatherback nests

less than green turtle nests because of the greater depth of leatherback nests (Pritchard, 1971; Schulz, 1975). Our results showed that leatherbacks may be subjected to greater predation than green turtles, perhaps because of their longer incubation period. However, it is also possible that in leatherback nests, especially nests that were washed over, the higher embryonic mortality in intact eggs leads to more rotten eggs than in green turtle nests, which then break or are ruptured by emerging hatchlings.

Nest-site selection and hatching success

While leatherbacks nested almost exclusively in the sand zone, green turtles nested most frequently in the border zone (Table 1). As the hatching success of green turtle nests was similar in the sand and border zones, it may be that the green turtles have responded to competition from leatherbacks for nest sites in the sand zone by selecting sites further back on the beach, in the border zone. Green turtle nests are, on average, shallower than leatherbacks' and are more likely to be destroyed by leatherbacks nesting on the same site than *vice versa*. Where the two species nest on Trengganu beach, Malaysia, a spatial separation of species between nesting beaches is found (Hendrickson & Balasingam 1966). The difficulties of orientation and entanglement in vegetation are worse for leatherback hatchlings than for the faster moving green turtles so that the risks of predation would be greater for leatherback hatchlings trying to reach the sea from nests sited in vegetated areas (Mrosovsky & Shettleworth, 1975; Mrosovsky, 1983*a*). Also, the larger size of the adult leatherbacks compared to the adult green turtles may make the length of the crawl on land more critical for the leatherbacks. Sand temperatures at nest depth in the border and sand zones on Krofajapasi beach were found to have very little difference and no striking differences in sex ratio were found in leatherback nests which were washed over by extreme high tides, or between green turtle nests laid in the sand and border zones (Mrosovsky *et al.*, 1984). Clearly there must be other factors which led the leatherbacks to nest near the high tide level, a strategy which resulted in a large proportion of nests being destroyed by high tides (Dutton & Whitmore, 1983) and lowered the hatching success of nests laid above SHTL: from our data we estimated that the mean hatching success of the leatherback nests above SHTL was reduced by 11·6% because a proportion of these nests (40%) were occasionally washed over by high

tides. Since green turtles generally nested further away from the SHTL, only 12 % of nests were washed over and the reduction in mean hatching success of green turtle nests laid above SHTL was only 1·8 %.

Implications for conservation

In the absence of any conservation measures the mean hatching success of all leatherback and green turtle clutches laid on Krofajapasi would clearly have been lower than that of our sample, as it would have included the *ca.* 40 % leatherback and 20 % of green turtle nests which are laid below SHTL and would be completely destroyed (Schulz, 1975; Dutton & Whitmore, 1983).

The eggs that were incubated in styrofoam boxes and reburied clutches were from 'doomed' nests (i.e., below SHTL), so using artificial incubation clearly improves the hatching success of these clutches. Since we found reduced hatching success in washed over nests laid above SHTL (Table 2), we might ask whether it would be useful to consider these nests as partially doomed clutches and to relocate them also. From our results we can speculate that hatching success could be improved by moving a leatherback clutch from a washed-over nest to either a styrofoam box or to an artificial nest, while moving a green turtle clutch would make little difference to the hatching success (Table 2). Given the possible ill-effects of relocation on embryonic development and sex ratio (Limpus, 1980; Stancyk *et al.*, 1980; Mrosovsky, 1983*b*; Dutton *et al.*, 1985) plus the difficulty of predicting at laying whether a nest will be washed over before emergence on the unstable beaches of the Guiana coast, very careful consideration should be given before relocating nests in possible danger of being washed over.

Our data show that although the hatching success of the styrofoam box incubated clutches is consistent with that reported in Schulz (1975), and similar to that of nests sited above SHTL (Fig. 2), this technique could still be improved. While predation was eliminated in the boxes, there was an increase in embryonic mortality in the boxes compared with nests. We suggest that investigation of dehydration, temperature fluctuation and removal of eggs from nests closer to the time of laying might reveal ways of reducing embryonic mortality in the boxes. It has recently been shown that movement-induced mortality in loggerheads can be reduced by cooling eggs to 10–14 °C (Miller & Limpus, 1983). Cooling eggs might

allow more time for workers to transport and relocate clutches before the critical period for movement-induced mortality is reached.

In the reburied leatherback clutches hatching success was higher than in nests or boxes, mainly because of less rupturing than in the nests and less late embryonic mortality than in the boxes. Schulz (1975) reports a much lower hatching success of only 12–18 % for reburied clutches. Low hatch rates can occur if eggs are exposed to the heat of the afternoon sun and not reburied during cooler times in the morning and evening (L. Auter, pers. comm.). The reduction of predation in our reburied clutches (Fig. 2) corresponds to the finding of Stancyk *et al.* (1980) that racoons *Procyon lotor* were unable to locate reburied loggerhead clutches until after hatchlings had emerged, and supports the theory that some predators can be deterred by careful relocation of clutches. This is probably because the cues normally used by such predators to locate eggs, such as disturbance in the sand surface and scent left by the female turtle around the nest, have been eliminated. Further study to identify the cues used by different predators could be of a great benefit to sea turtle conservation programmes.

ACKNOWLEDGEMENTS

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