

REPRODUCTIVE ECOLOGY OF THE GREEN TURTLE, *CHELONIA MYDAS*,  
AT ASCENSION ISLAND

BY

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The reproductive ecology and behavior of the green turtle, *Chelonia mydas*, were studied at Ascension Island, an isolated peak in the Central Equatorial Atlantic Ocean. Physical characteristics of the 32 cove-head beaches of the island were measured, and their influence on beach-choice by gravid females, on the behavior of females during nest construction, and on viability of the eggs and hatchlings was examined. Characteristics of the offshore approaches exert more influence on beach selection by nesting females than do features above the high tide line. Nesting is most dense on beaches with approaches unobstructed by submerged rocks. The turtles avoid beaches with foreshores cluttered by rocks, or where there is artificial lighting nearby.

Females have difficulty digging egg chambers in the coarse, dry Ascension sand. Typically, they emerge repeatedly, on two or three successive nights, and dig multiple trial nest holes before depositing eggs. Successive egg clutches are laid at intervals of about 14 days. Although females may lay as many as seven clutches in a season, the average number recorded was between two and three. The numbers of eggs

laid by individual females during a season decreases with successive nestings; the average clutch size measured was 120.9 eggs. Four years, followed by three years, are the predominant remigratory intervals recorded in Ascension turtles.

During renesting emergences, the females usually land at the same beach, often to within a few meters of their previous nesting place, or at an adjacent beach. Stronger site tenacity was evident in renestings separated by less than seven days (assumed to be repeated attempts to lay the same clutch of eggs), than in those separated by longer time intervals. These differences correlate with predictable patterns of behavior observed in females, the movements of which were visually tracked during their internesting intervals. After successful oviposition, tracked females travelled to a shallow area off the northwest coast of the island. The frustrated nesters remained in the vicinity of the nesting beach that they had just abandoned. Both rarely entered water more than 18 m deep.

Nesting occurs on all the beaches, although on some, hatching success approaches zero. No correlation between nesting density and percent hatchling emergence on the beaches was found. Reproductive success is influenced by characteristics of the beach sand, especially particle size distribution. Sand that is too fine, or too poorly sorted inhibits gas diffusion. Coarse sand causes cave-ins. A positive correlation between hatching success and depth of the nest was observed, probably because higher moisture levels occur at great depths. Elevated levels of salinity in the sand, most frequently seen in poorly sorted sand, may induce desiccation through osmotic stress. The positive correlation between hatching success and distance from the sea may be

related to inundation by rollers. There is a relative dearth of both terrestrial and offshore predation upon the eggs and hatchlings. Heavy mortality is caused by edaphic and density-dependent factors--beach erosion, inundation, and females digging up previously laid clutches.

An estimated 2,600 females nested at Ascension during the 1976-77 season, and 1,800 during the 1977-78 season.

## CHAPTER I INTRODUCTION

### Background for the Study

When Linnaeus introduced *Chelonia* to science in 1758, he based his description on a specimen from Ascension Island. It probably did not occur to Linnaeus that the population on which he based his new genus was, biologically, probably the most interesting in the world. Ascension lies in the Central Equatorial Atlantic, midway between the coasts of Africa and Brazil. It is a true oceanic island with no littoral platform to support the marine vegetation on which green turtles (*Chelonia mydas*) normally feed. The fact that turtles show up there each season poses a number of biological questions: Where do they come from? Why do they go out there to nest? By what route do they travel? By what mechanism is the open-sea travel guided? To what extent has speciation been induced by isolation and the selective demands of their long migration to a mid-ocean speck of an island?

It was to shed light on these questions that the tagging program of the University of Florida was extended in 1958 from Tortuguero, Costa Rica to Ascension. The origin of the seasonal nesting colony was soon shown to be the coast of Brazil. In the Spring of 1960, Harold Hirth spent nine weeks on the island. Of 206 turtles that he tagged, four were recovered in Brazil (Carr and Hirth, 1962). During the years between 1960 and 1976, a total of 2,236 turtles were tagged by other collaborators--students sent to the island for brief periods, local residents

who tagged during spare time--and by personnel of the Mariculture, Ltd. turtle farm who visited the island in 1972, 1973 and 1974 to collect turtle eggs for the farm. Morphometric data on the adult turtles and descriptions of the nesting behavior of the population are given by Carr and Hirth (1962) and Simon and Parkes (1976). Carr and Hirth (1962) and Carr (1975) reported on nesting periodicity. Stancyk and Ross (1978) correlated physical characteristics of each beach sand at Ascension with density of nesting observed on the beaches. Carr *et al.* (1974) described movements of a few turtles tracked in the interesting habitat.

As tag returns accumulated, Carr published several papers documenting the Brazil-Ascension migratory pattern, and suggested possible sensory mechanisms for the open sea navigation involved (Carr, 1962; 1964; 1967a; 1972; 1975 and Koch *et al.*, 1969) and theories to explain the evolution of such long distance migration (Carr and Coleman, 1974). These studies have shown the migration of the Ascension colony to be one of the most remarkable in the animal world. Although it is not as extensive as that of some birds (ex. the golden plover or arctic tern) there can be no doubt that it entails true open sea navigation; the turtles have access to no landmarks. Tracking experiments with Ascension females to test the sensory mechanisms involved in open sea navigation were discontinued because equipment failed (Carr, 1972).

I chose the Ascension Island colony as the subject of my research because of these unique attributes and the many unanswered biological questions that they pose. A major asset is that the colony is unexploited, having in 1926 become the first sea turtle population in

history to receive complete protection from human depredation on the nesting beach (Hart-Davis, 1972). Moreover, the island is the sole breeding place for the turtles nesting there, and is small enough that nesting activity can be effectively monitored.

The nesting ground at Ascension is discontinuous, being divided into a series of covehead beaches. These differ from each other in terms of their size and shape, offshore configuration and approach, and sand characteristics. A central effort of my research was to determine what effect these variables may have on nesting density and beach preferences, on reproductive homing, on the process of nest construction, and on hatching success. In every phase of the study, I looked for behavioral characteristics that could be used to distinguish the members of the Ascension Island population from those of the other major green turtle populations in the Atlantic Ocean system--the mainland Tortuguero, Costa Rica, and Surinam populations. I studied interesting movements of turtles in the sea by tracking (Carr *et al.*, 1974) and have compared the interesting behavior of the insular Ascension population with that recorded for the mainland Tortuguero colony.

My work has materially supplemented the meagre data previously gathered on within-season nesting periodicity and remigration intervals. The record of long distance migration has also been extended--although not beyond the borders of Brazil. The Ascension Island green turtle colony is now the best documented insular sea turtle population in the world. It is still by no means thoroughly understood, however, and continued research at Ascension would surely be very rewarding.

## The Island

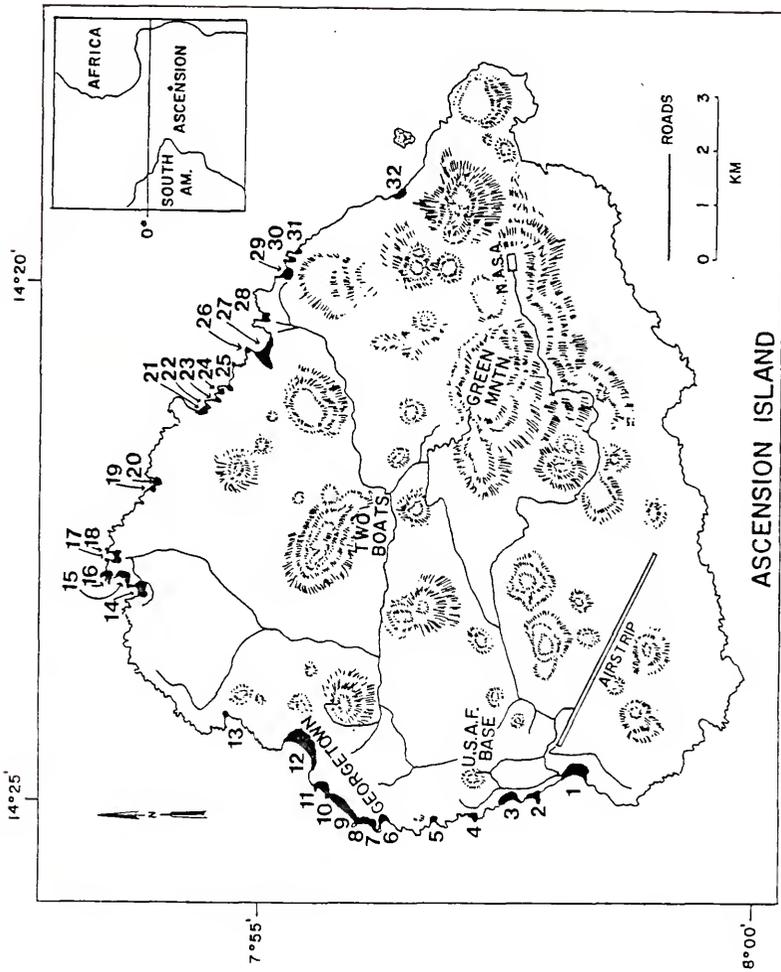
### Geology and Topography

Ascension Island is an isolated volcanic peak on the mid-Atlantic ridge in the South Atlantic Ocean ( $7^{\circ}57'S$ ,  $14^{\circ}22'W$ ). It is roughly triangular in shape, covering an area of about  $97 \text{ km}^2$ , and measuring approximately 14.0 km from east to west and 11.2 km from north to south (Fig. 1). The nearest points of land are the island of St. Helena, 1304 km to the south, Liberia on the African continent, 1536 km to the northeast, and the easternmost bulge of Brazil, 2200 km due west. The highest elevation, 860 m, is the Peak of Green Mountain; about two-thirds of the island is below 255 m (Duffey, 1964). The terrestrial ecology of the island is described in detail by Duffey (1964), and its geology by Darwin (1896) and Daly (1925). More than half of the island-- principally the coastal areas and the flat northern portion--is covered with flows of basaltic or trachdoleritic lava, forming an extremely rough terrain (Daly, 1925). There is no continental shelf, and the sea bottom drops away abruptly on all sides. The central equatorial current flows past the island from the east at speeds averaging from 0.4 to 0.9 knots (Anon., 1975).

Along the northern and western coastline are scattered 32 cover-head beaches, ranging in length from 10 m to 915 m and in area from  $110 \text{ m}^2$  to  $63,064 \text{ m}^2$ . The topography of the beaches is described in Chapter 4. On most of them the sand is a combination of crushed shells and algae nodules. On some, however, the sand is derived from pulverized lava and volcanic ash. Physical characteristics of the various beach sands are described in Chapter 5.

Figure 1. Nesting beaches of Ascension Island. The beach clusters referred to in the text are the following: South West Bay cluster (beaches 1-4); Long Beach cluster (beaches 6-12); English Bay cluster (beaches 14-18); North East Bay cluster (beaches 21-31). Turtles were not tagged on the following beaches: 5, 13, 19, 20 and 32. The numbers correspond with the following beaches:

1. South West Bay; 2. Turtleshell; 3. Clarkes; 4. Payne Point; 5. Mitchell's Cove; 6. Blowhole; 7. P.O.L. South; 8. P.O.L. North; 9. Deadman's; 10. Fort Hayes; 11. Georgetown; 12. Long Beach; 13. Comfortless Cove; 14. English Bay; 15. EB 1; 16. EB 2; 17. EB 3; 18. EB 4; 19. Ladies Loo West; 20. Ladies Loo; 21. Porpoise Pt 1; 22. Porpoise Pt 2; 23. Porpoise Pt 3; 24. Porpoise Pt 4; 25. Porpoise Pt 5; 26. Porpoise Pt 6; 27. North East Bay; 28. Beach Hut; 29. Hannay; 30. Pebbly West; 31. Pebbly East; 32. Spire.



### Seasonality of Climate and Turtle Nesting

Ascension lies in the zone of steady southeasterly trade winds. Wave action is exceptionally heavy. At times, huge swells called "rollers," believed to originate from distant storm centers, pound the shoreline, coming in predominantly from the northwest and less commonly from the southwest. The roller season coincides with the turtle nesting season (Chapter 5).

The average annual precipitation measured by the weather station near the airstrip (see map, Fig. 1) between 1962 and 1978 was 193.7 mm (S.D. = 129.6). Figure 2 shows the average monthly precipitation recorded there. For comparative purposes I mounted raingauges behind South West Bay beach, Long Beach, English Bay beach and North East Bay beach (Fig. 1). Rainfall measured by the weather station at an altitude of about 75 m, is similar to what I measured at nearby South West Bay beach and Long Beach, and to what the Cable and Wireless Office measured in Georgetown. Rainfall was somewhat higher at North East Bay beach, and lower at English Bay beach than at the other sites.

Predictable levels of precipitation occur during most of the year, but the months of December, March and April are subject to unusually heavy downpours. Five out of the 16 months of March for which precipitation was measured, and three of the 17 months of April, received more than 55 m of rainfall (ranging from 57.4 to 294.6 mm). During one of the Decembers, 176.5 mm of rain fell. In no other single month was there more than 55 mm (Fig. 2). The heavy rains are not predictable on an annual basis, but they seem to be so over longer periods of time. It is not surprising that the turtle nesting season (December through

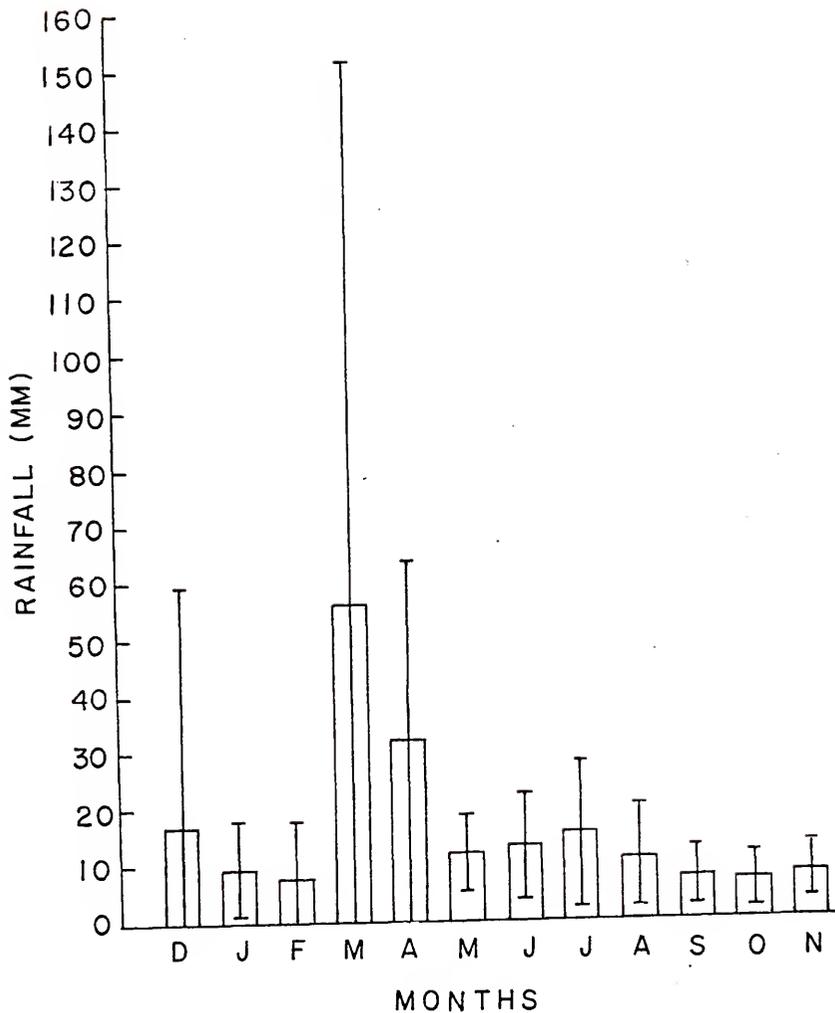


Figure 2. Average monthly precipitation between 1962 and 1978 recorded by the U.S. Base Weather Station near the airstrip.

May) coincides with the wettest time of the year (cf. Figs. 2 and 25), in view of the low levels of precipitation that occur at Ascension, and the difficulty turtles have in constructing their egg chambers in the dry sand (Chapter 2).

Relative humidity measured on the southwest side of the island at an elevation of about 50 m, ranges from 56-61% during the day, to the 70's and 80's at night (Duffey, 1964). Air temperatures remain relatively constant from month to month throughout the year. Figure 3 shows the average daily maximal and minimal temperatures per month recorded at Georgetown. The turtle nesting season, which peaks in February, March and April, coincides with the warmest part of the year (cf. Figs. 3 and 25).

#### Human Inhabitants

Ascension Island was not permanently inhabited until 1815, when the British erected a Garrison at what is presently Georgetown. In 1899 the first submarine cable was laid to Ascension, and from then until 1964 the island was administrated by the Eastern Telegraph Company (later Cable and Wireless Co.). During World War II the airstrip was built, and Ascension served as a stop-over point for aircraft flying between South America and Africa. About 4,000 U.S. servicemen were stationed on the island. In 1957 the island became part of the Air Force Eastern Test Range, and various satellite tracking installations were erected.

Today Ascension Island is part of the British colony of St. Helena, which includes the islands of Ascension, St. Helena and Tristan da Cunha. The human population consists of approximately 1,000 people--St.

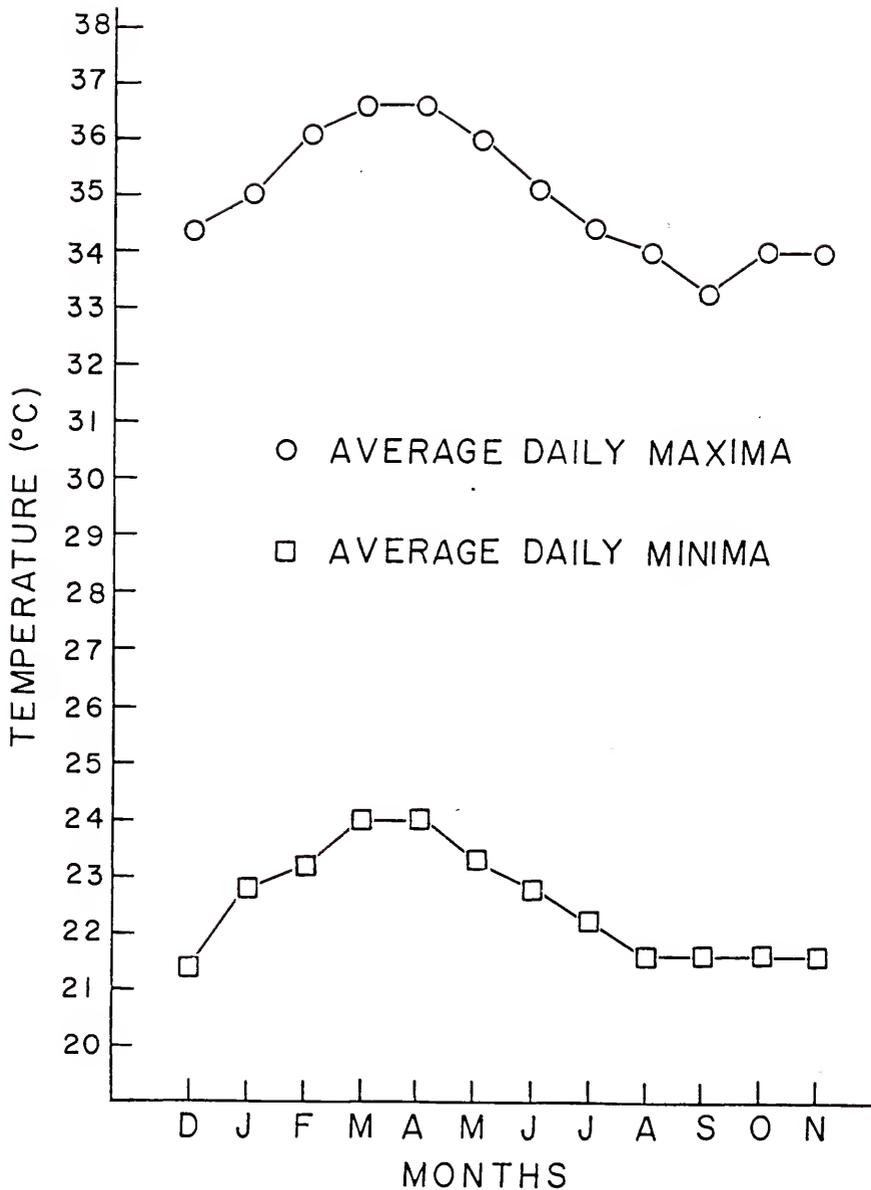


Figure 3. Monthly temperature maxima and minima for Georgetown, during the years 1899-1954 (Duffey, 1964).

Helenian, British, American and South American--who live in the British villages of Georgetown and Two Boats, on the U.S. Air Force Base, and near the top of Green Mountain (Fig. 1).

CHAPTER 2  
NESTING, RENESTING, MIGRATION AND REMIGRATION

Introduction

The nesting behavior of female sea turtles at the beach is well documented (see review by Ehrhart, in press). Behavioral studies of nesting turtles along with tagging studies have yielded information about nesting periodicity, reproductive homing, clutch size, long-distance migration and remigratory intervals.

Nesting Periodicity

During a nesting season, green turtles usually lay from one to seven clutches of eggs. There is strong evidence, however, that some females may lay only once or twice (Hendrickson, 1958; Bustard, 1972; Schulz, 1975; Carr *et al.*, 1978; Balazs, 1980). The average interval between nestings varies among green turtle populations. The following interesting intervals (in days) were recorded at other nesting grounds: Sarawak (Hendrickson, 1958)--10.5 (8-17); Heron Island, Australia (Bustard, 1972)--14.5 (9-21); French Frigate Shoals, Hawaii (Balazs, 1980)--13.2 (11-18); Surinam (Schulz, 1975)--13.4 (11-16); and at Tortuguero, Costa Rica (Carr *et al.*, 1978)--12.1 (9-15). Carr and Hirth (1962) estimated the interesting interval for Ascension turtles as 14.5 days, with a range of 10 to 17 days (N = 76). Simon and Parkes (1976) did not calculate the average number of days between nestings at Ascension, but observed that 41.0% of the turtles (N = 75)

nested after intervals of 11 to 12 days, and 25.3% after 13 to 14 days. I was the first investigator to tag intensively at Ascension throughout an entire nesting season, and my data thus make possible the first estimate of the number of clutches laid by individuals during a season, and also enhance knowledge of interesting periodicity.

#### Clutch Size

Average clutch size varies among populations of green turtles and has been found to be: 104.7 in Sarawak (Hendrickson, 1958); 110 at Tortuguero, Costa Rica (Carr and Hirth, 1962); 115.5 at Ascension (Carr and Hirth, 1962); 78.0 in the Galapagos Islands (Pritchard, 1971a); 110 at Heron Island, Australia (Bustard, 1972); 138 in Surinam (Schulz, 1975); and 104 in Hawaii (Balazs, 1980). Clutch size has been shown to be positively correlated with the size of the turtle both within and between populations (see review by Hirth, 1980). Carr and Hirth (1962) and Pritchard (1971a) observed that the sizes of successive clutches laid by individual females tend to decrease during the season. At Tortuguero, Bjorndal (1980) found evidence that the egg clutches of remigrant turtles are larger than those of untagged "recruit" turtles.

#### Reproductive Homing

Most populations of green turtles have been shown to have homing urge and ability (Hendrickson, 1958; Carr and Ogren, 1960; Carr and Hirth, 1962; Carr and Carr, 1972; Schulz, 1975; Carr, 1975; Balazs, 1980). At the linear coastline rookery at Tortuguero, Costa Rica, three levels of reproductive place-finding, perhaps involving three different sets of orienting cues, have been identified. These have been designated as

regional return, philopatry and site-fixity by Carr *et al.* (1978). The ability of Tortuguero turtles to find the coast of Costa Rica represents the regional return. Although most of the Atlantic coastline of Costa Rica is a nearly uniform stretch of beach, green turtles nest only on one 35 km segment of the shoreline, bounded at each end by a river mouth. Site discrimination at this level is termed philopatry. The phrase site-fixity refers to the tendency of individual turtles to make emergences modally no more than 0.2 km from previous emergence sites (Carr and Carr, 1972). The Tortuguero analysis is at least partly applicable to the levels of nest-site discrimination shown by members of other populations of turtles, even where the topography of the nesting grounds differ greatly from that at Tortuguero. At Ascension the nesting grounds consist of a series of covehead beaches that vary in size and shape, and are located at irregular intervals along the leeward side of the tiny island and are separated from each other by rugged rock promontories. Thus at Ascension the island-finding phase of the reproductive migration, which involves crossing more than 2,000 km of open sea that separate the island from the feeding grounds on the coast of Brazil can be considered the regional return (Carr, 1975). The term philopatry can logically be applied to the selection of a particular covehead beach, as previously documented by Carr and Hirth (1962) and by Carr (1967a; 1975), or of a cluster of beaches. Moving clockwise around the island from South West Bay, four clusters of beaches are easily identified. They are the South West Bay cluster, the Long Beach cluster, the English Bay cluster, and the North East Bay cluster (Fig. 1). Site-fixity in the restrictive sense would be the tendency to return to approximately the same place on one of the island beaches during successive nestings.

The present study does not address the problem of explaining the mechanisms by which the regional return to Ascension from the Brazilian coast is made. However, I have gathered considerable data on the two other levels of place-discrimination--the tendencies to return in successive nestings (a) to given beach or cluster of beaches, and (b) to a specific section of the beach selected. I have reassessed and tried to define the precision with which Ascension turtles are site-fixed in their three types of reneesting emergences, as follows: after roughly 14-day intervals; after abandoned nesting attempts; and after remigration intervals of two or more years. I have also attempted to examine possible sensory mechanisms by which such close range homing orientation is achieved.

#### Long Distance Migration

Meylan (in press b) summarizes available tag return data bearing on the migration of adult marine turtles. The migratory pattern of the Ascension turtles--along with those of the populations that nest at Tortuguero, Costa Rica (Carr *et al.*, 1978) and in Surinam (Schulz, 1975)--is more thoroughly documented than that of any other green turtle colony in the world.

#### Remigratory Intervals

The most commonly observed multi-annual reneesting intervals for *Chelonia* are two, three and four years. The predominant interval varies among populations: two years in Surinam (Schulz, 1975) and in Hawaii (Balazs, 1980); three years in the South China Sea (Harrison, 1956;

Hendrickson, 1958) and at Tortuguero, Costa Rica (Carr *et al.*, 1978); and four years in Australia (Bustard and Tognetti, 1969). Carr (1975) reported three years as the predominant remigratory interval in Ascension turtles. Returns that have accumulated since that 1975 report, however, suggest that longer intervals may be more typical.

### Methods

#### Beach Patrols and Tagging

The beaches were patrolled nightly and all turtles encountered were tagged on the trailing edge of the right front flipper, with cow ear tags of monel metal (Carr and Giovanolli, 1957). When previously tagged turtles were encountered, tag numbers were recorded. During the 1977-78 season all turtles were routinely checked for old tag scars. During the previous season, tag scars were only recorded when noticed by chance. In all cases, the point along the beach where the turtle was observed was recorded, and the stage of her nest digging process was recorded. An effort was made to estimate the number of trial pits that she had excavated when encountered.

Turtle taggers working on nesting beaches elsewhere (for example at Tortuguero, Costa Rica, and in Florida) routinely wait until a turtle has begun laying before they apply the tag. This is impractical at Ascension where successful nesting is delayed by the apparent difficulty turtles have excavating nests in the coarse dry island sand (see following section). Fortunately, Ascension turtles, which have evolved in an environment free of large terrestrial predators, tend not to be as skittish as their counterparts on the mainland. For this reason I was

able to devise a unique method of tagging. I found that if I approached a turtle quietly, from behind, while crawling on my belly, and avoided shining light in her face (I used a mouth-held penlight flashlight for illumination, and turned it on only to read the tag number) I could, in most cases, apply the tag during any stage of nest construction without frightening the turtle back into the sea.

Because of the long distances between them, I could not give equal attention to each of the 32 beaches, but instead tagged most intensively on beaches with the heaviest nesting activity. During the 1976-77 nesting season I tagged regularly on South West Bay beach, and visited the other beaches only sporadically. Twice during that season, for a period of about a week each time, I made all night patrols on South West Bay beach to monitor all the activities of the turtles which came up there. In order to recognize individuals from a distance without disturbing them, I painted a number on the rear of the carapace of each turtle with an orange cattle marking crayon, and applied the tag only after oviposition. Some turtles were also marked with crayon in the hope that divers might recognize them underwater. During the 1977-78 season I tagged regularly on South West Bay beach, Long Beach, North East Bay beach and Hannay beach, and patrolled most of the other beaches at less frequent intervals. Nesting activity on individual beaches was monitored over a period of several successive nights to determine the average number of times females emerge before laying eggs.

My aim to compare nesting behavior, in particular with respect to the number of trial nest holes dug, at different beaches with varying sand types, was hindered by the fact that nesting turtles making trial

holes frequently remain on the beach all night long. Accordingly, during my early morning track counts, I estimated the number of abandoned nest holes by counting pits associated with individual tracks. The high nesting density and looseness of the dry Ascension sand made it difficult to follow tracks above high tide line. For this reason, I was usually able to count pits only at the beginning or at the end of the season, when fewer turtles were nesting, or at other times when I encountered isolated tracks. By counting pits I was also able to identify emergences during which no digging occurred.

#### Long Distance Tag Recoveries, Remigration Intervals and Clutch Size

The present paper compiles all published and unpublished data on long distance tag recoveries and remigratory intervals accumulated by investigators at Ascension since 1960. The data on clutch size for the 1976-77 and 1977-78 nesting seasons were gathered during my hatching success study (see Chapter 5). Most of what we know about clutch sizes of Ascension turtles, however, was determined during previous seasons--especially during Harold Hirth's visit in 1960, and during the seasons that Mariculture Ltd. took eggs for the turtle farm on Grand Cayman.

### Results

#### Behavior on the Nesting Beach

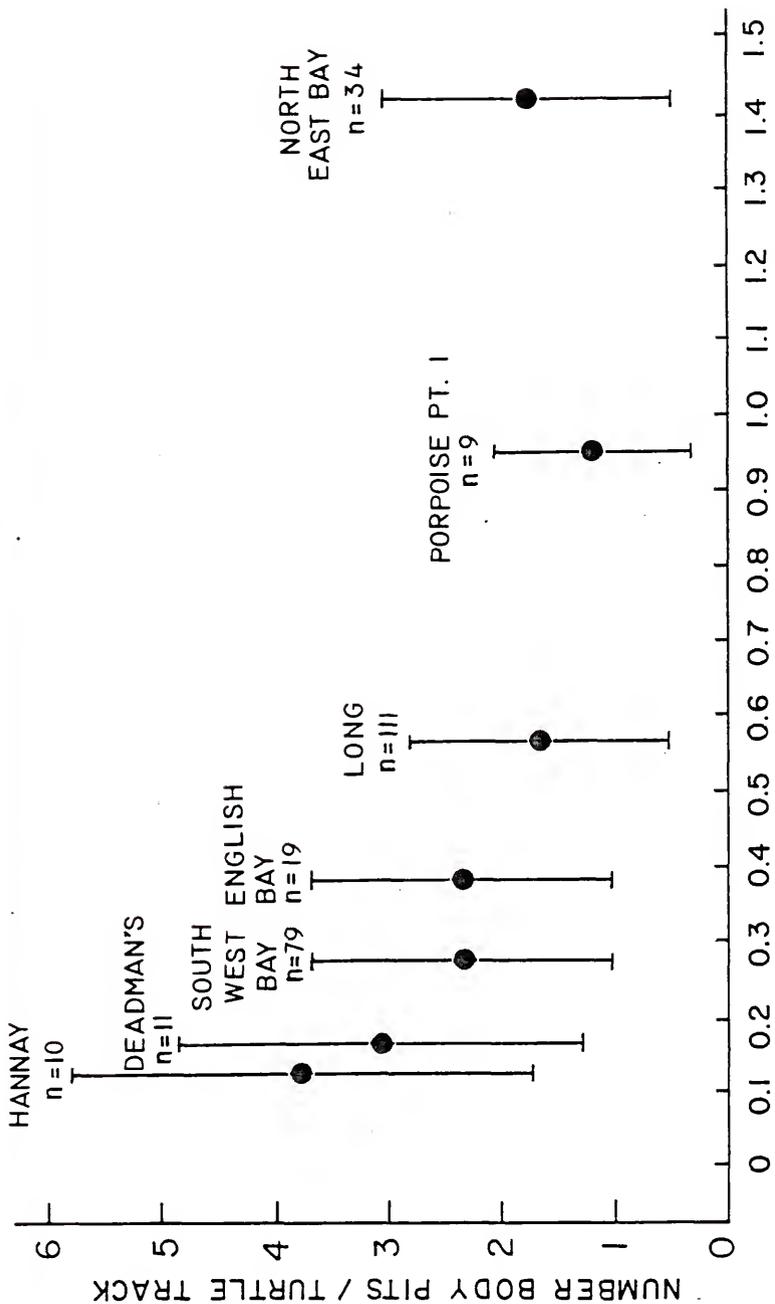
The nesting process of Ascension turtles follows the same general pattern as that at Tortuguero (Carr and Hirth, 1962) and at green turtle nesting grounds elsewhere. With the foreflippers the turtle digs a body pit, and when this has reached sufficient depth she delicately excavates

an urn-shaped egg chamber, using only the hind flippers. Into this the eggs are laid and then with the rear flippers, the nest is carefully filled with sand. When the egg chamber is covered, she uses her front flippers to throw large quantities of sand backwards over the nest site while slowly moving herself and her body pit forward.

The most noticeable differences between the behavior of Ascension females and those nesting at Tortuguero, are that at Ascension the body pits are deeper, and more than one body pit and egg chamber are usually dug before the eggs are laid (Fig. 4). The island turtles may remain on the beach from a few minutes to nine hours, and then return to the sea without laying eggs. As many as twelve body pits, with egg chambers in the bottom of most of them, may be dug. Presumably this activity is exhausting, and on occasion I have come upon females apparently asleep on the sand.

Figure 4 shows that the turtles dig more nest pits on beaches with coarse sand than on beaches with fine sand. The relationship between the average number of pits and the average mean sand particle diameter is also shown (see Chapter 5).

To estimate the numbers of emergences made prior to successful egg laying, over periods of three to seven successive nights I monitored nesting activity on South West Bay beach, where the sand texture is more or less typical for the island, and at Hannay beach which has very coarse grained sand. From each cohort of turtles observed nesting on a given night, I recorded the numbers that returned to the same beach on the second, third, fourth and fifth nights. I adjusted the latter figures upwards, using my percent tagging efficiency for those nights, computed



### MEAN PARTICLE DIAMETER ( $\phi$ )

Figure 4. Relationship between the average number of body pits per turtle emergence and the average mean particle size of the sand at each of the seven beaches. Brackets indicate range and standard deviation. The data were gathered during early morning beach surveys. Only beaches for which  $n \geq 9$  are included. Particle size is expressed in phi units, where  $\phi = -\log_2$  particle diameter (mm); thus, mean particle size decreases along the x-axis.

by comparing the number of turtles tagged each night with the morning track count (see Chapter 4). I found that about 79% of the turtles came back to nest at South West Bay beach a second night, 25% returned a third night, 12% a fourth night and 5% a fifth night. This gives an average of 2.2 emergences per turtle per nesting period. At Hannay beach, there was evidence that nearly 90% of the turtles returned the second night, 75% the third night, 50% the fourth night and almost 20% the fifth night--for an average of 3.3 emergences per turtle per nesting period.

There may be considerable error in these calculations. My tagging efficiency was rarely 100%, and site fixity is not perfect in Ascension turtles (see following section); turtles that may have returned to nest on any beaches other than South West Bay or Hannay would not have been recorded. Also, turtles that I recorded as first-night nesters might have emerged unrecorded on previous nights. In spite of these sources of possible error I feel that the figures are useful estimates.

#### Exploratory Crawls

Emergences during which no digging occurred were recorded most often early in the nesting season. They also occurred commonly after rollers had smoothed the beaches (see Chapters 1 and 5). During these emergences the turtles would crawl high up onto the beach platform. In the early part of the 1978 season, I counted 0.2 such emergences for each track associated with body pits.

#### Interesting Periodicity

Figure 5 shows time intervals between observed nesting emergences at Ascension. Of these returns, 67% were observed by me during the

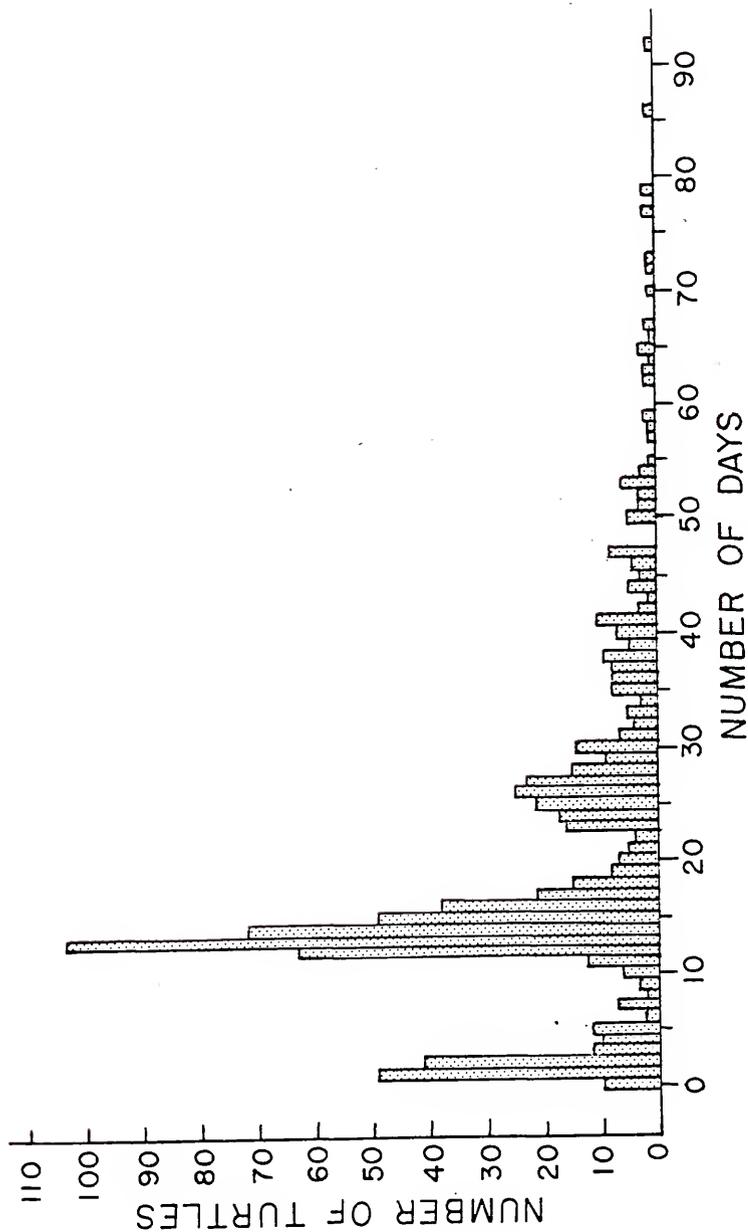


Figure 5. Time intervals separating consecutive emergences by Ascension turtles, recorded between 1960 and 1978. Emergences identified as unsuccessful nesting attempts are not incorporated into the figure.

nesting seasons of 1976-77 and 1977-78, and the remainder were recorded during 1960, 1964, 1966, 1967 and 1969.

#### Numbers of Nestings per Female

The numbers of days between the first and last observed emergences of turtles are shown in Figure 6. The longest interval is 92 days. Because my tagging efficiency never approached 100%, the intervals recorded are underestimates. The x-axis shows 14-day intervals corresponding to the interesting periodicity of the Ascension turtles. It is noteworthy that the bars on the histogram denoting the second through sixth nesting periods are nearly equal.

To improve the accuracy of the estimate of the number of nestings by each female, I restricted the sample to turtles tagged at South West Bay beach during the first 50 days of the 1977-78 season. My most consistent tagging effort was exerted there during the first four months of that season. Table 1 compares the total number of observed nestings by turtles first encountered in January ( $\bar{x} = 2.18$ ; 2.08 in 1977 and 2.27 in 1978) with those first seen in February ( $\bar{x} = 1.65$ ; 1.66 in 1977 and 1.63 in 1978). The average number of extrapolated nestings, derived by assuming that nesting occurs at regular 14-day intervals between the first and last observed nestings, was 2.82 (2.65 in 1977, and 3.0 in 1978).

A comparison of the total number of observed nestings by turtles bearing tags from previous seasons (remigrants) with the total number that arrived tagless (recruits) is shown in Figure 7. In both 1976-77 and 1977-78 more nestings were recorded for remigrants.

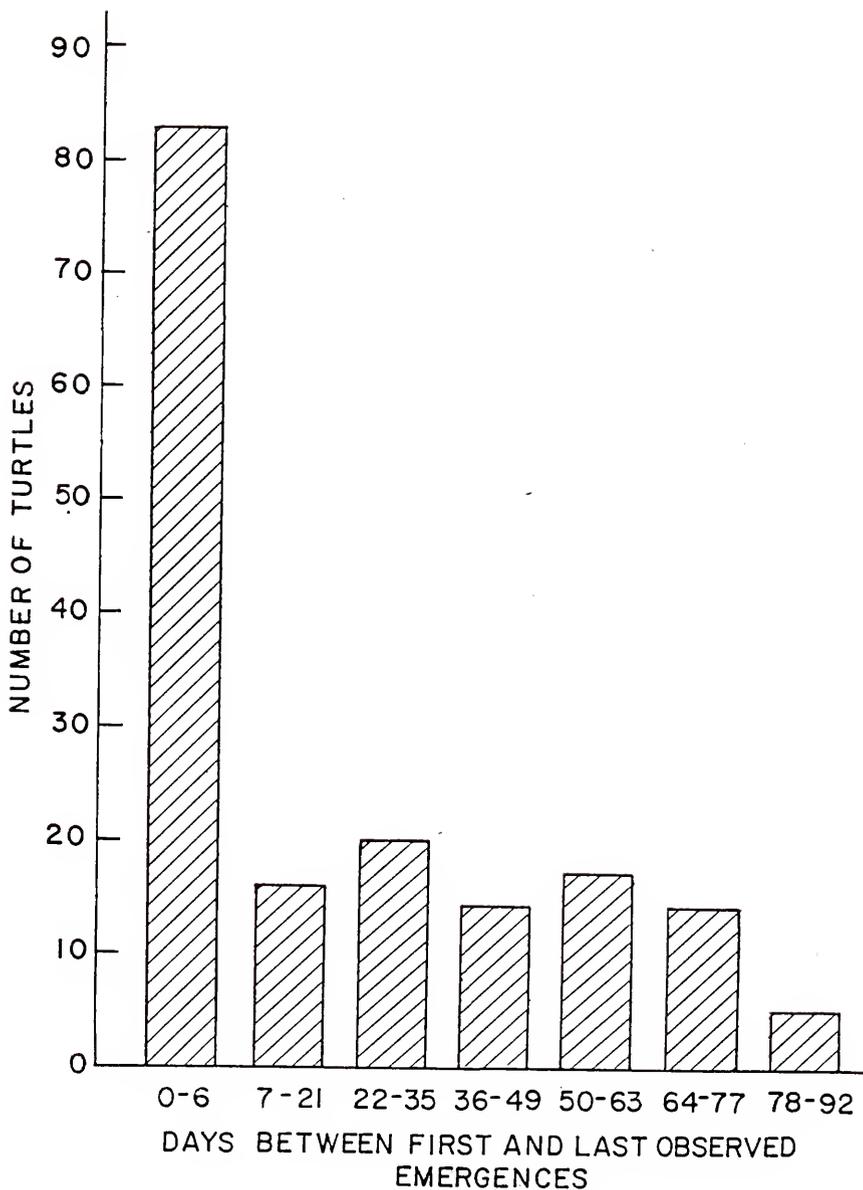


Figure 6. Number of days between the first and last observed emergences of turtles tagged during the first six weeks of the 1977-78 nesting season. The x-axis shows 14-day intervals corresponding to the interesting periodicity of Ascension turtles.

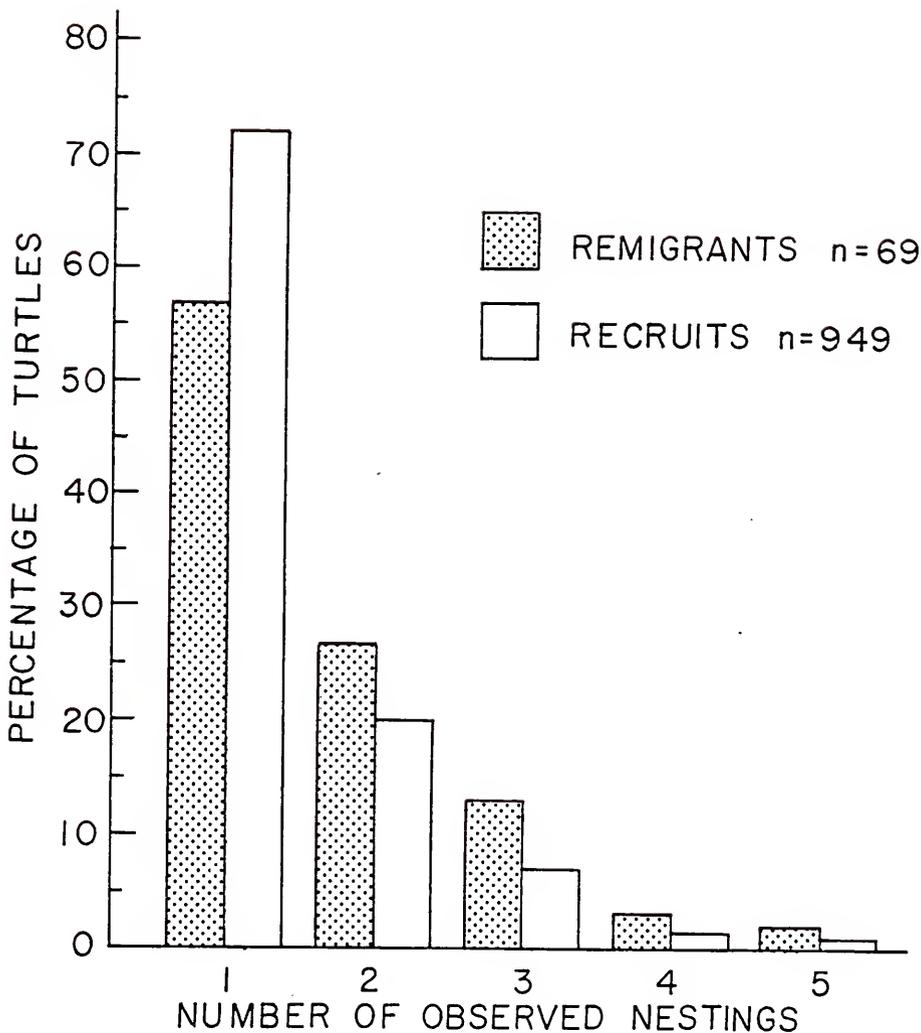


Figure 7. Comparison of numbers of observed nestings by remigrant turtles (those bearing tags or tag scars from a prior season) and the previously untagged recruit turtles. Data were collected during the 1976-77 and 1977-78 seasons.

Table 1. Comparison of total numbers of observed nestings by turtles first encountered at South West Bay beach in January and February of 1977 and 1978.

Number of Observed Nestings	Turtles First Encountered in January		Turtles First Encountered in February	
	n	%	n	%
1	23	29.5	36	57.1
2	29	37.2	15	23.8
3	17	21.8	10	15.9
4	7	9.0	2	3.2
5	2	2.6	0	0
Total	78	100	63	100
Mean Number of Observed Nestings	2.18		1.65	

### Reproductive Homing

During the 1976-77 and 1977-78 nesting seasons at Ascension I tagged 1,100 turtles. Of these, 371 were observed nesting at later dates, and were involved in a total of 973 multiple emergences, ranging from two to ten per turtle. Emergences separated by fewer than seven days were assumed to involve returns after aborted nesting attempts. Those occurring after intervals of seven or more days were considered to be successful nestings. In analyzing the data, I considered these two types of emergences separately. A third class of re-emergence is that made when a remigrant returns after an absence of two or more years. Although data are not extensive, reproductive homing is also evident in those returns. At Ascension Island the turtles show site fidelity for a cluster of adjacently located beaches; for a particular beach within a cluster; or to a less clearly demonstrable extent, for a restricted section of a beach.

### Site fidelity in remigratory returns

At other nesting grounds site fidelity in return nestings has been clearly proved for remigratory as well as re-nesting emergences. At Ascension, data on the former are meagre. For each remigrant turtle recorded at Ascension between 1960 and the present time, Table 2 indicates the cluster of beaches at which the last observed nesting during an earlier season occurred. The number of years separating emergences are also indicated. Many of the remigratory recoveries at Ascension have been made by part time collaborators, who did not usually keep precise locality records.

Table 2. Locations of the last observed emergences of the previous season, and the first observed emergences after remigration, for the 67 remigrant turtles. One turtle was recorded after two remigrations. The numbers indicate the years between each pair of sightings. The percentages indicate what portions of the total number of remigrants recovered at the beach clusters listed along the top row, were last seen at the beach clusters listed along the left hand side of the table.

		B E A C H C L U S T E R S		
		South West Bay	Long Beach	North East Bay
FROM	TO			
B E A C H C L U S T E R S	South West Bay	2,2,3,3,3,3, 3,3,3,3,3,3, 3,4,4,4,4,4, 4,4,5,6,6	2	4,9
		(79.3%)	(6.3%)	(8.7%)
	Long Beach	5	2,3,3,3,3, 4,4,4,4,5, 7	3,3
		(3.4%)	(68.8%)	(8.7%)
	North East Bay	4,4,4,5,7	3,3,6,6	3,3,3,3,3, 3,3,3,3,3, 4,4,4,4,4, 4,4,5,6
		(17.2%)	(25.0%)	(82.6%)
Total number of remigrants recorded per cluster		29	16	23

Site fidelity in within-season returns

Re-emergences occurring within a single nesting season are examined in terms of site fidelity for a beach cluster, for a given beach, and for points along a single beach.

Movements between clusters of beaches. In a preliminary assessment of site fixity, I assigned each re-emergence of each turtle a rating for "success" or "failure" depending on whether the turtle emerged at the same cluster of beaches on which it previously came out. Using a normal approximation of the binomial distribution (Mendenhall, 1975), I determined the 95% confidence interval for percentages of successful emergences, according to the formula:

$$\text{limit}_{0.95} = \hat{p} \pm 2\sqrt{\frac{\hat{p}(1 - \hat{p})}{S + F}}; \text{ where } S = \text{number of successes,}$$

$$F = \text{number of failures, and}$$

$$\hat{p} = \frac{S}{S + F}$$

The 95% confidence interval for the proportion of successive emergences on the same beach cluster separated by seven or more days was 84.1-90.6%. For those separated by less than seven days it was 91.0-97.9%. These data corroborate earlier evidence of philopatry at Ascension.

I then considered all the emergences of each turtle, and determined the beach cluster on which each nested most frequently. More than half of the emergences of each of 334 of the 371 turtles were confined to one cluster. Emergences of 37 turtles could not be categorized because only two were recorded, each at a different beach cluster.

I again assigned each re-emergence a score of "success" or "failure," this time depending on whether it occurred at the dominant beach

cluster. To see whether there were differences between the site-fidelity of turtles that nested predominantly at one cluster or another, I separated the turtles into four groups according to their dominant beach clusters, and used the same formula to determine the 95% confidence interval for the percentage of successful emergences within each group of turtles (Table 3). There was little difference between the performances of the four groups. However, emergences separated by less than seven days were more likely to occur within the same cluster of beaches, than those separated by greater time intervals.

Table 4 shows the location of each pair of consecutive emergences by individual turtles, separated by intervals of fewer than seven days; and Table 5 shows the same for those separated by intervals of seven or more days. In most cases, the two emergences occurred at the same cluster of beaches. In those instances in which a turtle strayed from the original cluster, she was more likely to re-emerge at a neighboring cluster than at one farther away. There was a greater tendency to re-appear at the same beach cluster when emergences were separated by less than seven days (Table 3).

Movements between beaches. For each turtle I determined which beach, if any, was used most often. Each emergence was given a score of "success" or "failure" depending on whether it occurred at the dominant beach. I then used the above formula to determine the 95% confidence interval for the percentage of "successful" emergences which occurred. When all the turtles are considered together, 77.4-85.1% of returns after seven or more days, and 81.6-91.7% of returns within a seven day interval, were successfully site-fixed.

Table 3. Accuracy with which turtles returned to the same cluster of beaches to nest. Each re-emergence was scored as a success or a failure, depending on whether it occurred at the same cluster of beaches as the majority of the returns of that turtle. Dashes indicate there were too few data in one or both categories to test significance.

Beach Cluster	Emergences Separated by < 7 Days			Emergences Separated by $\geq$ 7 Days		
	Number of Successes	Number of Failures	95% Confidence Limit for Proportion of Successes	Number of Successes	Number of Failures	95% Confidence Limit for Proportion of Successes
South West Bay	108	2	95.63 - 100.00%	248	10	93.72 - 98.53%
Long Beach	12	0	---	43	4	83.35 - 99.63%
English Bay	2	0	---	5	2	---
North East Bay	49	0	---	74	2	93.70 - 100.00%

Table 4. Locations of the members of each pair of successive nesting emergences separated by intervals of less than seven days. The beach clusters are listed in the order in which they occur at Ascension, moving clockwise along the shoreline, starting at South West Bay. English Bay cluster is not listed because no turtles were recovered there within a seven day interval. The percentages indicate what portions of the total number of turtles recovered at the beach clusters listed along the top row, were last seen at the beach clusters listed along the left-hand side of the table. The percentages across each row decrease as distance from the original cluster increases.

		B E A C H C L U S T E R S		
		South West Bay	Long Beach	North East Bay
FROM	TO			
	B E A C H C L U S T E R S	South West Bay	107/109 = 98.2%	6/21 = 28.6%
Long Beach		1/109 = 0.9%	14/21 = 66.6%	0/51 = 0%
North East Bay		1/109 = 0.9%	1/21 = 4.8%	50/51 = 98.0%
Total number of re-emergences recorded per cluster		109	21	51

Table 5. Locations of the members of each pair of successive nesting emergences separated by intervals of seven or more days. The beach clusters are listed in the same order in which they occur at the island, moving clockwise along the shoreline, starting at South West Bay. The percentages indicate what portions of the total number of turtles recovered at the beach clusters listed along the top row, were last seen at the beach clusters listed along the left-hand side of the table. The percentages in each row decrease as distance from the original cluster increases.

		B E A C H C L U S T E R S			
		South West Bay	Long Beach	English Bay	North East Bay
B E A C H C L U S T E R S	TO				
	FROM				
	South West Bay	240/254 = 94.5%	14/67 = 20.9%	1/13 = 7.7%	6/82 = 7.3%
	Long Beach	9/254 = 3.5%	42/67 = 62.7%	5/13 = 38.5%	2/82 = 2.4%
English Bay	0/254 = 0%	2/67 = 3.0%	4/13 = 30.8%	1/82 = 1.2%	
North East Bay	5/254 = 2.0%	9/67 = 13.4%	3/13 = 23.1%	73/82 = 89.0%	
Total number of re-emergences recorded per cluster		254	67	13	82

To determine whether site tenacity was greater at one beach than at another, I first grouped the turtles according to the cluster to which their dominant beach belonged. For each group the 95% confidence intervals were determined for the percentage of emergences which were site-fixed to the dominant beaches of the individual turtles (Table 6). A chi-square test was used to compare the proportions of successes and failures by each group of turtles--except the group nesting predominantly at the English Bay cluster for which too few data were gathered. No significant difference ( $p < 0.05$ ) was found between the performances of the three groups of turtles when emergences separated by intervals of fewer than seven days were considered. The chi-square test showed, however, that when renestings separated by seven or more days were considered, the turtles of the North East Bay cluster had significantly more failures than did those from the other clusters ( $p < 0.001$ ).

Site-fixity within the boundaries of a given beach. For each turtle recorded more than once on either South West Bay beach, Long Beach or North East Bay beach, an index of site-fixity was calculated. First, I determined the midpoint between the positions of her two most widely separated landings. Then I measured the distance of each emergence from that point, summed the distances, and divided by the total number of emergences made by that turtle. Figure 8 compares the indices calculated for turtles observed nesting at South West Bay beach, Long Beach, and North East Bay beach. It also compares site tenacity in emergences separated by less than seven days, with that of those separated by seven or more days. A z-test (Steel and Torrie, 1960) showed no significant difference between emergences occurring during the 1976-77 and 1977-78 seasons ( $p < 0.05$ ). At each beach a

Table 6. Accuracy with which turtles returned to the same beach to nest. Each re-emergence was scored as a success or a failure, depending on whether it occurred at the same beach as the majority of the returns of that turtle. Dashes indicate that there were too few data to test significance.

Beach Cluster	Emergences Separated by < 7 Days			Emergences Separated by $\geq$ 7 Days		
	Number of Successes	Number of Failures	95% Confidence Limit for Proportion of Successes	Number of Successes	Number of Failures	95% Confidence Limit for Proportion of Successes
South West Bay	104	7	89.08 - 98.31%	238	20	88.92 - 95.58%
Long Beach	11	1	75.71 - 100.00%	40	7	74.72 - 95.49%
English Bay	2	0	---	4	3	---
North East Bay	39	10	68.08 - 91.11%	58	20	64.47 - 84.25%

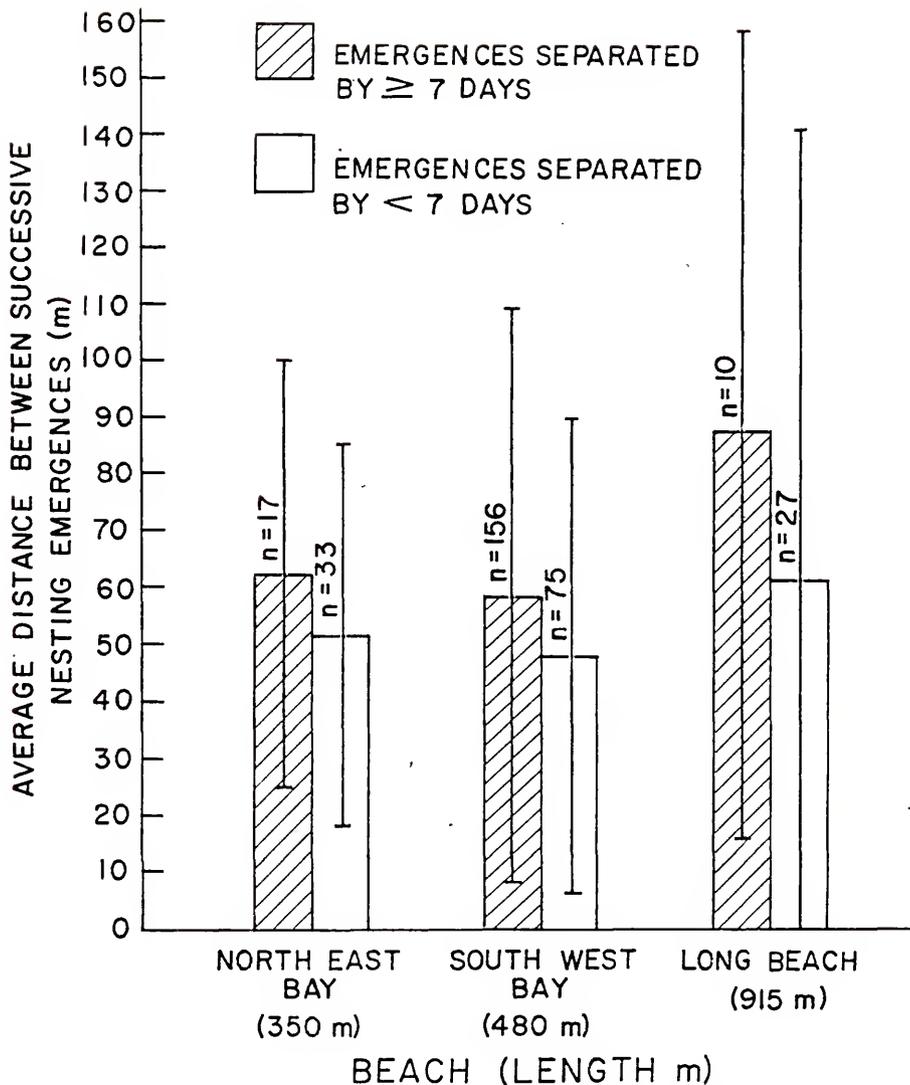


Figure 8. Means and standard deviations of the average distances between successive nesting emergences of turtles encountered on the three major beaches of Ascension Island. The distances were calculated by determining the average deviation of the emergences of each turtle from a point midway between her two most distant landings.

greater degree of site fixity tended to occur in consecutive emergences separated by less than seven days than in those separated by longer time intervals. However, a z-test showed these differences to be statistically significant only at South West Bay beach, where I had the largest sample size ( $N = 231$ ;  $z = -2.31$ ;  $p < 0.05$ ).

### Clutch Size

All available published and unpublished data on clutch size were compiled and the average clutch was found to be 120.9 eggs ( $N = 548$ ; S.D. = 26.8). The average varied from year to year: 115.5 eggs,  $N = 140$ , in 1960 (Carr and Hirth, 1962); 116.3 eggs,  $N = 169$ , in 1973, and 127.0 eggs,  $N = 163$ , in 1974 (Simon and Parkes, 1976); 128.9 eggs,  $N = 58$ , in 1977; and 125.6 eggs,  $N = 18$ , in 1978. A. Carr made available to me for recalculation, the raw data from Carr and Hirth (1962) in which clutch size in Ascension turtles is discussed. Egg counts of two clutches from each of 26 females were made by Hirth in 1960. The average egg number in the earlier of the two sets of clutches was 123 (S.D. = 15.7); in that of the later clutches it was 103 (S.D. = 20.91). A paired t-test showed a highly significant tendency for the second clutch to be smaller ( $t = 4.40$ ;  $N = 26$ ;  $p < 0.001$ ).

For an additional twelve individuals, Hirth counted the eggs of three or more clutches: for eight turtles, three counts were made; for two, four counts were made; and for two others five counts were made. In Figure 9 the number of eggs in each clutch is plotted against the number of days since the first observed laying by the corresponding female. A significant correlation was found ( $r = -0.55$ ;  $N = 42$ ;

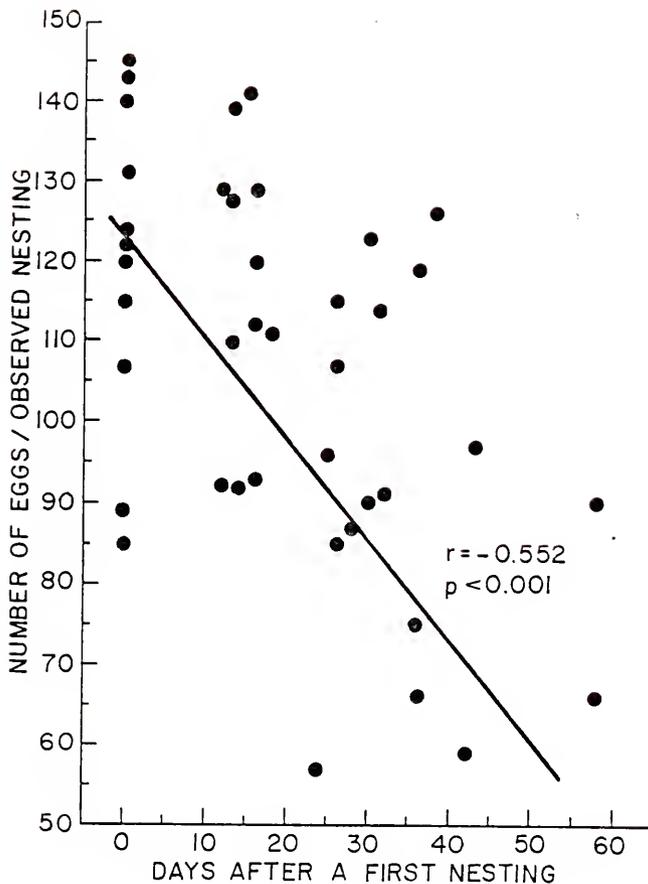


Figure 9. Relationship between the number of eggs laid by turtles at each recorded nesting, and the number of days elapsed since their first observed nesting during the season. Only cases involving three or more clutches with known egg count laid by the same turtle are considered.

$p < 0.001$ ) between number of eggs laid and the number of days elapsed since the first observed nesting.

I then compared all the egg complements counted by Hirth during the first part of the 1960 season (February 21-March 20), with those laid later in the season (March 21-April 30). A z-test (Steel and Torrie, 1960) showed no significant difference ( $z = -0.80$ ;  $df = 79$ ;  $p = 0.21$ ).

#### Remigration Intervals and Tag Loss

Since the initiation of the Ascension study in 1960, return migratory visits have been recorded for 68 tagged Ascension green turtles. Figure 10 shows the remigration intervals of these animals. Three and four year cycles predominate. During the 1977-78 season I systematically checked each turtle for old tag scars and found that 78% of the 42 remigrants had lost their tags.

#### Long Distance Recoveries

Since 1960, 3,384 turtles have been tagged at Ascension Island. At the present time, a total of 64 long distance tag recoveries have been made, all from the coast of Brazil (Fig. 11) where the turtles forage on benthic algae (Ferreira, 1968). The 39 Brazilian recoveries made prior to 1973 are summarized by Carr (1975). Elapsed time between the last recorded appearance of each turtle on the nesting beach and its capture on the coast of Brazil is shown in Fig. 12. Most recoveries occurred within three years after the turtle was tagged.

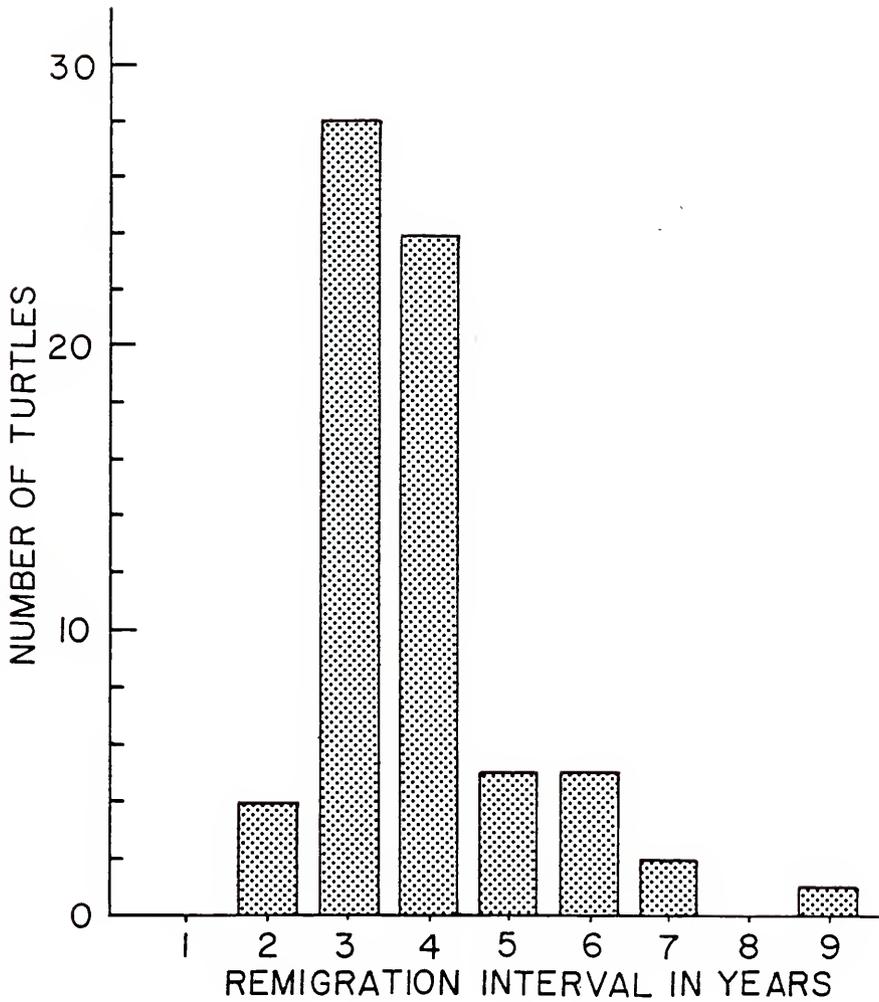


Figure 10. Remigration intervals between successive nesting seasons recorded for Ascension turtles.

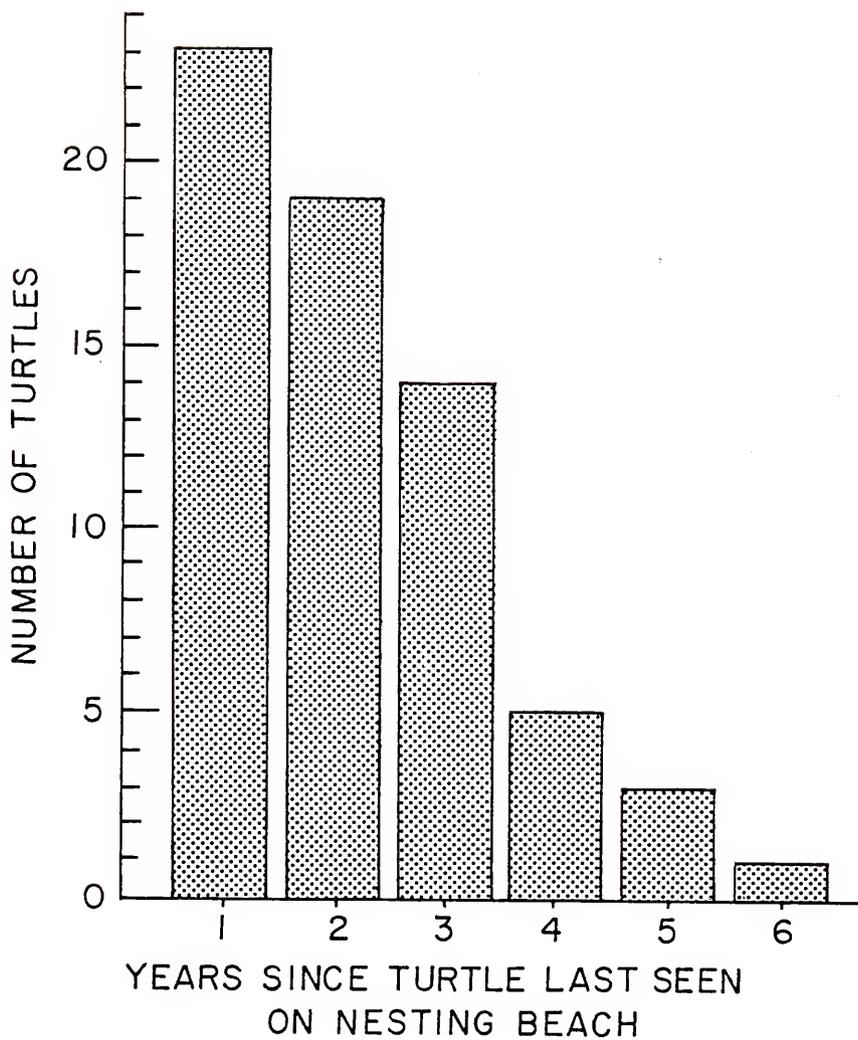


Figure 11. Number of years between last sightings of turtles on nesting beach and their capture off the coast of Brazil.



## Discussion

### Behavior on the Nesting Beach

All the Ascension beaches are characterized by coarse, dry and loose sand (Table 13). On the biogenic beaches in particular, the sand grains are rounded and slip over each other easily. It would obviously be difficult to form an egg chamber with nearly vertical walls in such a medium. Because the angle of repose increases with moisture content, and because water content increases with depth, it is reasonable that the Ascension turtles would have to dig deep body pits. In addition, the higher moisture levels found at greater depths would benefit the incubating eggs, which at Ascension are subject to dehydration (see Chapter 5). Possibly their need for deeper body pits, and their long distance migratory patterns explain why the turtles of the Ascension colony are larger than those of other green turtle populations (Hirth, 1971).

Because cave-ins are frequent, it is not surprising that turtles dig more trial nest holes in beach sands with larger mean particle diameters (Figure 4). An exception was found at North East Bay beach, where the turtles dig more nest pits in the relatively fine sand than would be expected based on the observations made at the other beaches (Figure 4). Perhaps this is explained by the low moisture content of the North East Bay sand (Table 13), a condition which would decrease the angle of repose. Bustard (1972) and Balazs (1980) believe that at Heron Island, Australia, and at French Frigate Shoals low moisture content of the sand impedes digging.

It was sometimes obvious why a turtle stopped digging a particular egg chamber; the walls had caved in. Often, however, the original egg chamber appeared well formed and some other quality of the sand or site must have prompted her to move out of the body pit and resume digging a few meters away. One wonders whether the viability of egg clutches laid in such egg chambers would have been significantly lowered. In Sarawak, Hendrickson (1958) found evidence that vibrations in the sand caused by the activities of females digging nearby cause turtles to abandon egg chambers. I doubt that this is a major cause of abandonment by Ascension turtles, because multiple nest holes are often dug by isolated individuals.

Many egg clutches at Ascension are destroyed by turtles digging new nests, as was observed at Heron Island, Australia, by Bustard and Tognetti (1969). Such density dependent mortality is greatest on the beaches with coarser grained sand, where more trial nest holes are constructed. In light of this, it seems curious that a strong site fixity (see following section) should be a characteristic of the Ascension population. If a turtle returns to lay eggs at the same point on the beach where she laid another clutch two weeks earlier, and if she makes numerous trial nest pits there, she obviously risks digging up her own eggs. It also seems curious that a turtle once having failed to construct a suitable nest on a given night, should return to the same point on the same beach the following night. There is also the question, what happens if a turtle is never able to construct a suitable egg chamber. Does she drop her eggs in the sea, as has been suggested by Simon and Parkes (1976) and Balazs (1980), or does urgency force her to accept a suboptimal egg chamber?

### Exploratory Crawls

"False crawl" is a somewhat misleading term that for want of a better phrase has been used to indicate an emergence during which eggs are not laid. Carr *et al.* (1978) discussed the various degrees of completion to which unrealized nestings advance at Tortuguero, and recognized three distinct types. These are, in order of their prevalence at Tortuguero, the smooth arcing "half-moon" and the angular "half-moon" (in which a turtle emerges to a point on or just beyond the wave-washed flat and then returns to the sea), and the abandoned prospecting venture far up into nesting sand. Only rarely do turtles at Tortuguero dig complete nest cavities and then abandon them, as occurs so commonly at Ascension. Somewhat more frequently, Tortuguero turtles crawl up onto the beach, make a few trial scrapes, and then return to the sea without nesting. This type of behavior is observed more commonly at Ascension, especially early in the season when one finds long, meandering tracks high on the beach platform, with little or no evidence of digging except for a shallow body pit. Possibly, these tracks only seem to be more numerous at that time because later on, as nesting activity increases, they are not as easily discernible among the tracks left by other turtles. However, I found other evidence that recent nesting activity on a beach may encourage turtles that arrive later to begin nest construction.

Virtually without exception, as soon as an Ascension turtle, crawling along a beach, begins to descend into a body pit left by another turtle, she will start throwing sand with her front flippers, and often will construct her own body pit and egg chamber there.

Similar behavior was also observed by Hendrickson (1958) in Sarawak. It seems possible that a turtle encountering only smooth sand, might actually be discouraged from nesting because she receives no possible stimulus to dig. In any case, after wandering about, such individuals return to the sea. This reluctance to dig in smooth sand might be adaptive. For example, the body pit left by a turtle after she covers her nest is usually located one or two meters from the site of the egg clutch. Turtles subsequently nesting in that pit will therefore not threaten the eggs (Hendrickson, 1958). A second advantage may be that segments of beach regularly subjected to smoothing by inundation would be avoided. For example, one night after a series of rollers had smoothed the surface of an Ascension beach, the only four turtles that emerged that night, wandered extensively over the beach without digging nest holes.

It is noteworthy that the two most frequent types of false crawl occurring at Tortuguero, the half-moons, are the least prevalent both at Ascension and in Hawaii (Balazs, 1980). The smooth arcing half-moon, which leaves a curving track on the wave-washed flat seems to be a pre-programmed sensory appraisal of the shore. In the other type, the angular half-moon, the two limbs of the track meet at an angle, suggesting that the turtle abandoned the emergence after receiving some discouraging stimuli. In neither case is there any evidence of digging, nor that the turtles aborted the emergence because they had been startled. Half-moons seem to be sensory, probably chemical or tactile, appraisals of the shore (Carr *et al.*, 1978).

During the 1979 season at Tortuguero, approximately 1.1 false crawls were recorded for each complete nesting emergence. At Ascension

they were less prevalent. Carr and Hirth (1962) discuss differences in the topography of the two nesting grounds which may account for the divergent behavior. In 1978, during the first month of the season at Ascension, when false crawls are most commonly observed and most easily discernible, I counted only 0.2 false crawls for each normal emergence. Because Ascension beaches are steeper than that at Tortuguero the wave-washed littoral zone is also less extensive. For this reason, most of the exploratory emergences that occur at Ascension may go unrecorded. On many occasions I saw turtles crawl distances of one or two meters onto the wave-washed sand, in the classic half-moon pattern, but their tracks were erased by waves within seconds. On nights when the moon was full, I could sometimes see turtles swimming back and forth in the surf just offshore. Presumably these were females investigating the shoreline prior to making a landfall (see Chapter 3).

#### Interesting Periodicity

Carr and Hirth (1962) based their estimate of the average inter-nesting interval at Ascension (14.5 days) on 76 observations. I calculated a new estimate using all the re-emergences observed at Ascension since 1960 (Fig. 5). The majority of the 405 turtles represented in the first peak in Figure 5 nested after intervals of 11 to 18 days (range 7-20). The predominant interval was 13, followed by 14 days, and the average interval was 13.9 days. Lesser peaks can be seen in Figure 5 at points roughly corresponding to multiples of 13-14 days. Nesting emergences observed within six or fewer days were assumed to be re-emergences after aborted nesting attempts.

Figure 5 shows the intervals between recorded nesting emergences, but in most cases egg laying was not observed. To test the accuracy of my estimate, I examined the 53 emergences recorded during the 1960, 1970, 1977 and 1978 seasons, in which eggs were known to have been deposited after intervals ranging from seven to 20 days. The average of these, 14.1 days (S.D. = 2.49), is very close to the 13.9-day estimate derived from Figure 5.

#### Number of Nestings per Female

In Surinam, where the tagging efficiency was reported to be nearly perfect, Schulz (1975) estimated that the average green turtle nested 2.9 times in a season. Turtles first observed nesting during the initial six weeks of the season laid more clutches--an average of 3.6 nests. At other localities where it has been impossible to monitor every emergence, the minimum average number of clutches laid per female must be estimated. At Tortuguero, Costa Rica, Carr *et al.* (1978) estimated that turtles first encountered early in the season lay an average of 2.8 clutches.

At Ascension, the longest interval between the first and last observed emergence by a turtle was 92 days, during which time she could have laid seven egg clutches at 14-day intervals. The nesting season lasts approximately six months, so individuals nesting early in the season are not the same that nest at the end of the season. I recorded an average minimum of 2.2 clutches per season laid by turtles first observed early in the season, and like Schulz (1975) and Carr *et al.* (1978), I found evidence that more clutches are laid by turtles first observed at the beginning of the season than later in the season (Table 1).

It is important to realize that my numbers are probably underestimates because my beach coverage was by necessity incomplete. My estimate increases to 2.8 clutches per season when the number of nestings is extrapolated on the assumption that nesting occurs at regular 14-day intervals. In the past, some investigators have assumed that to calculate the number of actual nestings, it was only necessary to divide the time between the first and last observed emergences, by the known interesting interval. In Surinam, Schulz (1975) recorded large numbers of turtles nesting at intervals corresponding to multiples of the average two-week interesting interval. One might assume such extended intervals to be artifacts of the sampling caused by unrecorded emergences. Schulz, however, believes that his monitoring of the nesting beach is so complete that the tagging crew could not have missed that many nestings. Thus, it would appear at least in Surinam, and maybe at other nesting grounds, that turtles occasionally refrain from nesting, but then re-emerge on schedule at a later date, thus preserving the expected two week cycles.

At Ascension, more nestings were recorded for the remigrants than for the recruits in both 1976-77 and 1977-78 (Fig. 7). Schulz (1975) in Surinam, and Carr *et al.* (1978) at Tortuguero, also found that remigrant turtles laid more clutches than did the new recruits. Both authors believe that many turtles probably nest only once during the season. My data also suggest this (Table 1; Fig. 6). Carr *et al.* (1978) postulated that recruits may begin their reproductive life with a migration that culminates in only a single nesting.

### Reproductive Homing

My data reveal three degrees of precision in re-emergent site tenacity, depending on the time interval separating the emergences. Emergences separated by fewer than seven days were probably separate attempts to lay the same clutch of eggs, and were characterized by a higher degree of site fidelity than were re-nestings separated by longer time intervals. This is in accord with results of my tracking experiments (see Chapter 3), which suggest that during the first 24 hours after abandoning a nesting attempt turtles generally remain within the vicinity of the nesting beach. Those which have deposited their eggs travel greater distances. Obviously the chances that a turtle will re-locate a site at which she previously emerged would be enhanced if she does not leave the area between emergences.

Site fidelity would logically be expected to decrease with an increase in time between emergences. A Pearson correlation demonstrated no significant correlation between the time interval and the amount of geographic displacement separating emergences that occurred during a season ( $N = 601$ ;  $r = -0.01$ ;  $p = 0.80$ ). This is consistent with the findings of Carr and Ogren (1960) at Tortuguero, that there was no decrease in site fixity over time.

Similarly, site fidelity would be expected to decline even more sharply in returns after migratory intervals of two or more years. At Tortuguero, however, Carr and Carr (1972) found a similarity between nest-site intervals for the 12-day re-nesting returns and those for the remigrant turtles. Because the tagging effort at Ascension has been so uneven from year to year (Table 7), it is difficult to compare the site tenacity in re-nestings within the same season, with that in

emergences separated by a remigration interval. Carr (1975) reported a tendency for the precision of remigratory homing to exceed that of the renesting returns, based on 24 remigrant returns at Ascension. Today, the data base has increased to 68 remigrants, and the data now suggest that there may be a very slight decline in site fidelity after a remigratory interval (cf. Tables 2 and 5).

For emergences separated by less than seven days, site tenacity at the level of the beach cluster is nearly perfect, but it is lessened when longer time intervals separate the emergences (Table 3). To determine whether the turtles showed stronger site fidelity to one beach cluster than to another, I grouped the turtles according to the beach cluster at which most of their nesting emergences occurred and compared the performance of turtles within the group. A Chi-square test showed there is no significant difference in site fidelity to a cluster between turtles from the three major beach clusters--South West Bay, Long Beach and North East Bay. Proportionally more individuals from the English Bay cluster may have strayed to other beach clusters, but the results are inconclusive (Table 3). It would be reasonable for English Bay cluster turtles to stray more frequently, because the distance between the extreme ends of the cluster is only 1,375 m; whereas the corresponding distances along the South West Bay, Long Beach and North East Bay clusters are respectively 2,690, 3,440 and 4,000 m. In cases in which a turtle did stray between beach clusters during successive emergences, she was more likely to go to an adjacent beach cluster than to one farther away (Tables 4 and 5).

Besides their tendency to return to a particular cluster, the Ascension turtles showed a tendency to nest repeatedly on the same

beach within a cluster, especially when the emergences were separated by less than seven days (Table 6). Although the North East Bay cluster turtles showed no greater tendency to emerge to nest on other beach clusters than did those from either South West Bay or Long Beach, they did show a greater tendency to re-emerge at different beaches within that cluster (Table 6). This was true regardless of the number of days between emergences. It seems likely that the number of beaches that make up a beach cluster, and the lengths of those beaches, may be influential in determining whether turtles return to the same beach. There are eleven separate beaches in the North East Bay cluster, compared to four in the South West Bay cluster and seven in the Long Beach cluster. The average length of the North East Bay beaches is only 83 m (median 45); for South West Bay beaches 248 m (median 175), and for the Long Beach beaches 349 m (median 290). These data support the assumption that it may be easier for a turtle to home in on a longer beach than on a shorter one.

The weaker site fidelity for a specific beach at the North East Bay cluster is consistent with the behavior of the individuals I tracked. Although the two turtles tracked after they abandoned a nesting attempt at North East Bay beach remained within the offshore waters of the North East Bay beach cluster, they travelled away from North East Bay beach itself, and even briefly crawled ashore on other beaches within the cluster (Fig. 18 and 19). In comparison, all six turtles tracked after abandoning a nesting attempt at South West Bay beach (Figs. 16, 20-24) remained in the vicinity of South West Bay beach itself, and any brief emergence occurred on that beach (Figs. 20-21).

To determine whether individual turtles homed to a location within the boundaries of a single beach, I used an index of site fixity. The

index is a measure of the average distance the collective emergences of each turtle strayed from a point midway between her two most extreme emergences. Using these calculations, Figure 8 compares the site fixity of turtles nesting at the three most important beaches--North East Bay beach, Long Beach and South West Bay beach. The lengths of the beaches are, respectively, 350 m, 915 m, and 480 m. A Kruskal Wallis test (Siegel, 1956) showed no significant difference ( $p < 0.05$ ) between the average distances calculated at the three beaches. There were only small increases in the mean distances. This suggests that at Ascension, once a turtle locates a beach at which she nested previously, her ability to locate a particular point within the boundaries of that beach is not substantially hindered by the overall length of the beach.

My site fixity index only considered those emergences occurring within the boundaries of a given beach. Because the nesting ground at Ascension is broken into short segments of beach, it would have been unrealistic to use an index that would incorporate all the emergences of a turtle. Re-emergences occurring on different beaches which were separated by expanses of rock shoreline would have distorted the values obtained.

#### Clutch Size

Hirth (1980) published a regression of the mean clutch sizes and mean carapace lengths in eleven green turtle populations. The average clutch size for Ascension turtles, 120.9 eggs ( $N = 548$ ), fits Hirth's regression line better than the figure of 115.5 eggs ( $N = 140$ ) (Hirth and Carr, 1962) which he plotted on his graph.

My analysis of the data gathered by Hirth during his visit to Ascension clearly demonstrates that within a season, the number of eggs laid by individual turtles tends to decrease with each successive nesting. However, the trend does not manifest itself as an overall decrease in the average size of clutches laid from month to month as the season progresses. Schulz (1975) also found no significant differences in clutch sizes for different periods during the nesting season. This is probably because new turtles arrive at the nesting beach throughout the season, and their larger clutches compensate for the smaller clutches being laid by turtles that had already deposited clutches earlier in the season. Hirth's 1960 data (Carr and Hirth, 1962) suggests that a turtle's first clutch of the season is large regardless of whether it is laid near the beginning or the end of the season.

#### Remigration Intervals

Three and four years are more clearly dominant among remigration intervals recorded for 68 Ascension turtles between 1960 and the present (Figure 10), than they were in 1973 when only 24 remigrants had been recorded (Carr, 1975). The tagging effort at Ascension has been erratic over the years (Table 7) so the question arises whether the observed proportions of their cycles reflect the true situation or are artifacts of the sampling procedure.

Tag loss also influences observed remigratory intervals. The percentage of remigrants in my study that had lost their tags, 78%, is high compared with the 23% recorded among 462 remigrants to Tortuguero in 1976 (A. Carr, pers. comm.); but is comparable to that observed in populations elsewhere (Mrosovsky, 1977). There was correlation between

Table 7. Number of turtles tagged at Ascension Island each year. Numbers indicate tagging effort and do not reflect levels of nesting activity.

<u>Year</u>	<u>Number of Turtles Tagged</u>
1960	203
1961	0
1962	0
1963	0
1964	159
1965	83
1966	122
1967	145
1968	0
1969	124
1970	100
1971	36
1972	96
1973	567
1974	511
1975	25
1976	65
1977	564
1978	457
1979	<u>127</u>
Total	3,384

numbers of turtles recaptured on the coast of Brazil and numbers of years elapsed since the last observed nesting emergence; all the recaptures of turtles in Brazil occurred within six years after tags had been applied (Fig. 11). This trend probably reflects rates of tag loss. Although mortality on the feeding grounds is an alternate explanation for this trend, the implications are the same with respect to remigration intervals. The largest number of observed remigrations would be expected after shorter time intervals, especially after one year. Remigrations by green turtles after intervals of one year, have rarely been observed anywhere, however, and no one-year remigrants were reported at Ascension (Fig. 10). Thus, we can assume that the observed numbers of turtles returning to nest after intervals of two and three years do not include one-year remigrants overlooked during a previous nesting season, and our observation that three-year remigrants outnumber two-year remigrants by at least seven to one (Fig. 10) is probably valid.

It is more difficult to estimate the relative number of four-year remigrants reliably. The figure for this group is probably inflated by the inclusion of two-year remigrants whose previous remigration had been overlooked. Since tag loss is greater after four years (Fig. 11), than after two, however, the data in Figure 10 probably under-represent the number of four-year remigrants. In actuality, the four-year remigratory interval is probably dominant, and the three-year interval the next in frequency. A long remigratory interval seems reasonable in view of the great distance between the nesting and feeding grounds of the population.

Only one Ascension turtle was recorded as a double remigrant. She nested after three years, and then again two years later. Such modulated periodicity has also been observed in other populations (Carr and Carr, 1970; Schulz, 1975; Carr *et al.*, 1980; Balazs, 1980).

#### Long Distance Recoveries

There is no correlation between the sites where turtles nested on Ascension and sections of the coast on which they were later intercepted off Brazil (Fig. 12). Neither was any correlation observed between places on the beach at Tortuguero where the turtles nested, and the areas where they were later recaptured (Carr *et al.*, 1978).

All the Brazilian recoveries of Ascension turtles were made within six years of the time they were tagged on the nesting beach (Fig. 11). The four Brazilian recaptures that occurred within 100 days of a last-observed nesting clustered around the easternmost part of the bulge of the continent (Fig. 12). However, there was no correlation between the point along the Brazilian coastline and the period of time that had elapsed since it was last sighted on the Ascension beaches (Carr, 1975). This suggests that the first landfall of a migrating turtle after it has left Ascension is the bulge of Brazil, and that the turtles subsequently disperse northward and southward along the coast.

The quickest recovery of an Ascension turtle was made 56 days after it had been observed nesting on March 22, 1977. This rapid crossing suggested oriented travel. To swim the straightline distance of 2,300 kms, this turtle travelled at an average rate of 41.1 km per day. During the months of February, March and April the mid-equatorial

current from Ascension to the bulge of Brazil flows at speeds of 0.4 to 0.9 knots (Anon., 1975). At this rate an object drifting with the current would take from 58 to 129 days to reach Brazil. Thus, the turtle which took a maximum of 56 days probably did not travel passively in the current. The speeds of travel of turtles captured shortly after leaving nesting beaches have been calculated for other populations (literature reviewed by Carr *et al.*, 1978). Schulz (1975) estimated an average travel speed of 35-80 km per day (or 0.8-1.8 knots) for green turtles travelling against the current from the Surinam nesting grounds to the feeding grounds of Brazil. Thus, it seems likely that turtles travelling from Ascension with the current can easily reach Brazil in less than 56 days.

## CHAPTER 3 INTERESTING BEHAVIOR

### Introduction

Female green turtles spend most of their adult lives at their foraging pastures, migrating to the nesting grounds once every two, three or four years, or even less frequently (Carr, 1975; Carr *et al.*, 1978). During a season, a female usually lays from one to seven egg clutches (literature reviewed by Ehrhart, in press). Since consecutive layings are separated by intervals of about two weeks, a turtle may spend as much as four months at the nesting grounds. Little is known about the behavioral ecology of female green turtles during that time. Most of what we know about interesting ecology has come from the visual tracking experiments performed by Carr at Tortuguero (Carr, 1967a; Carr, 1972) and at Ascension (Carr, 1972; Carr *et al.*, 1974) and by Meylan (1977; in press a) at Tortuguero. Julie Booth made underwater observations of interesting females in Australia (Booth and Peters, 1972).

Tracking does not only provide information about the occupancy of the interesting habitat. It can also be a tool with which to evaluate how a turtle reacts to features within its environment (topography of the seabed, water depth, etc.), which may in turn lend clues to the mechanism of sea turtle orientation. Sea turtles guide themselves through long distances between their foraging and breeding

grounds, and also show clear, though variably precise site fixity in returning to the nesting beach (Carr *et al.*, 1978). Ascension Island turtles usually return to the same beach for repeated nestings--often close to the same point on that beach (Chapter 2). The sensory cues that mediate this behavior are unknown. Investigation is handicapped by the fact that data can usually only be obtained when a tagged female is up on the nesting beach, or when her tag is returned after she has been killed at the feeding grounds. It has generally not been possible to plot the exact routes taken by turtles during their goal-finding activities.

The present study is an attempt to learn more about the behavioral ecology of female turtles during their interesting intervals. I visually tracked the movements of turtles after they left their nesting beaches, using polyurethane foam tow-floats. From shore, the positions of the floats at sea were recorded. Although the use of a tow-float has drawbacks, and may seem a primitive technique, it is virtually the only way to get detailed information about the movements of turtles at Ascension. Sophisticated radio tracking devices using either surface to surface, or satellite transmission would also require that the transmitter be elevated above the surface of the water. Ireland (1980) successfully followed the movements of turtles on their feeding grounds in Bermuda by using sonic devices attached directly to the carapace of the turtles. At Ascension, this method would not be practical because the turtles often swim close to shorelines pounded by heavy surf, and the air bubbles in the water would reflect sonic signals.

Most previous tracking experiments with interesting females have focused on movements after egg laying (Carr, 1967a; Carr, 1972; Carr *et al.*, 1974; Meylan, 1977 and in press a). In the present study, two types of experiments were conducted. Turtles were tracked after successful nesting, and also after abandoned nesting attempts. By tracking the turtles after abandoned nesting attempts, I was able to examine the manner in which the nesting beach was reapproached, and to gather clues that might suggest the sensory basis of nest site selection. The turtles in my experiments abandoned their nests because they were frightened by me. On Ascension, however, even when there is no human interference, nesting females often return to the sea without having laid their eggs. This is probably because of the difficulty they have excavating a satisfactory egg chamber in the coarse, dry sand (Chapter 2).

An understanding of sea turtle behavior after abandoned nesting attempts will help in evaluating what level of disturbance is tolerable on the nesting beach. Moreover, to help protect the breeding turtles from such hazards as incidental catch, trawling, and pollution, it is necessary to define the interesting habitat and to determine the activities of the animals within it.

#### Materials and Methods

The travel of each turtle in the interesting habitat was recorded by visually tracking a float attached by a 20 m nylon line to the posterior margin of the carapace. Simultaneous compass bearings were taken at intervals of about 3 minutes, from two points on the shore. The positions of the float were determined by triangulation.

The floats, made of polyurethane foam, were elliptical in shape, and measured 19 x 12 x 7 cm. A fiberglass fishing rod served as a mast, and to the middle of this a small piece of foam was affixed, to prevent the float from turning over. At the top of the mast there was a 3 volt light bulb, wired to a flasher circuit. As a back-up in case of light failure a chemical light stick (Cyalume) was taped to the mast. Ballast was provided by a lead disc and a 6 volt battery. The body of the float was waterproofed with bright yellow epoxy (Boat Renu) paint. Daytime visibility was enhanced by fluorescent orange spray paint and by yellow-and-orange flagging attached to the mast.

The float line was fastened to the shell of the turtle by 1.5 mm ungalvanized baling wire, threaded through a hole drilled in one of the posterior marginals. Because jagged rock reefs are abundant around the perimeter of the island, I chose wire weak enough to break and free the turtle if the float became snagged.

Compass bearings were taken with an Embeeco compass-bearing monocular from promontories around the island perimeter. For maximum accuracy, care was taken to choose positions from which lines of sight would be approximately perpendicular to each other. In a few cases, it was necessary to estimate the position of the turtle using only a single compass bearing. Turtles that had nested at the English Bay beaches were not tracked. The difficult terrain and lack of suitable promontories would have made continuous observation impossible. Likewise, at Long Beach an offshore fuel line that would have entangled the tracking device made tracking impracticable. Only turtles found nesting at either South West Bay or North East Bay beaches (Fig. 1) were tracked.

These included four that had successfully nested, and eight others that had not been permitted to lay eggs before returning to the sea. One individual of the latter group was continuously tracked from the time it abandoned its nest, until two days after it had successfully laid eggs the following night (a total of 60 hours).

### Results and Discussion

The movements of four turtles after successful nesting are shown in Figures 13-15, 17. Movements of eight turtles that were frightened at uncompleted nest holes before laying are shown in Figures 16, 18-24. Figures 16 and 17 are consecutive tracks of the same individual, the first after abandoning a nesting attempt, and the second after laying eggs the following night. All compass bearings taken on the tracking floats were incorporated into the tracks in Figures 13-24. Times are indicated at fifteen minute intervals, unless otherwise specified. Table 8 gives the nesting history of turtles before and after they were tracked.

The travel-patterns of turtles that had laid eggs were consistently different from those of turtles that had abandoned a nesting attempt. All the turtles that laid eggs initially moved into water 12-16 m deep, and then travelled parallel to the shoreline for distances of up to 7 km, and did not venture into water less than 8 m deep during the first 3 to 11 hours (Figs. 13-15, 17). The frustrated nesters on the other hand, stayed in the vicinity of the beach from which they had been frightened, and travelled back and forth in near-shore waters (Figs. 16, 18-24). Both patterns of behavior were clearly shown by the

Figure 13. Movements of turtle 15426 during the first 5.6 hours after laying eggs at North East Bay beach in the second egg chamber that she dug. Tracking ended when the float could no longer be seen in the glare of the morning sun. The mast from the float was later found washed up on the shore at the point indicated by the symbol ⊕. There were no other observed nesting emergences by 15426.

TURTLE NO. 15426

23 APRIL 1977

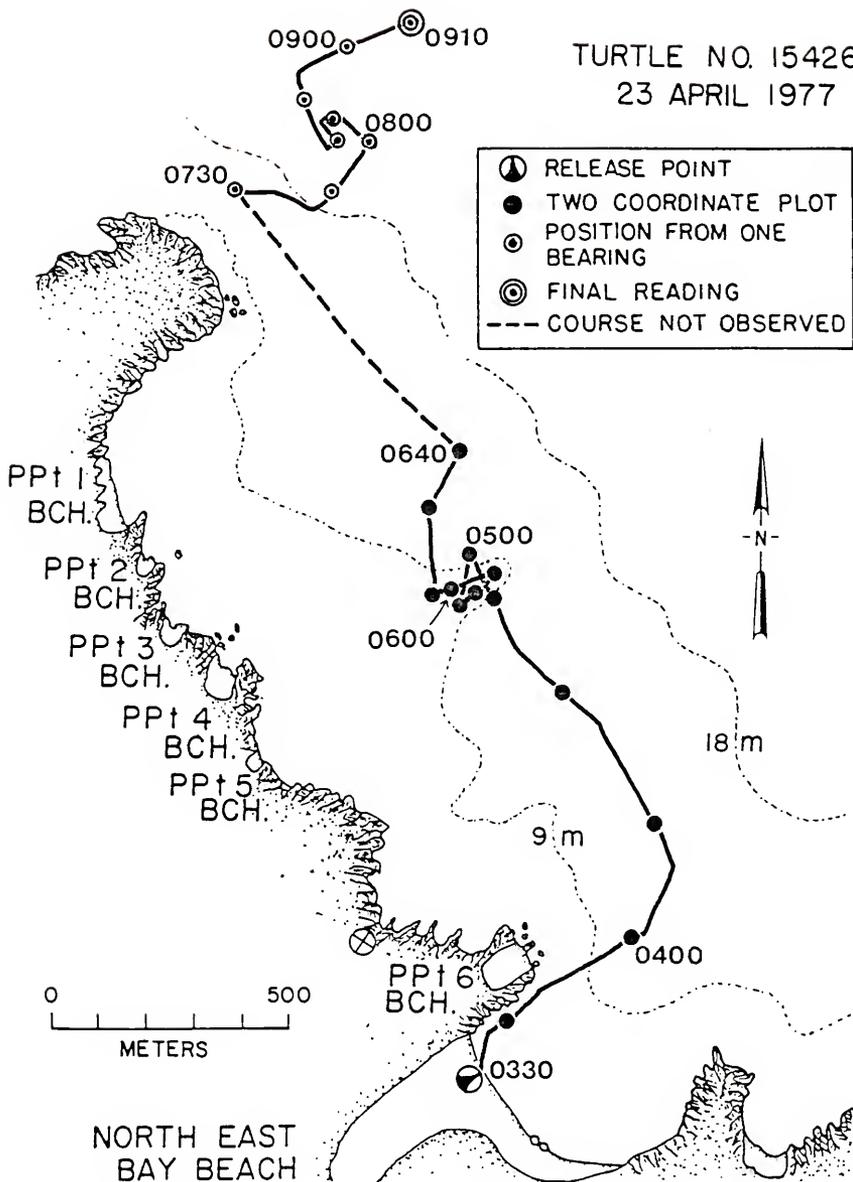


Figure 14. Movements of turtle 15139 during the first six hours after laying on South West Bay beach. Tracking terminated when she freed herself after the tow-line snagged on submerged rocks. All earlier and later nesting emergences recorded during 1977 occurred at South West Bay beach (Table 8).



Figure 15. Movements of turtle 15153 during the first 38 hours after laying eggs at South West Bay beach. Tracking terminated when the turtle was cut free after the float tangled on the fuel line near Long Beach. There were no other recorded nesting emergences.

TURTLE NO. 15153  
25-26 FEB. 1977

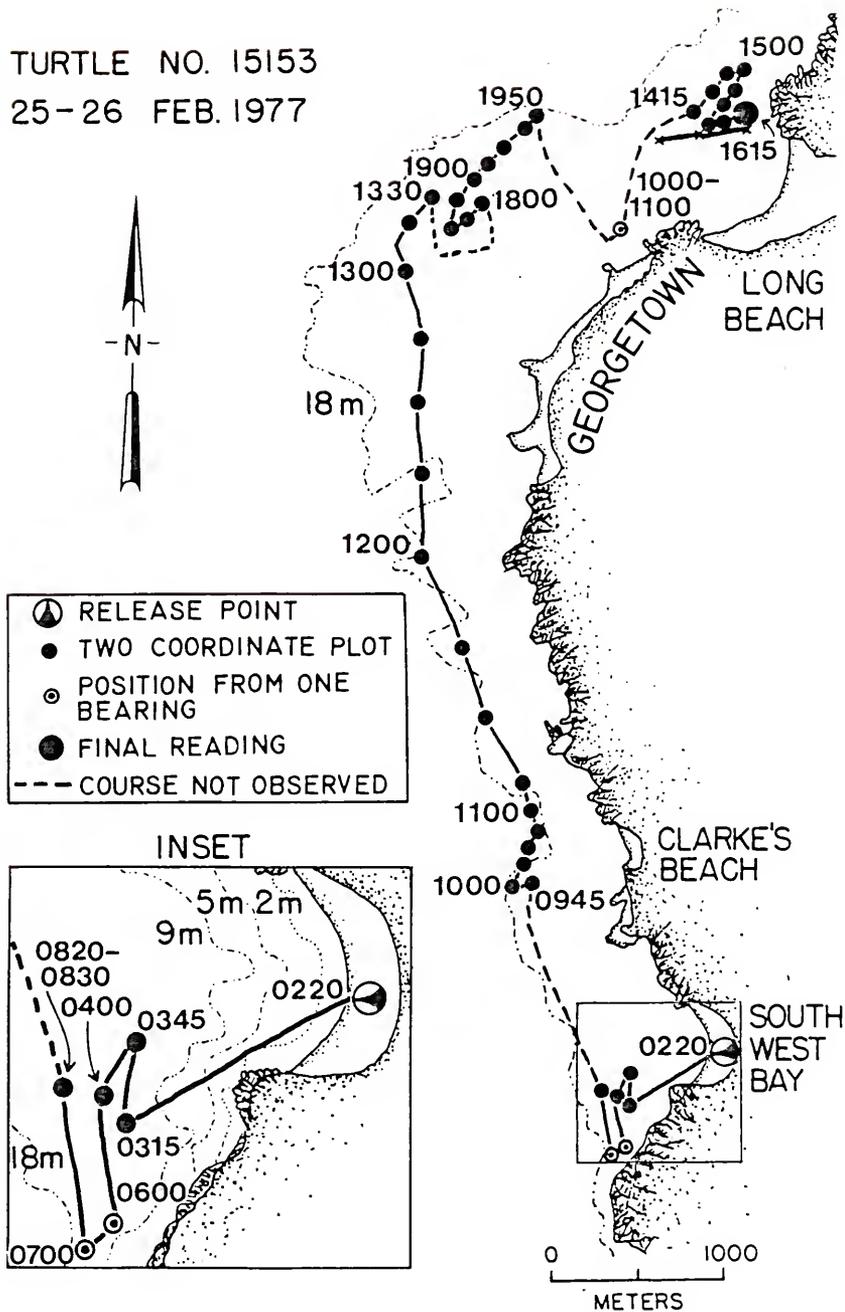


Figure 16. Movements of turtle 15206 during the first 17.3 hours after she abandoned a nesting attempt at South West Bay beach. Eggs were not laid. Tracking ended at sundown (1930 hours), because the light on the float had been smashed. At 2115 hours, 1.8 hours later, the turtle emerged from the surf towing the float, and nested at approximately the same point on South West Bay beach where she came out the previous night (see symbol ⊗ in Fig. 17). Figure legend 17 describes the rest of her nesting history.

TURTLE NO. 15206  
12 MARCH 1977

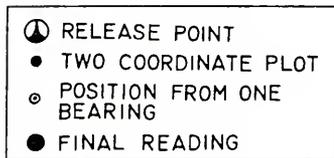
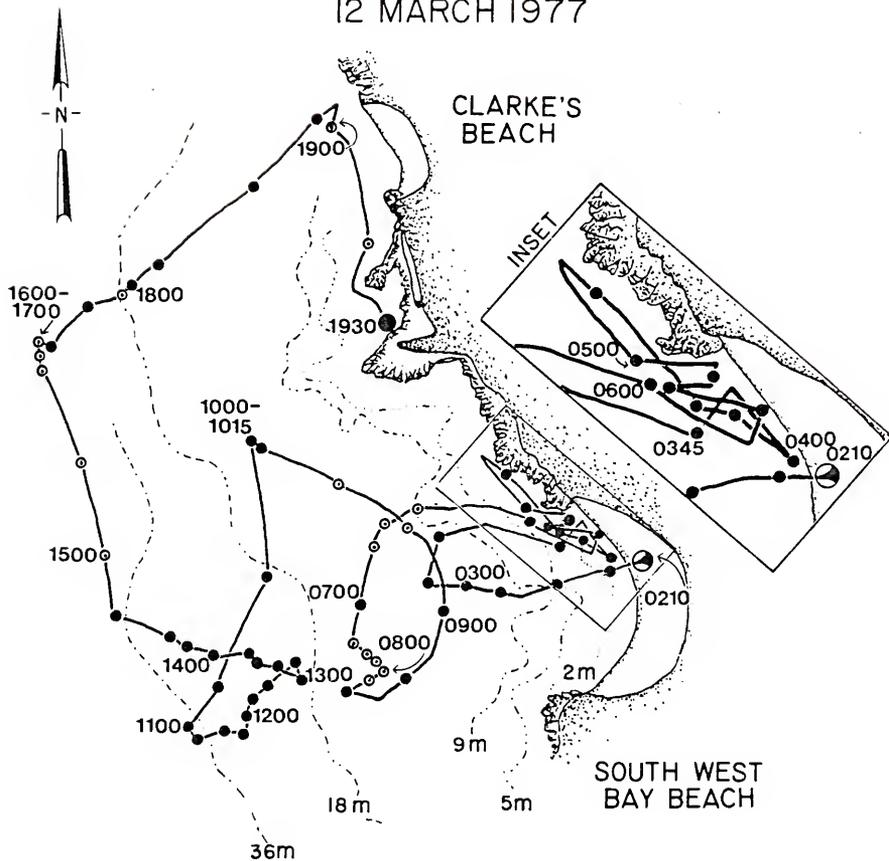


Figure 17. Movements of turtle 15206 during the first 36.3 hours after laying eggs at South West Bay beach (0330 hours), in her sixth egg chamber. Tracking ended when the investigator fell asleep. The only other observed nesting emergence of this turtle is shown in Figure 16.



TURTLE NO. 15206  
13-14 MARCH 1977

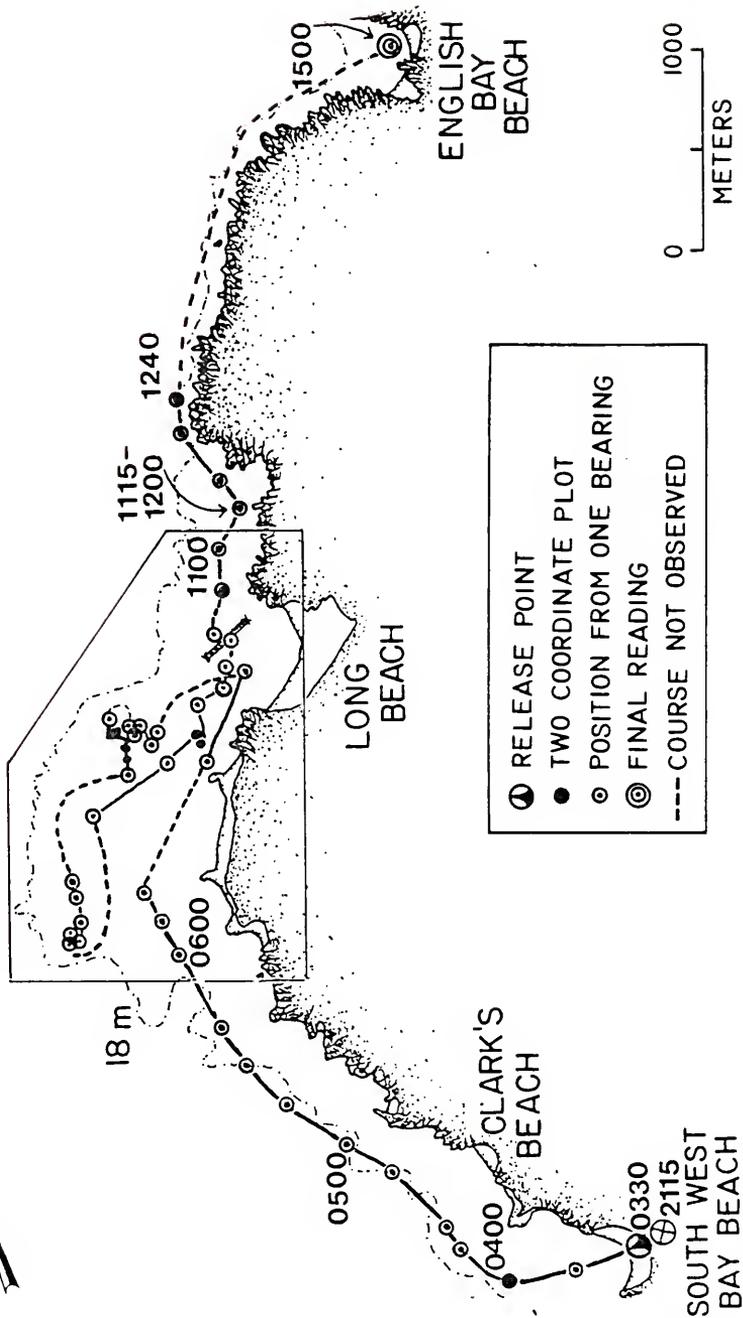


Figure 18. Movements of turtle 15985 during the first 7.2 hours after having been frightened away from her second nest hole at North East Bay beach. Eggs were not laid. The following night, 23 April, at 2130 hours the turtle emerged without her float at the north end of North East Bay beach, symbol ⊕, and laid eggs in the first nest hole dug. The tracking float was later found washed up on Ppt 2 beach. No other nesting emergences by this turtle were observed.

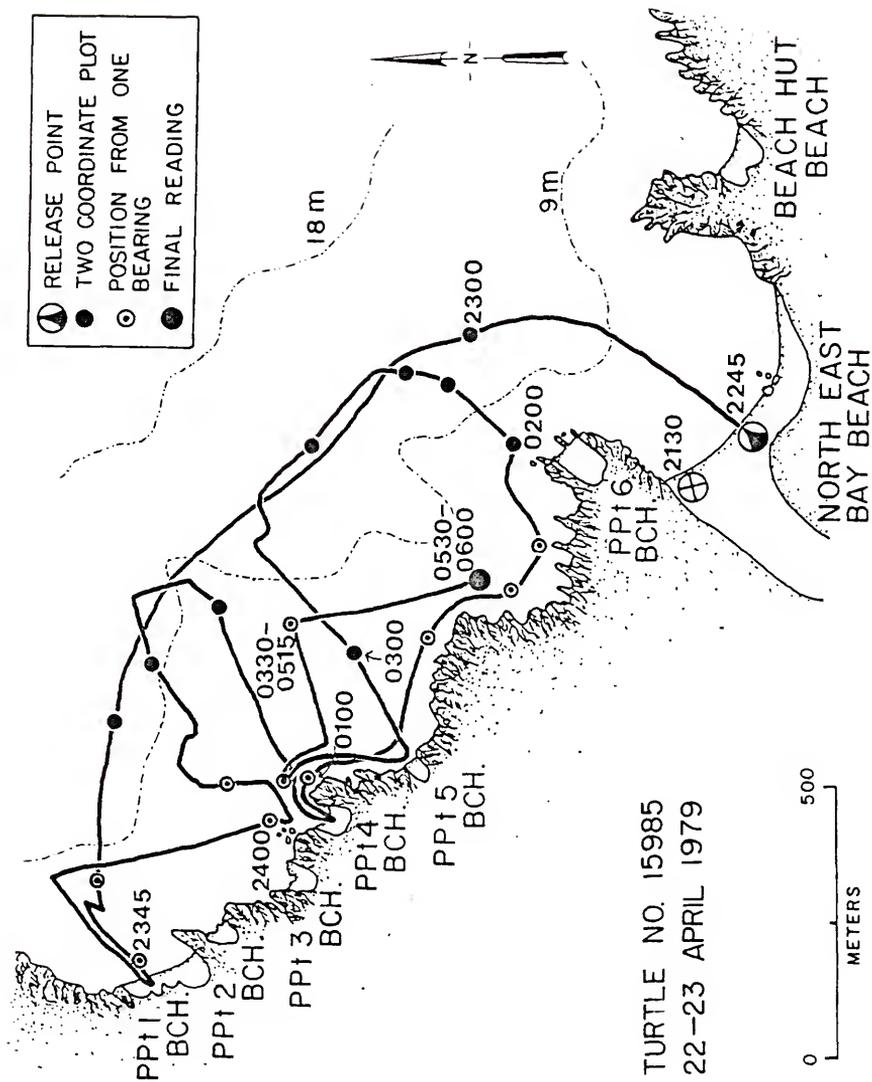
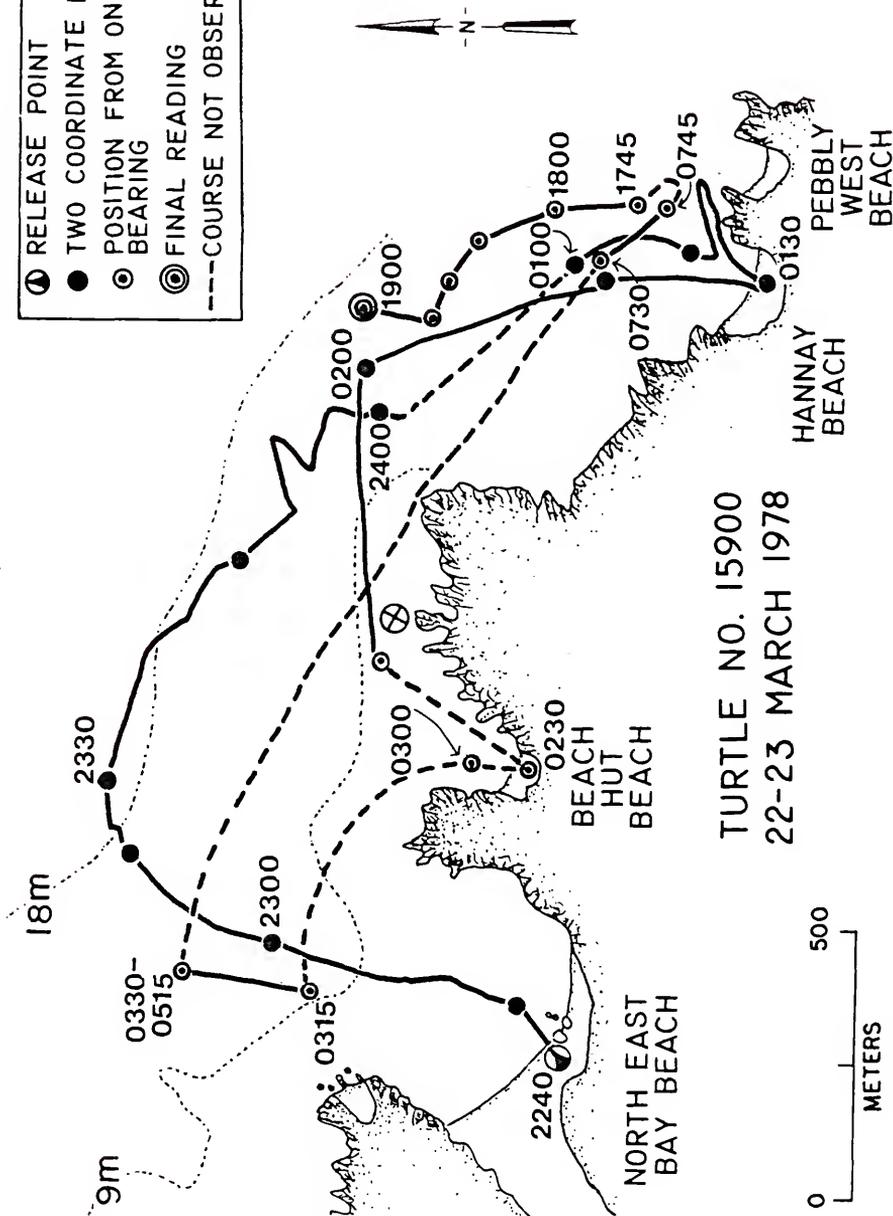


Figure 19. Movements of turtle 15900 during the first 20.3 hours after having been frightened away from her second nest hole at North East Bay beach. Eggs were not laid. Tracking ended at sundown when the float, whose light had burnt out, could no longer be seen. That night, she was not observed nesting on any of the beaches in the vicinity of North East Bay. However, several days later at a point east of Beach Hut beach (see symbol ⊗) the tracking float was found hooked on submerged rocks in 5-7 m of water, about 30 m offshore. There were no other observed nesting emergences.

- ① RELEASE POINT  
 ● TWO COORDINATE PLOT  
 ○ POSITION FROM ONE BEARING  
 ⊙ FINAL BEARING  
 --- COURSE NOT OBSERVED



TURTLE NO. 15900  
 22-23 MARCH 1978

Figure 20. Movements of turtle 15516 during the first 10.3 hours after having been frightened away from her third nest hole on South West Bay beach. She was reluctant to leave the beach and even began to dig a fourth body pit on her way to the water. Tracking was terminated when the float could no longer be seen in the glare of the morning sun. She was not observed nesting on the second night, although I checked the beaches in the vicinity of South West Bay throughout the night. All recorded earlier and later nesting emergences during 1978, except one, occurred at South West Bay beach (Table 8).

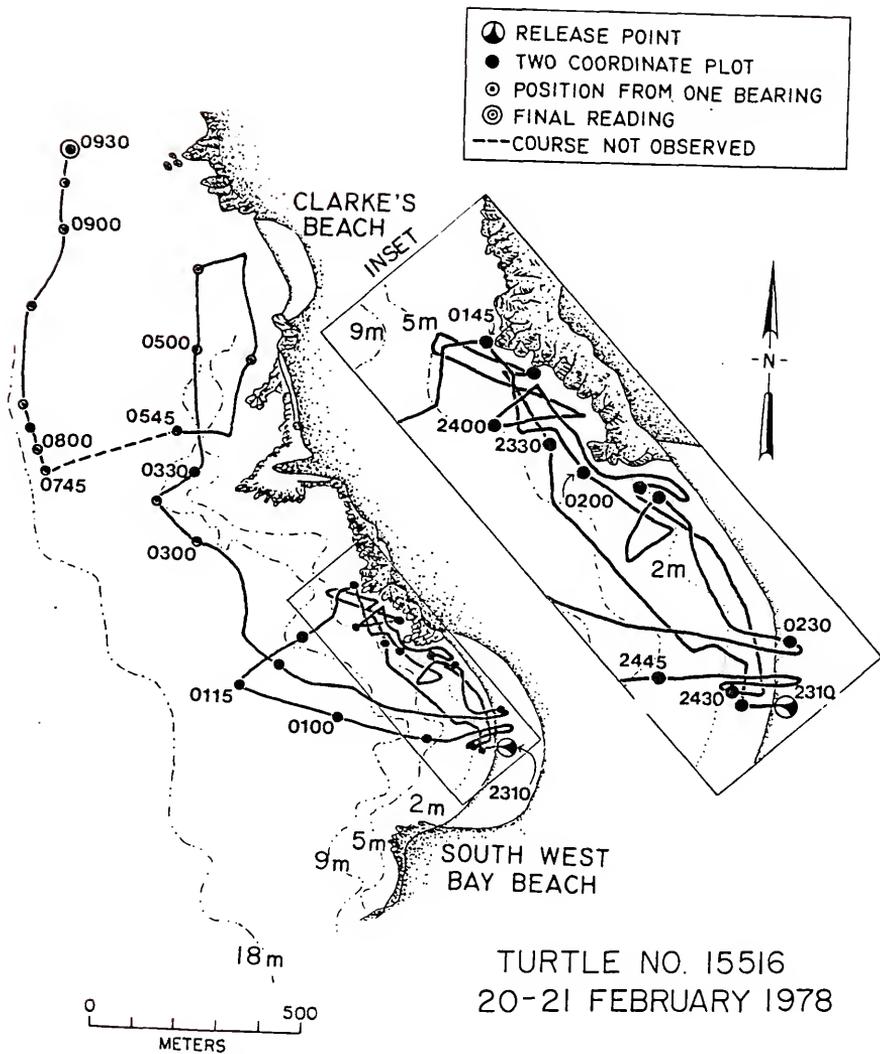


Figure 21. Movements of turtle 15923 during the first two hours after having been frightened away from her second egg chamber at South West Bay beach. Eggs were not laid. Tracking terminated when the tow-line snagged on submerged rocks, allowing the turtle to pull free. She was not seen nesting again. All her recorded nestings during 1977 were on South West Bay beach (Table 8).

TURTLE NO. 15923  
1-2 JUNE 1978

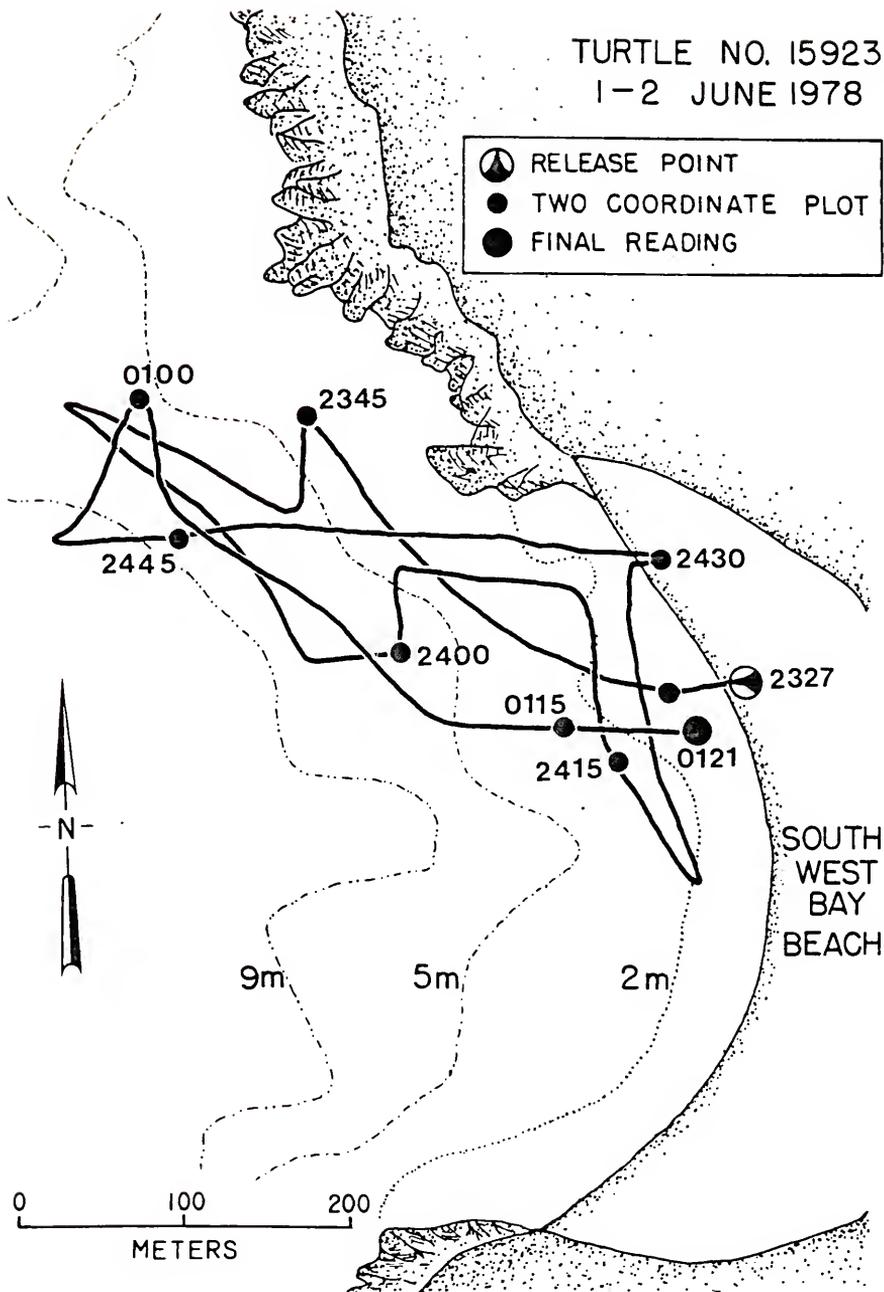


Figure 22. Movements of turtle 15465 during the first 8.2 hours after abandoning her second nest hole at South West Bay beach. Eggs were not laid. The turtle emerged without her float at 2240 the following night, 12 May, on South West Bay beach at the point marked by the symbol ⊗, and laid eggs in the first egg chamber constructed. She made no other observed nesting emergences.

TURTLE NO. 15465  
11-12 MAY 1977

RELEASE POINT  
 TWO COORDINATE PLOT  
 FINAL READING

SOUTH  
WEST  
BAY  
BEACH

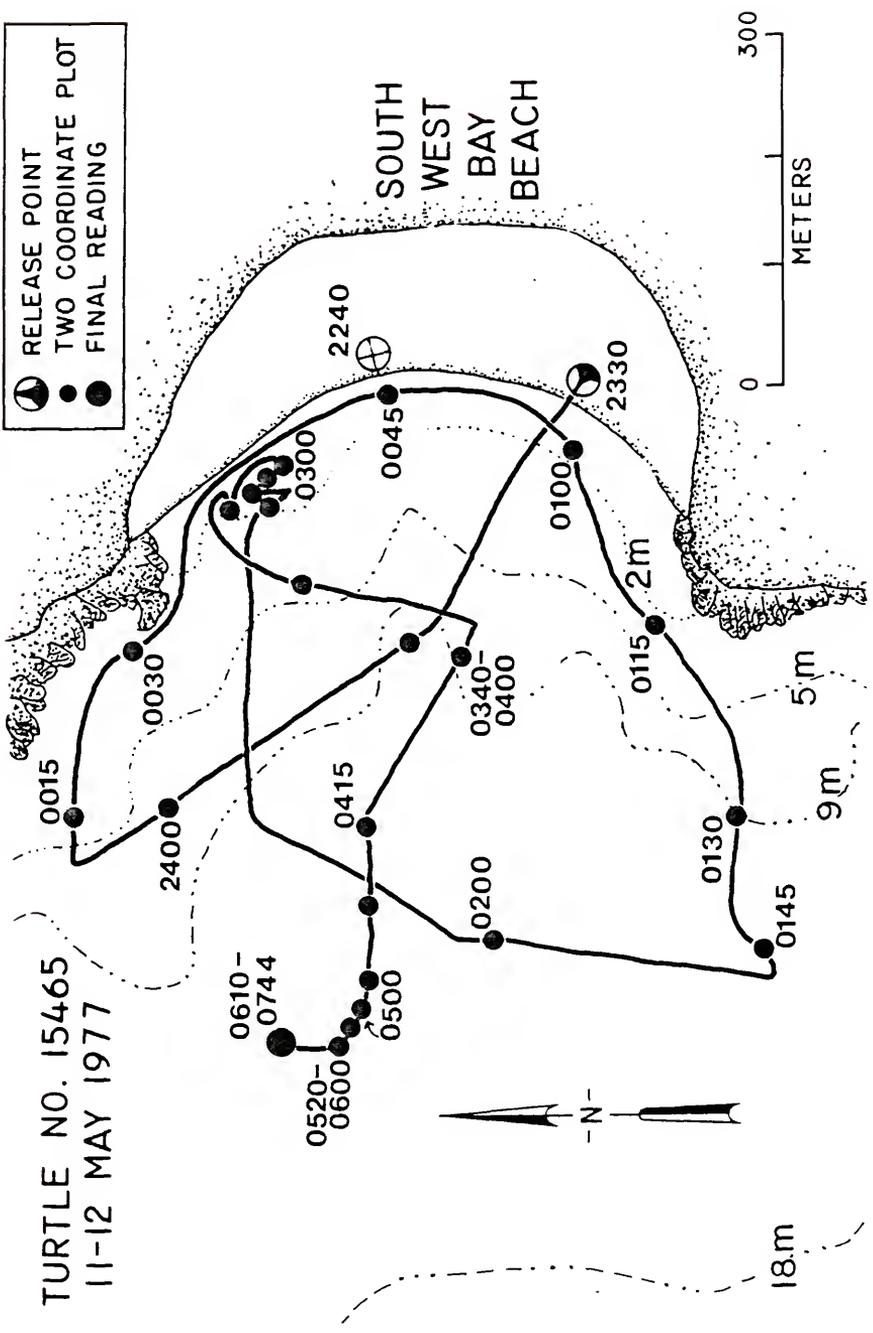


Figure 23. Movements of turtle 16019 during the first 3.3 hours after having been frightened away from her first egg chamber at South West Bay beach. Eggs were not laid. Tracking ended when heavy surf broke off the float as she approached shore. She emerged to nest the following night, 27 May at 2230 hours, on South West Bay beach (symbol ⊗). She dug at least three egg chambers before laying. No other nesting emergencies were observed.

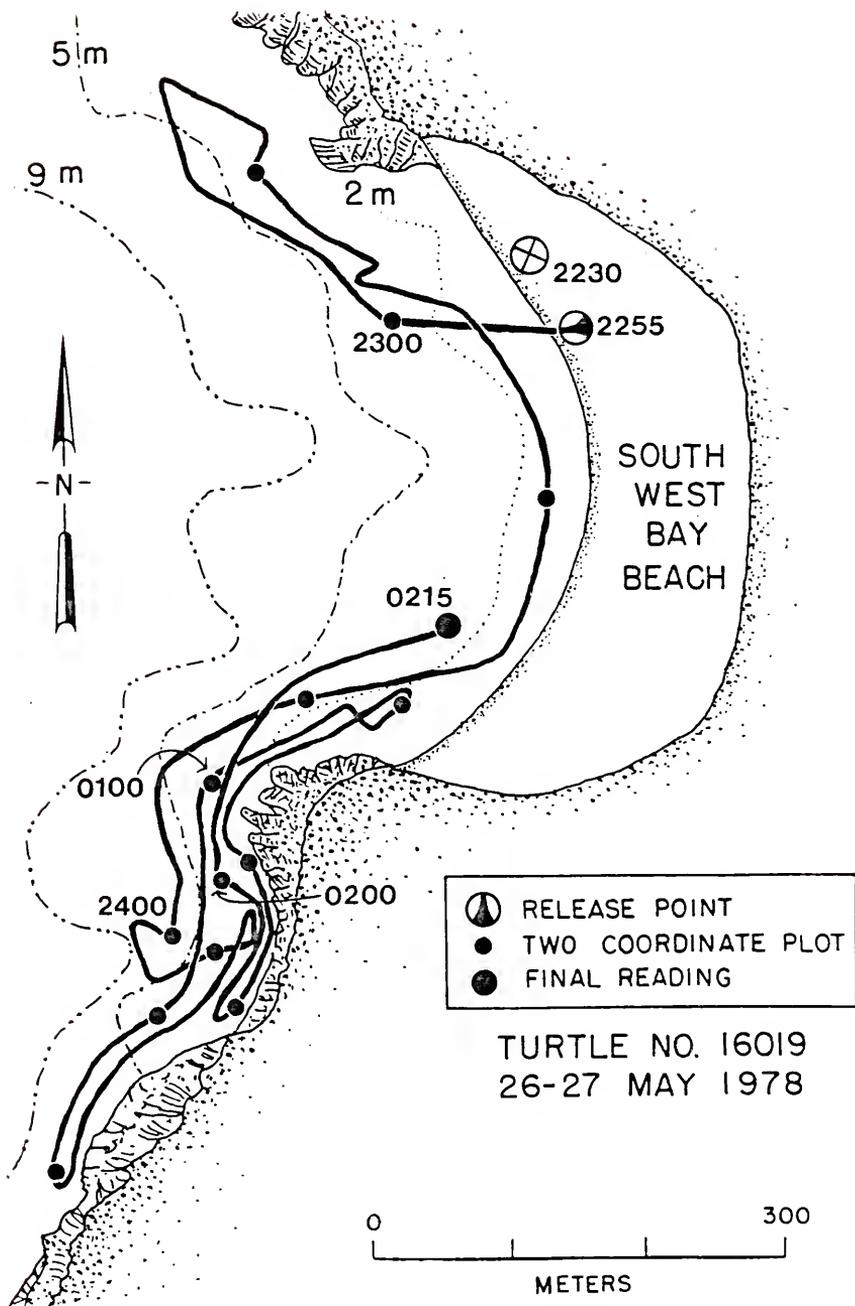


Figure 24. Movements of turtle 15415 during the first two hours after having been frightened away from her fifth nest hole at South West Bay beach. Eggs were not laid. Tracking terminated when the float became snagged on submerged rocks. Turtle 15415 was not recorded nesting again. She had been observed nesting at approximately the same point on South West Bay beach one month earlier, on 21 April.



Table 8. Recorded emergences of turtles on the nesting beaches before and after they were tracked. The Figure numbers indicate the interesting track plots. Distances from the south end of the South West Bay beach (SWB) are shown in meters.

Turtle Number	Release Point	Dates Tracked	Nesting History
15516* (Fig. 20)	SWB	20-21 Feb 78	3 Jan 78; SWB 40 m 18 Jan 78; SWB 455 m 19 Jan 78; SWB 460 m 3 Feb 78; SWB 290 m 5 Feb 78; SWB 195 m 6 Feb 78; SWB 195 m 7 Feb 78; SWB 440 m 20 Feb 78; SWB 180 m 4 Mar 78; Turtleshell Bch 5 Mar 78; SWB 160 m
15923 (Fig. 21)	SWB	1-2 June 77	28 Mar 77; SWB 35 m 31 Mar 77; SWB 112 m 15 Apr 77; SWB 112 m 1 Jun 77; SWB 400 m
15415 (Fig. 24)	SWB	20 May 77	21 Apr 77; SWB 280 m 20 May 77; SWB 280 m
15139 (Fig. 14)	SWB	5 Mar 77	17 Feb 77; SWB 60 m 4 Mar 77; SWB 195 m 18 Mar 77; SWB 85 m 20 Mar 77; SWB 190 m

\* Repeated emergences made by this turtle before successful oviposition, probably occurred because part of her right rear flipper was missing.

individual (number 15206) that was tracked under both circumstances (Figs. 16 and 17).

#### Travel After Egg Laying

Similar patterns of movement were recorded for six turtles after they laid eggs at South West Bay beach--three tracked during the present study (Figs. 14, 15, 17); and three turtles previously tracked by Carr (Carr, 1972; Carr *et al.*, 1974). I will discuss my results with those published by Carr.

One of the six experiments was terminated after only six hours (Fig. 14), and one after nine hours (Carr *et al.*, 1974). Contact with the other four turtles was maintained for 15 (Carr, 1972), 36 (Carr *et al.*, 1974), 36.3 (Fig. 17), and 38 (Fig. 15) hours. All six turtles initially cruised slowly (averaging 1.2 km/hr) northward towards the expanse of shallow water off Georgetown, a site that I will call Georgetown Ledge. This area is adjacent to the series of beaches between Blowhole beach and Long Beach (Fig. 1). The three turtles which continued to be tracked after they reached the Georgetown Ledge swam more slowly (averaging 0.5 km/hr) once they reached it. They travelled back and forth across the Ledge, remaining within the 18 m depth contour, for periods of 22 (Carr *et al.*, 1974), 28 (Fig. 15), and 29 (Fig. 17) hours. Two of the tracks were terminated at this point (Carr *et al.*, 1974; and Fig. 15). The third turtle (Fig. 17), after spending 29 hours on the Ledge, began to travel in a northeasterly direction, parallel to the shoreline, in water about 18 m deep. She was seen three hours later moving past English Bay beach, having

maintained approximately the same rate of travel between Long Beach and English Bay as she had between South West Bay and Long Beach (about 1.2 km/hr).

After laying eggs at South West Bay beach, another turtle tracked by Carr *et al.* (1974) remained within a radius of 0.3 km, in 9-16 m deep water directly off South West Bay, for about 30 hours. This behavior was never repeated by any other turtle tracked at Ascension.

I tracked a turtle after she had laid eggs at North East Bay beach. She moved offshore and then slowly travelled parallel to the coastline in a southwesterly direction (Fig. 13) for 5.6 hours, until the observations were terminated. The float and tow-line were found one week later wrapped around a different turtle just off Blowhole beach on the other side of the island (Fig. 1). This circumstantial evidence suggests that she may have travelled to Georgetown Ledge after laying eggs at North East Bay beach.

#### Travel-Patterns After Abandoned Nesting Efforts

For the entire time that they were observed (2 to 19 hours,  $\bar{x} = 9.1$ ), all eight turtles tracked after abandoning a nesting attempt remained within the general vicinity of the beach from which they had been frightened. The six tracked from South West Bay beach (Figs. 16, 20-24) strayed no more than about 500 m from either end of that beach, moving back and forth along the shoreline. During the hours of darkness, with the exception of the turtle shown in Fig. 24, they each stayed in water less than 9 m deep for 80-100% of the time.

The two turtles tracked from North East Bay beach were less restricted in their movements. One swam directly northwest to Ppt 1

beach (Fig. 18), and the other went in the opposite direction to Hannay beach (Fig. 19). In both cases, after entering the sea, they spent their seven remaining hours of darkness travelling slowly along the shoreline, back in the direction of North East Bay, occasionally moving very close to shore or even briefly crawling out onto a beach. At Tortuguero, Meylan (in press a) found that both the nesting and non-nesting turtles left the region adjacent to the emergence site within 24 hours of returning to the sea.

On only seven occasions have I recorded tagged turtles emerging twice during a single night--either onto the same beach, or on different beaches. None of my tracked subjects nested during the same night that they abandoned their first nesting. However, four briefly crawled out of the sea (Figs. 18-21) during that first night. These emergences may have been exploratory "half moons" (Carr *et al.*, 1978; Chapter 2), or possibly the drag of the tow-floats or the flashing lights discouraged the turtles from crawling all the way out to nest. Although turtle number 15206 failed to re-emerge on the first night, she emerged and laid eggs on the following night, pulling her tow-float behind her (Figs. 16 and 17). Carr and Giovannoli (1957) and Meylan (1977) have also recorded nesting emergences by turtles dragging floats.

Between 2115 and 2240 hours on the second night, four (Figs. 16-18, 22 and 23) of the eight turtles emerged and laid eggs on the same beach that they had abandoned the previous night--in two cases (Figs. 17 and 23) almost at the same point on that beach. This causes me to doubt that the convoluted tracks recorded the night before represent searching behavior on the part of the turtles, and makes it seem likely

that the turtles were simply waiting until motivated to emerge. This waiting phase generally takes place in inshore waters, and may be typical of behavior just prior to nesting. On full moon nights, I have stood on the beach and watched turtles swim back and forth over the white sand just offshore, sometimes in water less than a meter deep; Hendrickson (1958) and Bustard (1972) made similar observations in Sarawak, and at Heron Island, Australia.

It seems clear that the turtles are familiar with the nesting grounds, and can locate a specific place without extensive trial and error searching. For example, during the 1.5 hours just before her nesting emergence, the movements of turtle number 15206 (Fig. 16) were not recorded, because at 1930 hours sunset ended the experiment, and she was not seen again until 2100 hours, when she emerged onto the beach. Assuming she maintained the same average speed as she had during the previous two hours (0.9 km/hr), in order to reach the point at which she finally emerged, she would have had to travel directly, and with little hesitation. This was a remarkably precise landfall; her two emergences occurred within about ten meters of each other. Similarly, after departing North East Bay beach, the turtles in Figures 18 and 19 seemed to travel directly to PPt 1 beach and Hannay beach, respectively. They obviously were either aware of the locations of these beaches before they left North East Bay, or were somehow able to detect them from a distance.

#### Periods of Rest

Resting seemed to occur both during the daytime and at night with no clear diel cycles detectable. There were intervals of 15 minutes to

two hours ( $\bar{x}$  = 1.2 hours; S.D. = 0.6; N = 15) during which turtles remained completely stationary (Figs. 13-19 and 22). In all but one case (Fig. 22) this occurred in water more than 7 m deep. They were probably resting under rock ledges or at rock-sand interfaces--the habitats where, while skin and SCUBA diving, I regularly found turtles resting. A t-test showed that during the first eight hours after entering the sea, the average resting interval (1.5 hours) recorded for turtles that had laid eggs was significantly longer than that for turtles that had been frustrated during their nesting attempt (0.9 hours) ( $p < 0.005$ ;  $t = 2.87$ ;  $N = 15$ ). At other times, although the turtles were not completely stationary, their speeds of travel were so slow (less than 0.2 km/hr) that resting or drifting with local currents must be assumed (Figs. 16, 17 and 22). During the period that the turtles were under observation, they spent an average of 14.6% of their total time resting (range: 0-31.0%; S.D. = 12.4; N = 12).

Some turtles rested on returning to the sea after laying eggs (Figs. 13-15). Others, having laid at South West Bay beach travelled to Georgetown Ledge before they rested (Fig. 17; and Carr *et al.*, 1974). Not enough data were gathered to do a statistical analysis, but there was no apparent relationship between the number of trial nest holes dug, and the amount of time spent resting.

After laying eggs on North East Bay beach, turtle number 15426 moved into water about 12 m deep and travelled southwestward along the shoreline (Fig. 13). This course carried her to a shallower, rocky zone, about 9 m deep, where she remained for 1.5 hours, evidently resting.

### Rates of Travel

During the first four hours after they entered the water, I recorded higher maximum rates of travel for the eight turtles that had abandoned their nesting attempt ( $\bar{x} = 2.08$  km/hr; range 1.3-4.0) than for the four turtles that had successfully nested ( $\bar{x} = 1.4$  km/hr; range 1.0-1.8). A t-test, however, did not show the difference between the two groups to be statistically significant ( $p < 0.05$ ). Turtles that had laid eggs maintained speeds of 1.1-1.7 km/hr for up to four consecutive hours. Their average speed of travel, 1.2 km/hr, was slower than the averages previously reported for turtles tracked after laying, by Carr *et al.* (1974) at Ascension--1.5 km/hr, and by Meylan (in press a) at Tortuguero--2.0 km/hr. After they reached the Georgetown Ledge, turtles tracked in the present study travelled more slowly, at speeds averaging only 0.5-0.6 km/hr (Figs. 15 and 17).

### Departures from the Beach

On entering the sea after a nesting emergence, all the turtles initially swam under water in a direction approximately perpendicular to the shoreline. Without exception, on reaching points about 40 m from shore, they stopped briefly, raised their heads above the surface, breathed, and then submerged. Because sea turtles can go for long periods without breathing, it is unlikely that they found it necessary to blow immediately after getting through the breakers. Thus I conclude that they were visually orienting. After submerging, they often would not surface again for several hundred meters, usually continuing to travel straight out to sea, although in some cases altering their courses significantly (Fig. 20).

### Correlation Between Travel and Depth

In only one case did an Ascension turtle venture into water deeper than about 20 m during the interesting period. At 1015 hours turtle number 15206 (Fig. 16) was disturbed by the crew of a navy launch, who, unaware that the float was part of a tracking experiment, hauled her up to the surface to see what was at the end of the tow-line. On being released she headed for deeper water. At French Frigate Shoals, Balazs (1980) affixed depth gauges to turtles after they nested. The maximum depth he recorded during the interesting interval was 12.8 m.

At Tortuguero, Meylan (in press a) found that the turtles travelled parallel to the shore and within the 24 m contour, but she found no evidence that Tortuguero turtles followed specific isobaths in their longshore travels. At Ascension, however, the tracks of the movements of the turtles commonly coincided with the depth contour lines offshore. When travelling between South West Bay beach and Georgetown Ledge, for example, turtles stayed close to the 18 m contour line (Figs. 14, 15 and 17; Carr *et al.*, 1974). While on the Georgetown Ledge, the turtles sometimes seemed to be following shallower contour lines. For example, turtle 15206 (Fig. 17) followed the 5 m contour between 0645 and 0715 hours, and the 9 m contour line from 0945 to 1523 hours, and again from 1930 to 2200 hours. Turtle 15415 (Fig. 24) stayed in water 12-14 m deep from 0045 to 0130 hours. The 12 m isobath was followed closely by turtle 15206 from 0800 to 1000 hours (Fig. 16).

The turtles spent their daylight hours in deeper water than at night. Those that had abandoned nesting attempts passed most of the night in shallow water (less than 9 m). In fact, contact with them

often ended prematurely when the tow-line snagged or the float was damaged as the turtle moved close to shore. Only three of these frustrated nesters were tracked during the hours after sunrise (Figs. 16, 19 and 20). In each case the turtle either moved into deeper water when the sun rose at about 0600 hours (Figs. 16 and 20), or was already in deep water at that time and remained there. Some turtles probably wait until after dark before moving back inshore. For example, turtle number 15900 (Fig. 19) was still in deep water when tracking ended at sunset. However, about 2.5 hours before sunset, turtle number 15206, having spent the entire day since sunrise in water 9-39 m deep, (Fig. 16) moved slowly, but directly, inshore to water less than 5 m deep. Similar diel migrations between deeper and shallower water were also observed for Tortuguero turtles (Carr, 1972; Meylan, in press a).

#### Influence of Food Availability on Activity Patterns

Because green turtles eat benthic flora (literature reviewed by Mortimer, in press), virtually no forage exists for them off most nesting beaches (Hirth, 1971). The high-energy surf required to form suitable beaches tends to inhibit the development of good feeding habitat (Carr and Coleman, 1974). At Ascension the dearth of vegetation is aggravated by the abundance of the voracious blackfish (*Melichthys niger*) which devour all plant growth in longshore waters.

Forage is probably also unavailable to the turtles during their open ocean migration between Ascension and Brazil (Carr, 1975). Females may spend more than 16 weeks at the breeding grounds, so the length of time spent fasting is substantial. This suggests that during the interesting period the turtles might be found to limit their

activity and save energy. Although my observations indicate that the females by no means remain immobile, they do spend a lot of time resting or travelling slowly.

If this is correct, one might expect to find different degrees of interesting activity in populations with shorter and longer migratory journeys. Comparison of the interesting movements of Ascension and Tortuguero turtles, the nesting and feeding grounds of which are respectively separated by distances of 2,500 and 400 km, seems to support this idea. At Ascension, turtles were rarely observed farther than about 0.8 km from shore, while at Tortuguero they regularly moved as far as 3.8 km out to sea (Meylan, in press a). The turtles there usually disappeared from sight when they made extended trips southward along the coast.

I calculated, from the interesting tracks plotted during the present study, and the studies of Carr *et al.* (1974) and Meylan (1977), the average distance covered while the turtles were under direct observation, including those times when the turtles were resting as well as travelling. As an index of comparison, I used the average distance travelled during an hour. As expected the average distance travelled by the Tortuguero turtles was greater ( $\bar{x} = 1.05$  km; S.D. = 0.56; N = 23) than that travelled by the Ascension turtles ( $\bar{x} = 0.78$  km; S.D. = 0.23; N = 14) during the same interval. Although the Mann Whitney *U* test did not show a significant difference between the two populations ( $p < 0.05$ ), there was a trend.

It also seems possible that there is a difference in the distance travelled by males and females. In a given season females may produce

and lay up to seven clutches, each comprising about 121 eggs (Chapter 2). This places a heavy energetic burden on her, so one would expect her behavior to be more subdued than that of the males, in order to conserve her energy. I found this to be the case; males were rarely seen resting. They appeared to spend most of their time at the nesting ground searching for mates.

### Sexual Behavior

At most green turtle beaches, mating precedes nesting (Hendrickson, 1958; Carr and Giovannoli, 1957; Frazier, 1971; Booth and Peters, 1972; Balazs, 1980). At Ascension, copulation by green turtles begins early in November, reaches a peak in December and January, and is rarely observed after early April. Nesting activity usually does not start until mid-December. It peaks during February and March, and ceases by mid-July.

Copulating pairs were observed along most of the perimeter of Ascension Island, but were seen most regularly in the sandy bays off the major covehead beaches. The most concentrated mating activity appeared to occur off Long Beach. Ascension turtles mate both during the daytime and at night.

My observations of the sexual behavior of Ascension turtles generally agree with those of Hendrickson (1958), Carr and Giovannoli (1957), Frazier (1971), Booth and Peters (1972) and Bustard (1972), and I am unable to add much to their descriptions of courtship and copulation. I often swam close to the turtles, but was unable to devise a way to mark them underwater for later recognition. Since visibility

in the water was usually less than about 8 m, I could rarely keep track of individuals for more than seconds at a time.

Throughout most of the nesting season during daylight hours, females are usually found resting on interfaces of sand and rock, or under rock ledges, at depths greater than 6-7 m. At the peak of the mating season, however, I found aggregations of about 20-30 individuals, including males, females and mating couples, in shallow water only 2-10 meters deep, in an area off Long Beach where the sea floor is barren sand. The females that were not copulating, were lying on the sand bottom. Males, however, seldom rested, and were usually cruising back and forth, apparently looking for mates or following mated pairs, as described by Booth and Peters (1972). Although they would frequently try to mate with me, they seemed to ignore the females resting on the bottom.

In her study area, Booth identified a part of the lagoon where females rested on the sandy bottom, and, while there, were apparently immune from sexual advances by males (Booth and Peters, 1972). She labelled this zone the "female reserve." It seems possible that parts of the Georgetown Ledge serve a similar function for females at Ascension during their interesting intervals. I have seen females beach themselves at mid-day in an apparent effort to escape the attentions of one or more males. This type of evasive behavior was also described by Booth and Peters (1972), Bustard (1972), Hughes (1974b) and Balazs (1980). In spite of the advances that have been made over the past 20 years in our knowledge of the underwater activities of sea turtles, a great deal remains to be learned.

CHAPTER 4  
NESTING DENSITY, BEACH PREFERENCES AND  
POPULATION ESTIMATE

Introduction

Sea turtles nest on a wide variety of beach types, and it is not usually obvious why they choose one beach over another. Biologists have long tried to explain geographic patterns of beach utilization. Ascension Island is an excellent place to investigate how physical attributes of a beach influence a gravid female in her choice of nest site.

During my sixteen months on the island, I surveyed the beaches regularly and determined nesting density at each. I correlated density of nesting with various physical beach characteristics including: beach length, amount of rock cluttering the foreshore, amount of rock obstructing the offshore approach, and amount of artificial light visible on the shore. From the data on hatching success (Chapter 5) I was able to determine whether clutch survival and nesting density were correlated. Data from the beach surveys and from tagging turtles (Chapter 2) make possible an estimate of the number of females that nested on Ascension during each season.

Methods

Description of the Nesting Beaches

The entire coastline of Ascension Island was surveyed on foot, and every patch of sandy shoreline was evaluated as to its suitability

for turtle nesting. Beaches on which body pits had been dug were considered to be nesting beaches, regardless of the presence or absence of fresh turtle tracks. However, areas where turtles had left fresh tracks but had not dug body pits, either because the sand was too shallow or too hard, were not classified as nesting beaches.

After taking measurements using a string knotted at one meter intervals, and an Embeeco compass-bearing monocular, I mapped each nesting beach. The location of rock formations and major differences in the sand composition of the beach platform were plotted, as well as the sections of beach that had been destroyed by sand mining for construction. Plants growing on the beaches were identified to species, and their positions were mapped as accurately as possible (manuscript in preparation).

Ascension beaches show varying degrees of approachability by turtles. Some are completely unobstructed above and below the water line. At others there are horizontal beds of rock or strewn boulders either submerged or on the foreshore that partially obstruct turtle emergence. The percentage of the total length of each beach on which the approach of a turtle would be inhibited by each type of obstacle was measured.

#### Nesting Density

Nesting density on each beach was determined by counting turtle tracks. Counts were made just after dawn while the tracks were still damp; counts made later in the day were not reliable. At most of the 26 beaches monitored, counts were made at least once a week. For each beach, I estimated the total number of tracks during the season, by

plotting the morning counts against time and measuring the area below the curve with a planimeter (Figure 25).

## Results

### Description of the Nesting Beaches

Table 9 summarizes the physical characteristics of each of the Ascension Island beaches. Measurements include: beach length (m), area above the high tide line ( $m^2$ ), percent of beach destroyed by sand mining, percent of beach covered by vegetation, percent of the offshore approach obstructed by submerged rocks, percent of foreshore cluttered by beach-rock, and amount of artificial light visible on the beach at night.

### Nesting Density

Table 10 shows the estimated total number of turtle emergences onto each beach during the 1976-77 and 1977-78 nesting seasons, as derived from the morning track counts. More abandoned nestings are made on the coarser grained beaches, because turtles apparently have more difficulty digging nests there (Chapter 2). To estimate the total number of clutches laid on each beach, I divided the total number of emergences by the estimated average number of times a female comes out before successfully laying eggs on that beach (Chapter 2). The ratios are respectively 3.3 on biogenic beaches at which average mean particle diameter is less than 0.2 phi units, and 2.2 on finer textured beaches (Table 10).

Figure 26 shows the relationship between beach length and estimated total number of clutches laid at each beach during the season. The

Figure 25. Seasonal distribution of nesting activity on Ascension's three major nesting beaches--South West Bay, Long Beach and North East Bay--as shown by morning track counts. Data gathered during both the 1976-77 and 1977-78 seasons are shown. Not only did more turtles nest during the 1976-77 season, but nesting activity peaked at an earlier date. The early part of the 1976-77 season was missed because work was not begun until late January. The low track counts recorded at Long Beach on February 20-21 and March 10, 1978 are the result of heavy roller activity which prevented the turtles from coming ashore.

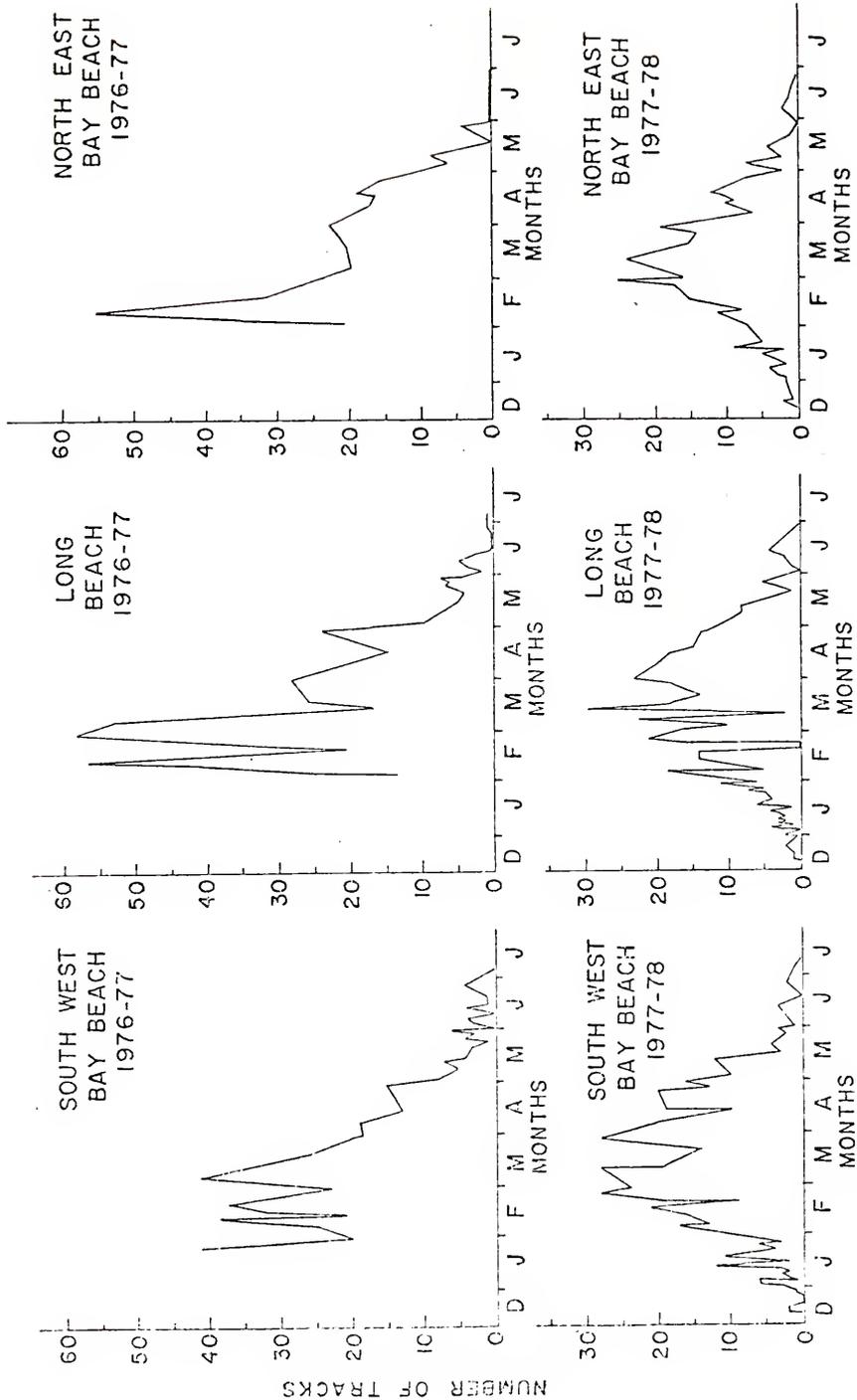


Table 9. Physical characteristics of each of the Ascension Island nesting beaches. Beaches are listed in the order in which they occur, moving clockwise around the island from South West Bay.

Beach	Beach Length (m)	Area Above High Tide (m <sup>2</sup> )	% of Beach Destroyed by Sand Mining	% of Beach Covered by Vegetation	% of Offshore Approach Obstructed by Rocks	% of Fore-Shore Cluttered by Rocks	Artificial Lights Visible*
South West Bay	480	20,290	4.4	31.6	0	49	P
Turtleshell	245	9,567	10.5	6.4	40	40	P
Clarkes	176	11,877	11.5-22.1	7.9	17	75	---
Payne Pt.	123	4,535	0	0	37	83	---
Mitchell's Cove	40	748	0	8.0	0	50	---
Blowhole	157	3,258	0	2.0	25	25	---
P.O.L. South	67	6,052	0	0.3	40	10	C
P.O.L. North	290	7,032	0	0	100	41	C
Deadman's	360	22,335	0	27.9	40	25	C
Fort Hayes	282	5,716	0	1.9	23	85	C
Georgetown	329	18,587	8.7	25.4	5	20	C
Long	915	63,064	14.7	3.0	0	2	C
Comfortless Cove	35	213	0	0	0	0	---
English Bay	185	10,890	3.0	1.4	10	11	C
EB 1	95	2,071	?	2.1	23	84	C
EB 2	56	1,729	0	0.7	0	100	C
EB 3	85	2,039	?	0	23	88	C
EB 4	16	284	0	0	25	100	---
Ladies Loo West	14	110	0	0	0	100	---

Table 9 continued.

Beach	Beach Length (m)	Area Above High Tide (m <sup>2</sup> )	% of Beach Destroyed by Sand Mining	% of Beach Covered by Vegetation	% of Offshore Approach Obstructed by Rocks	% of Fore-shore Cluttered by Rocks	Artificial Lights Visible*
Ladies Loo	11	1,542	0	0	0	0	---
Porp. Pt 1	80	2,497	0	0	0	0	---
Porp. Pt 2	55	361	0	0	100	100	---
Porp. Pt 3	10	1,032	0	0	30	100	---
Porp. Pt 4	18	1,548	0	0	20	20	---
Porp. Pt 5	30	723	0	0	0	0	---
Porp. Pt 6	32	1,961	0	0	90	100	---
North East Bay	340	23,471(±12,510)**	0	3.4	0	0	---
Beach Hut	107	2,503	0	0	16	21	---
Hannay	200	9,323	0	0	0	13	---
Pebbly West	45	846(+1,161)**	0	0	0	7	---
Pebbly East	40	303	0	0	95	100	---
Spire	20	404	0	0	0	100	---

\*p = periodic; C = constant; --- = none.

\*\* Gravelly area, which is not part of beach proper, but is accessible to turtles, and where nests are occasionally deposited.

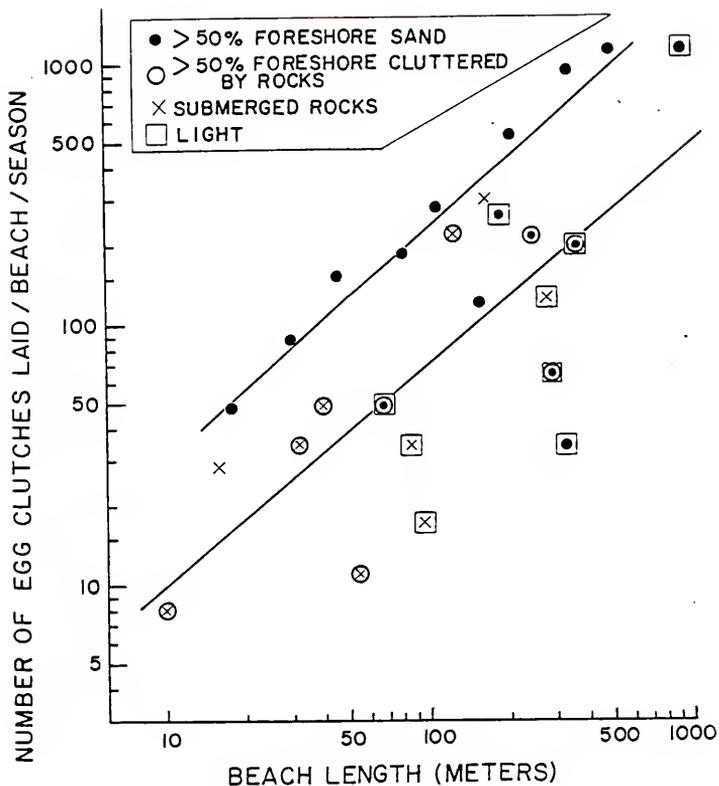


Figure 26. Relationship between estimated number of egg clutches laid on each beach during a season, and beach length, for 26 beaches at Ascension Island. The three symbols (X, ⊙, and □) indicating different obstacles to nesting are used in combination for some beaches. The upper line is a regression based on the nine beaches without obstacles ( $r = 0.92$ ;  $p < 0.001$ ). The lower line is from the remaining 17 beaches, where one or more obstacles occur ( $r = 0.76$ ;  $p < 0.001$ ).

symbols differentiate among beaches with respect to presence or absence of adverse factors such as submerged rocks offshore, artificial lighting, and obstruction by exposed slabs of rock on the foreshore. Linear regressions were performed on the nine beaches lacking obstacles to nesting, and on the 17 remaining beaches. The slopes of the two regression lines were nearly equal (0.90 without obstacles, and 0.84 with obstacles).

Figure 27 illustrates the relationship between each of three sets of adverse shore conditions (beach rock on the foreshore, submerged rocks, and lights), and track density. Some beaches are considered more than once because they fall into more than one category. Submerged rocks and artificial lighting seem to be the greatest hindrances to nesting, followed by the presence of low slabs of beach rock along the foreshore of the beach. Each beach is considered separately in Figure 28, which shows the relationship between nesting density and various combinations of factors.

The relationship between the distribution of nesting activity on each of the three major Ascension Island beaches and offshore contour lines, is shown in Figure 29. The heaviest nesting occurs on stretches of beach where the offshore approach is deepest.

#### Hatchling Emergence

Paradoxically, the turtles do not seem to prefer beaches on which my data show the higher levels of clutch viability. In fact, a Spearman rank test (Siegel, 1956) showed a negative correlation between percent hatchling emergence from each nest excavated, and the average nesting

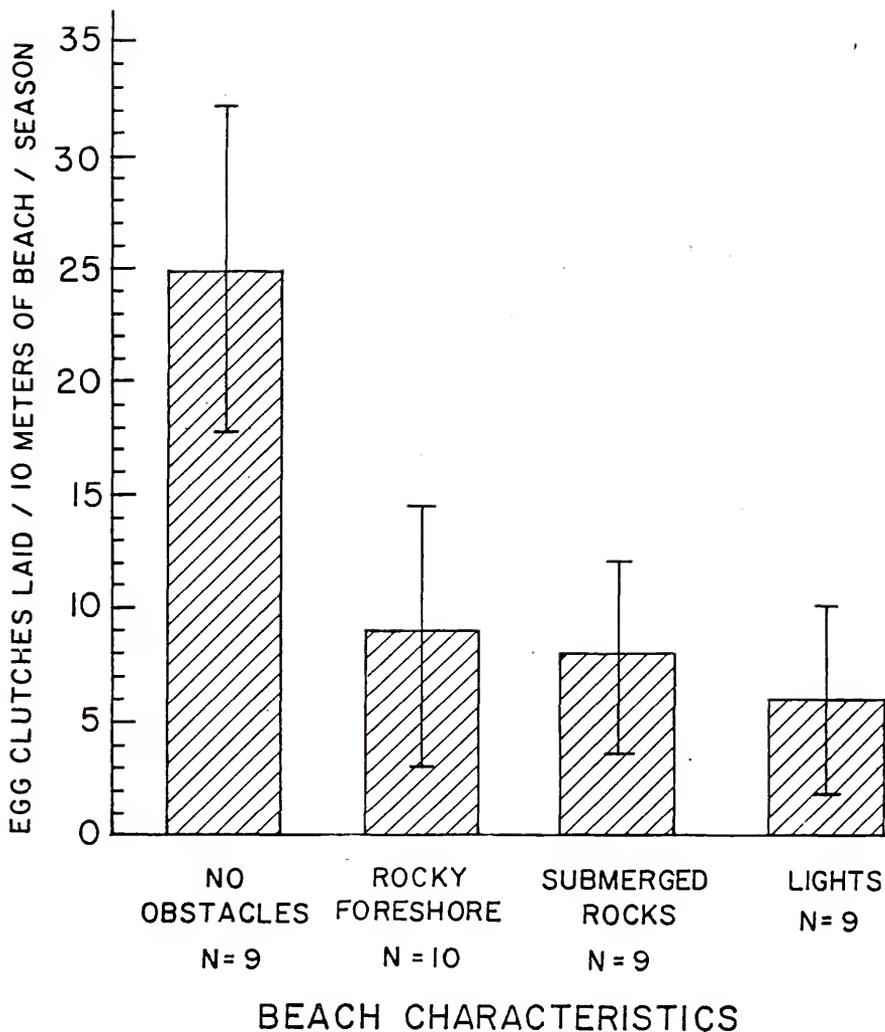
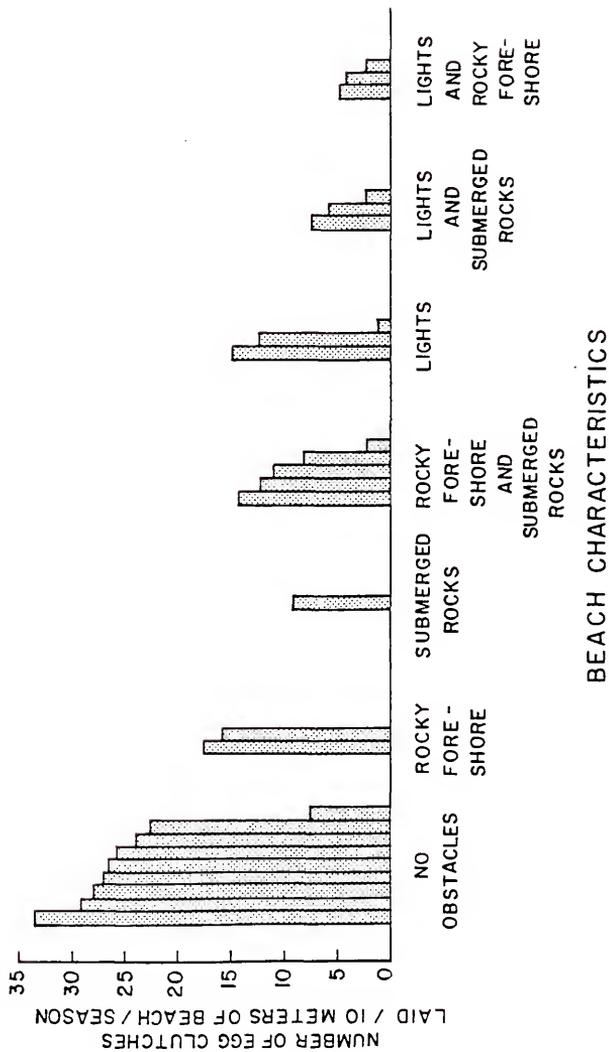


Figure 27. Relationship between physical characteristics of Ascension beaches and nesting density. Some beaches have more than one of the characteristics, and thus are included in more than one category. Brackets indicate standard deviation.



### BEACH CHARACTERISTICS

Figure 28. Relationship between combinations of beach characteristics and nesting density at Ascension Island. Each bar represents one beach.

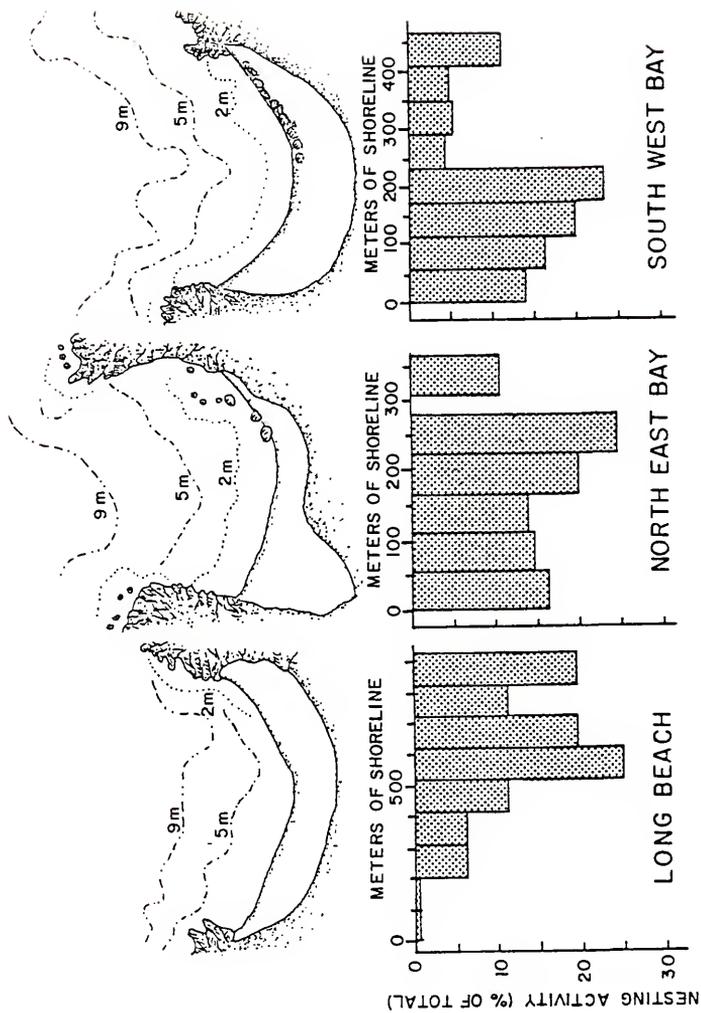


Figure 29. Relationship between nesting density along the shoreline, and the position of the offshore contour lines, at the three major Ascension beaches. Data were gathered by counting tracks during the 1977-78 nesting season.

density recorded for the beach at which the nest was located ( $r = -0.2582$ ;  $p = 0.02$ ;  $N = 77$ ).

#### Population Estimate

To calculate the number of turtles that nested at the island during each of two seasons, I divided the estimated number of clutches laid at each beach by 2.8--the estimated average number of egg clutches laid by turtles during a season (Chapter 2). Table 10 shows the estimated number of turtles nesting on each beach during each season.

### Discussion

#### Offshore Approach and Shoreline Composition

Data gathered at Ascension show that the heaviest nesting occurs on unlighted beaches, with open offshore approaches, and foreshores relatively free of rock clutter (Figs. 26-28). For such beaches the correlation between beach length and the estimated numbers of clutches laid per beach per season is highly significant (Fig. 26). On beaches characterized by the presence of obstacles to nesting, there is an overall decrease in the number of clutches laid. Within the boundaries of a given beach turtles also seem to prefer the deepest offshore approach to the beach (Fig. 29).

There are probably two main reasons why nesting females at Ascension avoid beaches with rock-strewn approaches. The most obvious is that the heavy Ascension surf makes coming ashore over or among rocks dangerous. Frequently, Ascension females have cracks and gashes in their shells (Carr and Hirth, 1962). The second reason is the

Table 10. Number of turtles and the percentage of total turtles nesting at each beach during the 1976-77 and 1977-78 nesting seasons. The estimated number of turtles nesting at each beach is obtained by dividing the estimated total number of emergences during a season (based on track counts) by both 2.8 (the estimated average number of egg clutches laid by turtles during a season), and by the estimated average number of emergences which occur before females successfully lay a clutch of eggs--approximately 3.3 at biogenic beaches whose average mean particle diameter is less than 0.2 phi units, and about 2.2 at finer textured beaches.

Beach	Estimated # Females Perching Laying	1976-77			1977-78			Average # Males at Each Beach
		Estimated Total Tracks	Estimated # Clutches	Estimated # Implies	Estimated Total # Tracks	Estimated # Clutches	Estimated # Implies	
South West Bay	2.2	2,195	1,270	453	2,195	998	356	18.3
Turtleshell	3.3	839	381	91	572	173	62	3.5
Clarks	2.2	658	299	107	570	259	93	4.6
Payne Pt.	2.2	324	147	53	427	194	69	2.9
Mitchell's Cove	---	---	---	3 <sup>a</sup>	---	---	---	0.1
Blowhole	3.3	400	121	43	400	121	43	2.0
P.O.L. South	3.3	198	60	21	32	12	12	0.8
P.O.L. North	3.3	261	79	28	163	49	18	1.0
Deadman's	3.3	847	257	92	460	139	50	3.1
Ft. Hayes	3.3	609	185	66	215	65	23	1.9
Georgetown	3.3	138	42	15	83	25	9	0.5
Long	2.2	3,118	1,417	506	1,760	800	286	17.4
Comfortless Cove	---	---	---	1 <sup>b</sup>	---	---	0 <sup>c</sup>	< 0.1
English Bay	3.3	1,129	342	122	612	185	66	4.6
EB 1	3.3	51	15	6	59	18	6	0.3
EB 2	3.3	0	0	0	0	0	0	< 0.1
EB 3	2.2	100	45	16	51	23	8	0.5
EB 4	2.2	61	28	10	61	28	10	0.5
Ladies Loo West	---	---	---	5 <sup>a</sup>	---	---	5 <sup>a</sup>	0.2
Ladies Loo	---	---	---	10 <sup>a</sup>	---	---	10 <sup>a</sup>	0.4
Porpoise Pt 1	2.2	452	205	73	350	159	57	3.0
Porpoise Pt 2	2.2	29	13	5	14	6	2	0.1
Porpoise Pt 3	2.2	18	8	3	18	8	3	0.1
Porpoise Pt 4	3.3	176	53	19	139	42	15	0.8
Porpoise Pt 5	2.2	192	87	31	192	87	31	1.5
Porpoise Pt 6	3.3	109	33	12	109	33	12	0.6
North East Bay	2.2	2,703	1,229	439	1,469	668	238	14.9
Beach Hut	2.2	804	365	131	420	191	68	4.4
Hannay	3.3	1,743	528	189	1,191	361	193	8.9
Pebbly West	2.2	343	156	56	349	159	57	2.6
Pebbly East	2.2	97	44	16	107	49	17	0.8
Spire	---	---	---	2 <sup>b</sup>	---	---	2 <sup>b</sup>	0.1
Total		7,409	2,624	872	4,872	1,824	684	

heightened predation pressure on hatchlings along rocky shores. More predators occur in the vicinity of rock-strewn bottom than over sand (Chapter 5).

For other species of turtles in other localities, the condition of the offshore approaches seems to be important in their choice of a nesting beach. For example, the heavy body and soft skin and plastron of the leatherback turtle (*Dermochelys coriacea*) make it particularly vulnerable to mechanical injury. Probably for this reason it almost invariably nests on beaches with obstruction-free approaches (Pritchard, 1971b; Hughes, 1974a). The leatherback has never been reported nesting at Ascension.

In contrast, loggerheads (*Caretta caretta*) in Tongaland (Hughes, 1974a) and at Mon Repos in Queensland (Bustard, 1968) seem to prefer beaches adjacent to outcrops of rocks or subtidal reefs. Hughes (1974a) suggests that this peculiar choice indicates the use of rocky approaches to orient to the site of emergence. He discounts the possibility that feeding is involved.

The gradient of the beach will determine the distance a turtle must crawl overland in order to reach a nest site. Nesting beaches of the leatherback often slope steeply, thus reducing the distance between the water line and the nest sites (Pritchard, 1971b; Schulz, 1975). In Surinam, leatherbacks as well as green turtles avoid beaches behind mud banks partially exposed during low tide, while those are the beaches actually preferred by the small olive ridley (*Lepidochelys olivacea*) (Schulz, 1975).

### Beach Vegetation

In some parts of the world, the presence of beach vegetation seems to affect the choice of a nesting site. On the Great Barrier Reef, green turtles reportedly nest where there is substantial beach-front vegetation--large bushes or even trees (Bustard, 1972). Bustard and Greenham (1968) suggest that turtles nesting in these locations are more successful in digging egg chambers because plant rootlets help bind the sand grains and thus prevent slippage. Hawksbills commonly dig their nests far back on the nesting beach, amongst vegetation (Garnett, undated report; Frazier, 1975; A. Carr, pers. comm.). In other places, however, roots in the substrate appear to constitute an important obstacle to digging. Vegetation does not seem to be a factor in beach selection at Ascension because there are no native plants on the beaches.

### Beach Sand

An important property of any nesting beach is the quality of its sand. One would assume that sand type would have a bearing on two vital aspects of the nesting biology of the turtle: beach selection by the females, and survival of eggs laid. The influence of sand type, especially particle size distribution, on choice of nesting beach has been discussed by a number of authors. Little attention, however, has been paid to the manner in which the physical parameters of beach sand effect hatching success (Chapter 5).

Surprisingly, not only does the particle size of the nesting medium vary from one nesting shore to another (Hirth and Carr, 1970; Hirth, 1971), but also a wide range of sand types may be utilized by the same

colony. Hughes (1974a) observed that on Europa Island, the beaches range in composition from fine sand to coral pebbles, and all are used by green turtles. At Ascension, Stancyk and Ross (1978) collected sand samples from 16 of the major nesting beaches and analyzed them for organic matter, water, and calcium carbonate content, pH, color, and particle size distribution. They found no correlation between any of these parameters and nesting frequency, estimated by a brief nesting survey, and from the Ascension nesting records collected by Mariculture, Ltd.

Hendrickson and Balasingam (1966) suggested that in Malaysia the texture of the sand might account for the selection of separate beaches by green turtles and leatherbacks because the beach chosen by *Chelonia* was composed of finer sand. However, the coarse sand of the *Dermochelys* beach is probably caused by an onshore current which strikes the beach perpendicularly, and produces a steep slope and a rapidly shelving bottom at the water line (Hendrickson and Balasingam, 1966). In as much as leatherbacks nest successfully in fine sand in other regions (Carr and Ogren, 1959; Hirth, 1963; Pritchard, 1971b) particle size is probably less important than the slope and offshore configuration of the beach.

Nesting media of hawksbills range from fine siliceous sand to coarse shell and coral fragments (Carr *et al.*, 1966; Hirth, 1963; Hirth and Carr, 1970; Bustard, 1974; Limpus, 1980; Ross, in press). At Ascension, although juvenile hawksbills are occasionally observed in the sea, adults have never been recorded. I doubt that hawksbills could nest successfully at Ascension. They are probably not large

enough to dig to the depth necessary to encounter sand that is sufficiently moist for egg chamber formation and to prevent desiccation of the eggs (see Chapter 5).

Throughout most of its range, the loggerhead shows a tendency to nest in silica sand (Hughes, 1974a; Caldwell, 1959; Cooke and Mossom, 1929). However, this apparent preference may simply reflect the fact that much of the range of the turtle is in temperate regions too cold for the formation of coral sand. Some colonies of loggerheads nest on coral beaches such as at Heron Island, Australia (Bustard and Greenham, 1968). In Tongaland, sand particle size seems to be of negligible importance to loggerheads in their choice of nesting beaches (Hughes, 1974a).

During my study at Ascension I tried to learn what influence particle size distribution has on both a female's choice of nesting beach, and on clutch viability. I found that there is an optimum range of grain sizes for hatching success (Chapter 5). Nests can fail in sand that is either too fine or too coarse. One would thus expect turtles to evolve an ability to select beaches at which their eggs would have the best chances of survival. Contrary to my expectations, I found no correlation between the average percent hatching emergence at Ascension beaches, and nesting density on those beaches (see result section). Ascension turtles lay eggs in media ranging in texture from that of dust to that of gravel. This provides further and quite anomalous evidence that grain size is not of over-riding importance to a turtle in her choice of a nesting beach. Characteristics of the offshore approach may be of greater importance.

### Biotic Factors Influencing the Utilization of Nesting Beaches

The nesting sites for many major sea turtle populations are islands, which are usually characterized by relative freedom from mammalian predators, at least prior to man's arrival. Even mainland nesting populations often utilize stretches of coastline that are in effect islands, in that they are partly cut off from optimal habitats of mammalian predators by barriers such as rivers and lagoons, or by environments hostile to predators. For example, the 32 km of coastline that serve as the nesting beach of the Tortuguero green turtle population is bounded at each end, and behind by rivers.

Competition from other species of sea turtles may also influence choice of nesting beach. Larger species, such as the leatherback, can easily destroy the nests of smaller sea turtles during the process of digging their own egg chambers. When leatherbacks and other species of sea turtles nest in the same vicinity, they tend to segregate either spatially, as is the case in Malaysia (Hendrickson and Balasingam, 1966), or temporally, as at Tortuguero, Costa Rica (Carr and Ogren, 1959). It is probably no coincidence that the most important nesting beach of the small olive ridley in the western Atlantic is a stretch of shoreline in Surinam, fronted by an extensive offshore mud bank (Schlulz, 1975). The mud bank seems to hinder the approach of the larger green and leatherback turtles which could destroy the shallow nests of the ridleys.

Probably in the course of the evolutionary history of sea turtles, such biotic factors as predation and competition have been more important than purely geological characteristics in determining which beaches were used for nesting.

### Human Alteration of Beaches

At Ascension, I found that nesting females tend to shun beaches where there is artificial lighting nearby, even if the light does not shine directly on the beach. Stancyk and Ross (1978) also found evidence of less frequent nesting on Ascension beaches near civilization. Artificial lighting has long been recognized as a disruptive agent at turtle nesting grounds (Carr and Ogren, 1959), but its effect has not been examined in sufficient depth.

Light has been shown to disorient newly-emerged sea turtle hatchlings of all species for which there are data--leatherbacks (Carr and Ogren, 1959), green turtles (Carr and Ogren, 1960), loggerheads (McFarlane, 1963; Mann, 1978; Fletemeyer, 1979) and hawksbills (Philibosian, 1976). However, the effect of artificial lights on nesting females seems to vary somewhat between species. Green turtles nesting at Merritt Island, Florida (Ehrhart, 1979), Tortuguero, Costa Rica (Carr *et al.*, 1978) and Ascension Island avoid beaches where artificial lights are visible. Although moving lights will frighten nesting females of all species, there is evidence that stationary artificial light has little effect on nesting female loggerhead turtles (Mann, 1978; Ehrhart, 1979). To establish controls that will limit human impact on nesting beaches, tolerable levels of light must first be determined.

In the past, not enough consideration has been given to the possible damage to incubating nests caused by vehicular and foot traffic on beaches. Recently however, Mann (1977) and Fletemeyer (1979) have independently demonstrated that compaction of sand by these two factors can preclude the successful emergence of hatchlings. Mining of beach

sand can also have a devastating and long term effect on nesting beaches (Sella, in press).

Unfortunately, some encroachment of human activities and development on beaches is unavoidable. Information that will enable us to develop coastlines in a manner compatible with sea turtle nesting requirements is badly needed.

#### Population Estimate

Seasonal and ontogenetic changes in habitat occupation make sea turtle populations difficult to census. The most feasible approach is to monitor the arrivals of females at the nesting beach (Carr *et al.*, 1978; Meylan, in press b). However, since nesting activity is subject to large annual fluctuations, data need to be gathered during more than one season for an estimate to be of much value.

I estimated that approximately 2,600 female green turtles nested at Ascension during the 1976-77 season, and 1,800 in 1977-78 (Table 10), averaging about 2,200 turtles per season. These data indicate that the Ascension green turtle colony is the second largest in the West Atlantic system. It is much smaller than the Tortuguero colony in Costa Rica which has been estimated by Carr *et al.* (1978) to range from 5,723 to 23,147 nesting females per year, but is larger than the one in Surinam for which Schulz (1975) reported an average of 1,500 to 2,000 green turtle females per season during the period 1968 to 1974.

Carr *et al.* (1978) proposed a formula for calculating the total sexually mature population from yearly arrivals at the Tortuguero nesting ground. However, as pointed out by Carr (Caribbean Conservation Corporation, 1980) there are several drawbacks to this method, the most

serious being that the equation is based on the assumption that the entire nesting population will make, or has already made, a nesting remigration. In fact, only about 30%-40% of each season's nesters are ever seen again at Tortuguero. Hughes (in press) suggests that the reason the majority of turtles tagged are never seen again may be either mortality or a natural tendency of females to nest only once in their lifetime. Until we come to terms with the problem of the "lost majority" no satisfactory estimate of the sizes of total populations can be made.

CHAPTER 5  
INFLUENCE OF PHYSICAL AND BIOTIC FACTORS ON  
EGG AND HATCHLING VIABILITY

Introduction

Hatching success has usually been studied under hatchery conditions. Relatively few investigators have measured survival of hatchlings in completely undisturbed nests. The most important such studies are those of: Baldwin *et al.* in South Carolina (Caldwell *et al.*, 1959); Ragotzie in Georgia (1959); Carr and Hirth at Ascension (1962); Gallagher *et al.* in Florida (1972); Bustard in Australia (1972); Schulz in Surinam (1975); Mann in Florida (1978); Balazs in Hawaii (1979); Fowler at Tortuguero, Costa Rica (1979); and Hopkins *et al.* in South Carolina (1980). Of these, only Baldwin *et al.*, Balazs, Bustard and Fowler indicated the mortality occurring at each developmental stage.

We know very little about the influence of chemical and physical environmental factors on hatching and emergence success. The effects of salinity, moisture, and sand temperatures were examined by Bustard and Greenham (1968); and McGehee (1979). Ackerman and Prange (1972); Ackerman (1975; 1977; 1980; and in press) and Prange and Ackerman (1974) described the process of gas exchange in sea turtle nests. Simkiss (1962) and Bustard *et al.* (1969) investigated the possibility of ion uptake from sources external to the eggs during embryonic development.

The diversity of the beach types at Ascension provides an ideal natural laboratory in which to study the effects of various

environmental parameters on hatching success. In the present study I compared the viability of clutches laid on different beaches. I recorded the amount of mortality and the stages at which death occurred, and determined whether hatching success was correlated with: depth of the nest, position of the nest on the beach, and several physical and chemical characteristics of the sand in which the clutch was incubated. These parameters were particle size distribution, salinity, moisture content, hydraulic conductivity, pH, percent organic carbon and percent calcium carbonate. The effect of predators on eggs and hatchlings was also investigated.

### Methods

#### Determination of Clutch Viability

Relative hatching and emergence success was determined by examining the contents of nests from which young had hatched and emerged from the sand. Initially, an attempt was made to mark clutches when they were laid and subsequently to excavate them at the end of their incubation period; but the heavy nesting density on most of the beaches, coupled with the propensity of Ascension turtles to dig multiple nest pits, resulted in so much shifting of sand that it was difficult to locate marked nests at a later date. I was able to locate only three of nearly twenty nests that had been marked.

Nests from which at least some young had emerged were found either by back-tracking the seaward paths of hatchlings or by looking for the saucer-shaped depressions in the sand indicative of hatchling activity below the surface. On Spire and Pebbly West beaches, poor

hatching success made successful emergence such a rarity, that to locate nests, I dug a trench across a portion of each beach and examined all egg clutches encountered. To insure even sampling among the beaches, data obtained in this manner are considered separately from those obtained by the first method.

For each nest, its location on the beach platform, its distance from the high tide line, and its depth from the surface of the sand were recorded. The position of hatchlings encountered in the sand column above each nest chamber was recorded. The likelihood of their successful emergence from the sand was assessed, on the basis of the apparent physical state of each turtle, its distance from the surface, and the number of individuals found together. Because vertical movement through the sand is a cooperative endeavor, successful emergence is unlikely in groups composed of less than about five individuals (Carr and Hirth, 1961).

The number of empty egg shells, unhatched eggs, embryos that died while in the process of pipping, and dead and living hatchlings remaining in the egg chamber were counted. In most cases the empty shells from hatched eggs were undamaged except at the point of exit by the hatchling. Unhatched eggs were opened and examined for signs of development, and the lengths of any embryos present were measured. Because about one third of the intact eggs were rotten, I could not confidently distinguish between those that died during early embryonic development and those that were infertile. However, it was always possible to distinguish late stage embryos that had died.

### Characterization of the Incubating Medium

Beach sand was analyzed by the methods described by the Soil Conservation Service, U.S.D.A. (1972) except as otherwise indicated. The samples were taken by two methods. To characterize nesting beaches, a minimum of three sand samples was taken from each beach at regular intervals along a transect paralleling the shoreline in the zone with the greatest density of body pits. Longer beaches were sampled at 50 m intervals. At each sample station, 500 g of sand were taken from the surface, from 30 cm and from 90 cm. All samples from the same level on the same beach were mixed and a subsample was selected and analyzed. Measurements were made of percent water content ( $\text{g H}_2\text{O/g dry sand}$ ), the pH (using the water dilution method), and the electrical conductivity of a saturation extract of the sand. Percent organic carbon present was determined by acid dichromate digestion, and calcium carbonate was determined by the titrimetric method (using HCl and NaOH). Particle size distribution was determined by the hydrometer method (Black *et al.*, 1965).

To evaluate the microenvironment in nests, a 500 g sample of sand was collected adjacent to the egg chamber of each of 56 nests at the time the nest was excavated for determination of hatching success. These samples were analyzed for percent water content, particle size distribution and electrical conductivity.

Hydraulic conductivity (*i.e.* the readiness with which water flows through a soil in response to a given potential gradient) was measured for the saturated beach sands from the eight beaches for which I had gathered the most complete data on hatching and emergence success. I

compared the hydraulic conductivities to estimate the relative rates at which gas would diffuse through the sands.

#### Predation Upon Eggs and Hatchlings

All observed incidents involving predation on eggs and hatchlings were recorded. With snorkelling gear I also trailed hatchlings at a distance of about 4 m, to see what preyed upon them in the inshore waters, as they swam away from the nesting beach. I did this in the daytime and at night, and followed the turtles until they were in water about 15 m deep.

### Results

#### Hatching and Emergence Success

Seventy six nests, distributed over 14 beaches, and all showing signs of hatchling emergence from the sand, were examined. I determined what percentage of each clutch met the following fates: successful hatching (*i.e.* emergence from the shell), successful emergence from the sand after hatching, death in the process of pipping, death within the intact egg; and death at a late developmental stage within the intact egg. The relationship between the amount of mortality in each developmental stage and various physical and chemical parameters of the incubation environment are examined below. Table 11 shows the fate of each of 9,987 eggs in the 76 emerged clutches. Table 12 summarizes, by beach, the data gathered from these nests, excluding beaches from which only one nest was excavated. The Duncan's multiple range test (Steel and Torrie, 1960) was used to determine whether the beaches differed

Table 11. Fates of eggs in 76 nests from which hatchlings emerged.

Egg Fate	Number of Eggs	Percent of Total Eggs	Number of Nests	Percent of Nests
<b>Hatched</b>				
Emerg'd from surface of sand	6956	69.65	76	100.00
Died, in nest	122	1.22	28	36.84
Died, above nest	237	2.37	20	26.32
Alive, in nest	147	1.47	38	50.00
Alive, above nest	95	0.95	27	35.53
Turtles with deformities, in or above nest	17	0.17	13	17.11
<b>Total Hatched</b>	<b>7574*</b>	<b>75.84</b>		
Died while pipping	886*	8.87	53	69.74
<b>Unhatched</b>				
Infertile/Undeveloped	407	4.08	60	78.95
Decomposed; age indeterminable	355	3.55	54	71.05
Normal embryos				
0-2 cm total length	48	0.48	19	25.00
2-4 cm total length	53	0.53	15	19.74
4-6 cm total length	34	0.34	16	21.05
Full term embryos	599	6.00	51	67.11
Deformed embryos	14	0.14	11	14.47
Albinos	3	0.03	3	3.95
Yolkless	14	0.14	6	7.89
<b>Total Unhatched</b>	<b>1527*</b>	<b>15.29</b>		

\* 9987 total eggs examined.

Table 12. Percentages and causes of mortality in eggs and hatchlings at Ascension beaches studied. The figures show means and standard deviations (in parentheses) of percentages of each mortality type recorded. Within each column, identical superscripts denote beaches that do not differ significantly (Duncan's multiple range test;  $p < 0.05$ ). Only beaches with sample sizes greater than two were considered by the Duncan's multiple range test. Spire beach was not considered because the sampling technique used there was used nowhere else.

Beach Sampled	N = No. of Nests	Emergence** Success	Hatching Success	Intact Eggs	Died While Pipping	Embryos That Died at Late Stage	Embryos That Died Pipping or at Late Stage	Died Between Times of Hatching and Emerging From Sand
South West Bay N = 14	71.09 <sup>a,b</sup> (24.77)	84.09 <sup>a,b</sup> (12.36)	9.03 <sup>a,b</sup> (9.03)	6.87 <sup>a,b,c</sup> (9.23)	2.79 <sup>a</sup> (4.14)	9.53 <sup>a,b</sup> (9.36)	12.99 <sup>a</sup> (24.12)	
Payne Point N = 2	79.79 <sup>†</sup>	81.11 <sup>†</sup>	18.89 <sup>†</sup>	0 <sup>†</sup>	10.23 <sup>†</sup>	10.23 <sup>†</sup>	1.32 <sup>†</sup>	
Long Beach N = 17	82.13 <sup>c</sup> (12.44)	85.52 <sup>a,b</sup> (12.28)	12.31 <sup>a,b</sup> (11.94)	2.16 <sup>c</sup> (3.26)	3.03 <sup>a</sup> (4.80)	5.19 <sup>b</sup> (6.66)	3.39 <sup>b</sup> (7.10)	
English Bay N = 6	63.93 <sup>a,b,c</sup> (14.49)	75.98 <sup>a,b</sup> (14.36)	18.66 <sup>a,c</sup> (15.83)	5.36 <sup>a,b,c</sup> (8.92)	2.44 <sup>a</sup> (2.78)	7.80 <sup>a,b</sup> (7.72)	12.06 <sup>a</sup> (13.57)	
Porpoise Point 1 & 2 N = 5	92.25 <sup>c</sup> (6.84)	94.57 <sup>c</sup> (3.23)	4.14 <sup>b</sup> (2.74)	1.29 <sup>b,c</sup> (0.60)	0.37 <sup>a</sup> (0.52)	1.66 <sup>b</sup> (0.94)	2.32 <sup>a,b</sup> (3.84)	
Porpoise Point 4 N = 2	76.42 <sup>†</sup>	83.75 <sup>†</sup>	12.01 <sup>†</sup>	4.25 <sup>†</sup>	2.03 <sup>†</sup>	6.27 <sup>†</sup>	7.33 <sup>†</sup>	
Porpoise Point 5 N = 2	88.29 <sup>†</sup>	89.75 <sup>†</sup>	8.79 <sup>†</sup>	1.46 <sup>†</sup>	2.44 <sup>†</sup>	3.90 <sup>†</sup>	1.47 <sup>†</sup>	
Hannay Beach N = 9	45.60 <sup>c</sup> (17.39)	50.04 <sup>c</sup> (20.38)	22.09 <sup>a,c</sup> (23.08)	27.87 <sup>d</sup> (16.79)	8.06 <sup>a</sup> (13.32)	35.92 <sup>c</sup> (20.08)	4.44 <sup>a,b</sup> (6.06)	
North East Bay N = 13	71.61 <sup>a,b</sup> (21.11)	74.73 <sup>b</sup> (19.59)	15.68 <sup>a,b,c</sup> (13.41)	9.59 <sup>a,b</sup> (10.64)	8.29 <sup>a</sup> (11.40)	17.87 <sup>a,c</sup> (18.82)	3.18 <sup>a,b</sup> (4.98)	
Pebbly West and East N = 4	50.59 <sup>b,c</sup> (24.90)	55.01 <sup>c</sup> (22.19)	30.89 <sup>c</sup> (18.17)	14.10 <sup>a,d</sup> (7.76)	21.85 <sup>b</sup> (14.60)	35.95 <sup>c</sup> (19.69)	4.42 <sup>a,b</sup> (7.13)	
Spire Beach N = 8	0 <sup>*</sup> (0)	0 <sup>*</sup> (0)	100.00 <sup>*</sup> (0)	0 <sup>*</sup> (0)	0 <sup>*</sup> (0)	0 <sup>*</sup> (0)	0 <sup>*</sup> (0)	

<sup>†</sup> Sample size too small for Duncan's multiple range test.

<sup>\*</sup> Data gathered by digging trench across beach.

<sup>\*\*</sup> Emergence from sand.

significantly with respect to the various types of egg and hatchling mortality observed (Table 12). A Spearman rank test (Siegel, 1956) showed no significant correlation ( $p < 0.05$ ) between clutch size and hatching success, or between clutch size and emergence success on any given beach or when all nests were considered together. Clutch size of Ascension turtles is discussed in Chapter 2.

#### Influence of Beach Sand on Clutch Viability

In the following sections, observed rates of hatching success of egg clutches are correlated with characteristics of the beach sand (particle size distribution, hydraulic conductivity, salinity, percent organic matter and pH) in which the eggs were incubated.

#### Particle size distribution

For each sand sample collected, the mean particle diameter, sorting coefficient, skewness and kurtosis were calculated, by equations developed by Folk and Ward (1957). Sand particle diameter is expressed in phi units:  $\phi = -\log_2 \text{diameter (mm)}$ . Only two of these mechanical properties, mean particle diameter and sorting (the measure of uniformity of the particles), seem to affect hatching success. Table 13 shows the average mean particle size, sorting coefficient, percent silt/clay and percent material greater than 2 mm in diameter by weight for each of the twelve Ascension beaches from which I obtained data on hatching success.

Based on the parent material and the sorting properties of their sand these beaches can be divided into two groups. The sand of eight of the beaches is primarily biogenic. It is light in color, consists

Table 13. Physical parameters of beach sand. The figures are the averages of all measurements taken from sand collected at nest level on each beach.

Beaches	Mean Particle Diameter ( $\phi$ ) <sup>*</sup>	Sorting Coefficient	% Silt/Clay	% > 2 mm Diameter	% H <sub>2</sub> O Content (g H <sub>2</sub> O/g Dry Sand)	% Organic Matter	pH	Electrical Conductivity (mmho/cm)	% Calcium Carbonate	Hydraulic Conductivity cm/min
Biogenic Origin										
Porpoise Pt. 1 & 2	0.95	0.67	0.98	0.99	4.56	0.26	8.7	0.44	96.1	3.94
Payne Pt.	0.68	0.86	2.24	4.77	5.55	0.24	8.8	1.36	93.6	--
Long	0.56	0.96	1.59	4.51	3.14	0.19	9.0	0.36	93.0	5.54
Porpoise Pt. 5	0.43	0.98	2.97	5.23	5.17	0.33	8.6	0.90	92.3	--
English Bay	0.39	0.53	0.97	1.43	3.56	0.22	9.0	0.24	97.4	15.71
South West Bay	0.27	0.85	2.01	5.30	3.76	0.28	9.2	0.41	93.5	8.17
Ilannay	0.14	0.63	0.70	2.85	4.45	0.26	8.8	0.56	73.7	17.35
Porpoise Pt. 4	0.06	1.02	2.08	13.84	6.78	0.36	8.5	1.04	88.4	--
Volcanic Origin										
North East Bay	1.43	1.01	1.07	2.51	3.47	0.22	9.0	0.44	47.6	1.42
Pebbly West	- 0.33	1.83	3.73	24.65	5.90	0.16	8.6	3.08	4.0	1.56
Pebbly East	- 0.91	1.78	2.76	33.93	11.41	0.24	7.9	6.10	17.6	--
Spire	0.79	2.82	10.65	26.38	5.91	0.10	7.0	7.25	0.9	0.33

\*  $\phi$  = - log<sub>2</sub> particle diameter (mm).

of more than 70% calcium carbonate, and is "moderately" to "moderately well" sorted (Folk, 1966), with mean sorting coefficients ranging from 0.53 to 1.02. (Higher sorting coefficients indicate poorer sorting, or less uniformity in particle size.) Table 13 shows the average percent calcium carbonate content measured for each beach. The remaining four beaches are dark in color, primarily volcanic in origin, with "poorly" to "very poorly" sorted sand in which mean sorting coefficients range from 1.01 to 2.82. Figure 30 shows the relationship between mean particle size, sorting properties, and the average emergence success in nests measured at each beach. Figure 31 plots the average mean particle diameter and average sorting coefficient measured at each of the 32 Ascension beaches.

The relationship between various types of egg mortality and mean particle diameter was determined only for the biogenic beaches. Mean particle size is not a good index for comparing sands whose sorting coefficients differ greatly, and it becomes less useful when applied to more poorly sorted sands.

A Spearman rank correlation was used to determine the relationship between the mean particle size of the sand samples and various aspects of hatching and emergence success for the 44 nests distributed over nine biogenic beaches for which samples of sand had been collected near the egg chamber. In those cases in which the correlation was statistically significant, survival increased as mean particle size increased. Mean particle size was positively correlated with total emergence ( $r = 0.3733$ ;  $N = 44$ ;  $p < 0.01$ ), and negatively correlated with the percent that died after hatching, but before reaching the surface ( $r = -0.3563$ ;  $N = 44$ ;  $p < 0.05$ ).

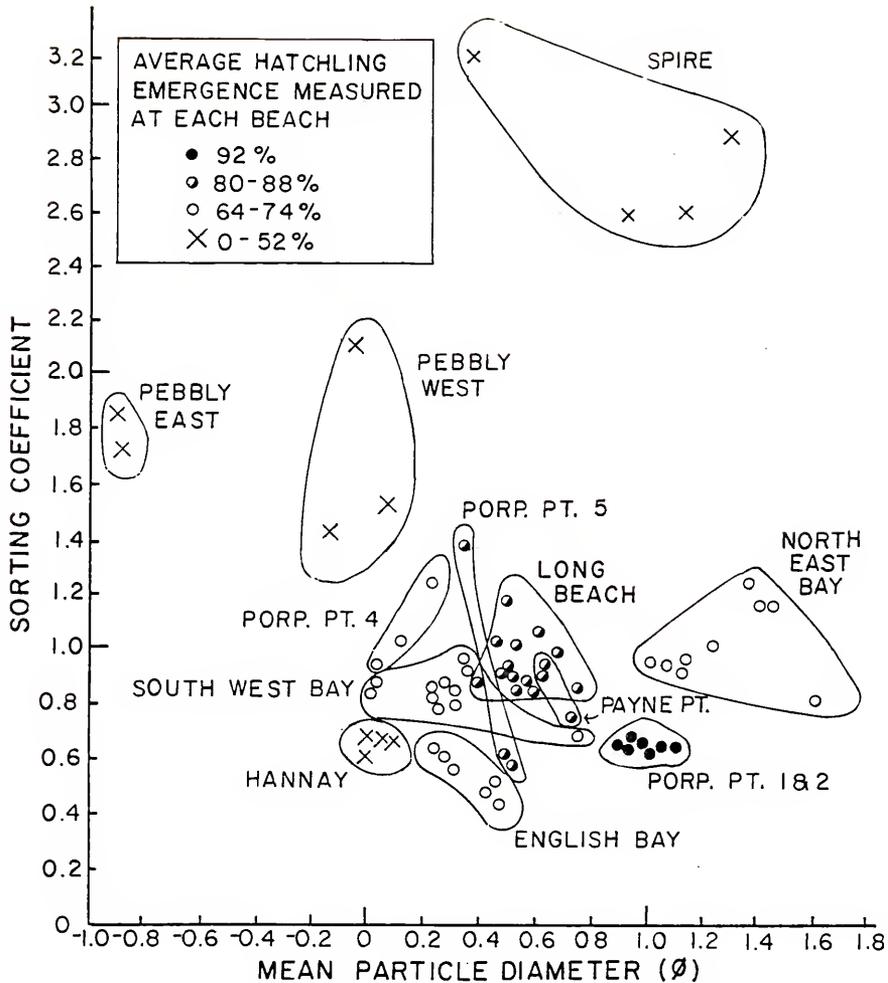


Figure 30. Relationship between mean particle size and sorting coefficient, and average emergence success of clutches. Each point indicates a sand sample, and is coded by a symbol that shows the mean percent emergence success of all clutches examined on the beach from which it was collected. The outlines group samples collected from the same beach. Mean particle diameter is expressed in phi units, where  $\phi = -\log_2$  particle diameter (mm); thus, mean particle size decreases along the x-axis.

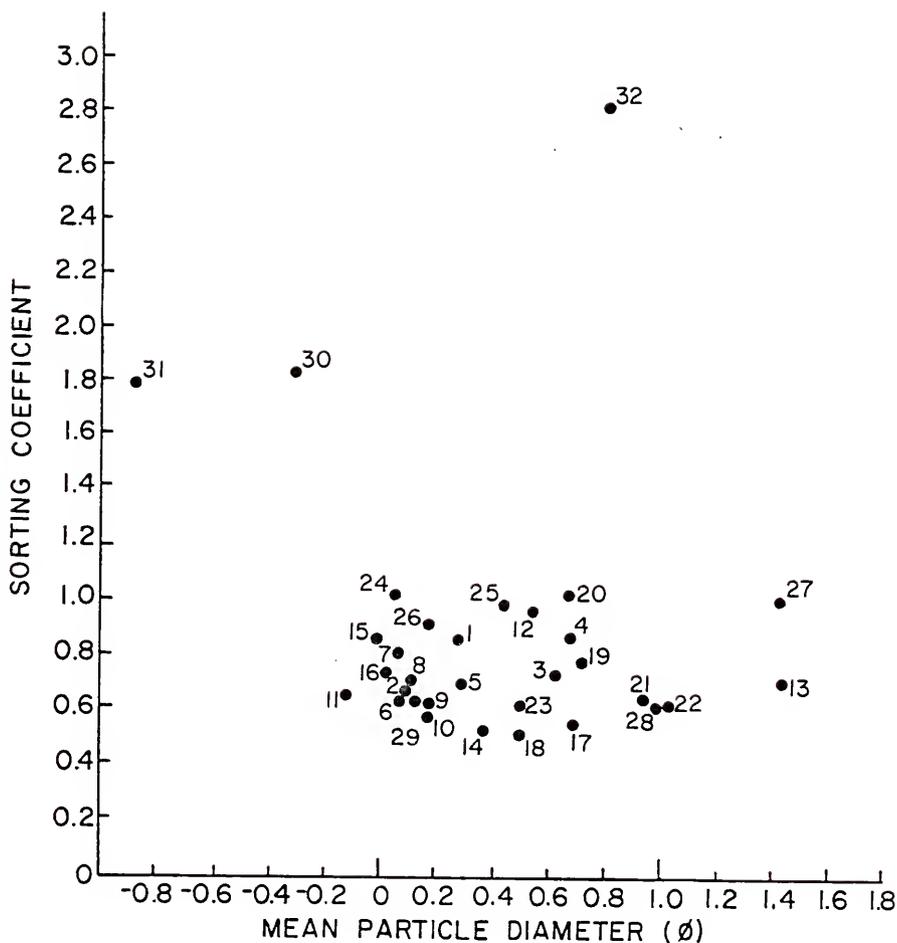


Figure 31. Average mean particle diameter plotted against the average sorting coefficient of sand collected at each of the 32 Ascension Island beaches. Mean particle diameter is expressed in phi units, where  $\phi = -\log_2$  particle diameter (mm); thus, mean particle size decreases along the x-axis. The beach numbers correspond to those on the map in Figure 1.

A Spearman rank test was also used to compare the average hatching and emergence success of all nests examined on each of the eight biogenic beaches, with the average value for mean particle size determined from all sand samples taken at nest level on each beach (cf. Tables 12 and 13). Mean particle size was positively correlated with percent total emergence ( $r_s = 0.74$ ;  $N = 8$ ;  $p < 0.05$ ); and negatively correlated with the percent which died in the process of pipping ( $r_s = 0.81$ ;  $N = 8$ ;  $p < 0.05$ ), and with the percent that died after hatching but before reaching the surface of the sand ( $r_s = 0.69$ ;  $N = 8$ ;  $p < 0.05$ ). The relationship between mean particle diameter and clutch viability in the volcanic sands was not examined because of the poor sorting properties of these sands.

#### Hydraulic conductivity

The hydraulic conductivity, measured in cm/min, of eight of the beach sands is shown in Table 13. The coarser grained sands generally have higher rates of hydraulic conductivity, indicating that water, and presumably also gases, would flow or diffuse more readily through them.

#### Salinity

Electrical conductivity (mmho/cm) was used as an index of beach sand salinity. On each beach, values obtained at the surface were often higher than those taken at either 30 or 90 cm depth. Table 13 shows the average values measured at nest depth for each beach. In general the volcanic sands were more saline than those of the biogenic beaches.

The Spearman rank test was used to examine the correlation between various measures of hatching and emergence success of nests and the level of conductivity in corresponding sand samples. When all 56 nests were

considered, a positive correlation was found between conductivity and both the percentage of total eggs which did not hatch ( $r = 0.3553$ ;  $p < 0.01$ ), and the percentage of eggs which had died unhatched at a late stage of development ( $r = 0.3288$ ;  $p < 0.01$ ).

#### Percent organic matter

The percent organic matter in the sand was estimated by multiplying the values obtained for percent organic carbon by the conversion factor 1.724 (Jackson, 1958). The amount of organic carbon measured was low in all cases with little variation among beaches (Table 13), and there was no significant correlation between percent organic matter and hatching success ( $p < 0.05$ ).

#### pH

The Ascension beach sands are slightly basic (Table 13). On most beaches the values at 30 and 90 cm depth were similar to each other, but sand measured at the surface tended to be about 0.2 to 0.4 units more neutral. There was no significant correlation between hatching success and pH ( $p < 0.05$ ).

#### Distance from the Sea

A Spearman rank test showed a positive correlation between hatching success and the distance of the nest from the high tide line both when all 56 nests were considered ( $r = 0.4436$ ;  $p < 0.001$ ), and also when only the 44 nests from the biogenic beaches were considered ( $r = 0.0160$ ;  $p < 0.05$ ). However, when each beach was considered separately, only on Long Beach was there a significant correlation between hatching

success and distance from the high tide line ( $r = 0.7666$ ;  $N = 12$ ;  $p < 0.005$ ).

#### Nest Depth

The distance between the floor of the egg chambers and the surface of the sand ranged from 50 to 155 cm ( $\bar{x} = 87.59$  cm; S.D.  $\pm 16.54$ ) at the time the nests were excavated. The relationship between hatching success and nest depth was tested with a Spearman rank correlation. Both the percentage that died while pipping ( $r = -0.2323$ ;  $N = 70$ ;  $p < 0.05$ ), and the sum of the percentage of those which died while pipping and those embryos which died intact at a late stage of development ( $r = -0.2567$ ;  $N = 70$ ;  $p < 0.05$ ), showed significant negative correlation with depth. There was no correlation ( $p < 0.05$ ) between nest depth and the percentage of individuals which died while making their way from the nests to the surface of the sand.

#### Predation upon Eggs and Hatchlings

The observed cases of predation are described in the Discussion section.

### Discussion

#### Effect of Particle Size Distribution

The hatching and emergence success of nests varies from beach to beach at Ascension, ranging from an estimated low of 0% viability at Spire Beach to 92.3% at Porpoise Point 1 and 2. Because most of my data deal with nests that had at least some successful emergence of

hatchlings, the figures obtained are over-estimates of the rate of hatchling production at each beach. Heavy nesting density made it impossible to monitor nests throughout their entire incubation periods, so I was unable to determine for each beach what percentage of clutches failed to hatch because of infertility, erosion, inundation, destruction by nesting females, or some other factor. However, I believe that my data accurately portray the relative survival in nests in the different beach sands.

Most of the variation measured appears to be attributable to differences in the composition of the sand in which the nests are incubated. Particle size distribution seems to be the most important single physical parameter involved. The data suggest that eggs are most viable (*i.e.* with better than 80% emergence success) when laid on beaches with both relatively well sorted sand (the sorting coefficients of which are smaller than about 1.3), and mean particle diameters ranging from about 0.38 to 1.08.

Clutch viability is very low in poorly sorted sand (Fig. 30), probably because the rate of gas diffusion is impeded. The hydraulic conductivity measurements made on the sands do not tell the absolute rate at which gas diffuses, but are used to compare the relative rates of gas diffusion in the beach sands. The lowest hydraulic conductivity was in sands from Spire, Pebbly West and North East Bay beaches (Table 13). No emerged nests were found on Spire beach, which has the least well sorted sand of all the beaches (Table 13), so a trench had to be dug across the beach to determine hatching success. None of the eggs from Spire beach showed signs of development beyond the formation of blood spots on the yolk. The data shown in Table 12 estimating success

at two other very poorly sorted beaches, Pebbly West and Pebbly East, are overestimates, because the information was obtained only from nests from which hatchlings emerged, whereas successful emergence is actually rare on those beaches. A trench dug across a portion of Pebbly West beach exposed seven nests, only one of which showed any sign of hatching success. On this beach also, the highest proportion (7%) of embryos died at intermediate stages of development, with total lengths of embryos between 0 and 55 mm. This evidence suggests that mortality occurs throughout the incubation period. The earliest mortality is probably suffered by eggs located near the interior of the egg mass. Individuals there would suffocate when their more favorably situated siblings outcompete them for oxygen.

Impeded gas diffusion only partially explains nest mortality. At Ascension, mortality while pipping seems higher than in other populations. An estimated 9% of the eggs examined in the present study died at this stage. Although it may have occurred, mortality at the pipping stage was not mentioned in any study except that by Baldwin *et al.* (Caldwell *et al.*, 1959), in which a figure of only 0.5% was reported. Mortality also is unusually high in Ascension hatchlings between the time they emerge from their eggs and when they erupt from the sand. I recorded an average rate of 6.2% mortality at that time, which is higher than that reported by other investigators--0.6% (Caldwell *et al.*, 1959) 5.9% (Balazs, 1979), and 3.4% (Fowler, 1979).

Sand cave-ins may at least partly explain both types of mortality at Ascension. Kraemer and Richardson (1979) showed that just prior to pipping, the volume of the egg mass decreases because of loss of turgor in the eggs. The resulting air space probably gives the pipping embryos

more room for movement, and facilitates their escape from the eggs. If sand collapsed the air space around them, they might be unable to free themselves. In 67.1% of the nests, I encountered half-pipped turtles with their head and one or two flippers out of the shell, or eggs in which the young turtles had died after only slitting the shell. Possibly, the unhatched individuals get trapped by cave-ins brought on by the movements of their already hatched siblings. Carr and Hirth (1961) demonstrated that during their vertical migration between the nest and the surface of the sand, groups of hatchlings maintain an air-space above them and move upward by scraping sand from the ceiling of the chamber and trampling it into the floor. If, however, the ceiling caves in on them they would eventually suffocate. Although I found no direct evidence of cave-ins, on eleven occasions at points between 10 and 30 cm from the surface of the sand, I found masses of dead hatchlings numbering between 4 and 162 individuals ( $\bar{x} = 34$ ).

Thus, cave-ins may explain why emergence success is relatively low even on such beaches as English Bay and Hannay, whose low sorting coefficients, large mean particle diameters, and low moisture content (Table 13) would enhance aeration. Although moisture inhibits gas diffusion, dry sand is more susceptible to slippage. Slippage also increases with particle size. The highest percentage of post-hatching mortality occurred at biogenic beaches with the largest mean particle sizes (Tables 12 and 13) and a significant correlation was found between mean particle size and post-hatching mortality. Correlation was also found between mean particle size and the percentage that died while pipping. The relatively low post-hatching mortality measured at Hannay beach

may be an underestimate caused by the extremely high density of nesting females on that beach. During the process of digging their own nests, turtles may have scraped away dead or dying hatchlings in the sand column above previously emerged nests that had not yet been excavated by me.

Figure 30 shows the relationship between the mean particle size and sorting properties of sand samples collected at each of twelve beaches, and average percent emergence success at each beach. These twelve beaches were the sites at which the most complete hatching success data were collected; they represent the extremes of beach conditions on the island. Actually, the average sorting coefficients of most of Ascension's beaches is below 1.02 and mean particle diameters in most cases range from almost zero to 1.08 (Fig. 31).

#### Nest Depth and Moisture Content

Because nesting is very dense on many of the beaches, there is much shifting of sand by the turtles, and the sand under which an egg clutch is buried can vary considerably in depth during the two months of incubation. Therefore, the nest depth measured after emergence may accurately represent the situation only during the latter stages of incubation. For example, two weeks after I marked one clutch, it was covered by less than 15 cm of sand, but when I excavated it upon emergence it was 155 cm deep, because nesting turtles had thrown sand over the nest site.

It was surprising that no correlation was found between nest depth and mortality among hatchlings as they moved between the nest and the surface of the sand, since the journey would surely take longer when the distance travelled is greater. In the 155 cm deep nest,

apparently healthy hatchlings were found at nest depth in the sand 73 days after the eggs were laid, the first hatchlings having emerged from the sand about seven days prior to that. Incubation usually takes about 60 days (Carr and Hirth, 1962).

There was significant negative correlation between nest depth and mortality during the pipping stage, and also between nest depth and the combined mortality during late-developmental and pipping stages. This is probably because moisture content increases with sand depth. Although precipitation data are not available for some nesting shores, Ascension beaches appear to be among the driest in the world, receiving only about 19.4 cm of rain annually. The average percent water content measured at nest depth in the biogenic beaches and at North East Bay, was 3.92 (S.D.  $\pm$  1.02); the more poorly sorted volcanic beaches were somewhat more moist (Table 13). Ascension eggs probably suffer stress from dehydration. The average percent moisture content at Porpoise Point 1 and 2, the beaches with the highest hatching success rates recorded for the island (Table 12), is above that measured for most of the island's biogenic beaches (Table 13). Ascension turtles experience particularly high mortality during the late stages of development just prior to pipping (Table 11). Possibly this is a response to desiccation. Cunningham and Huene (1938) found evidence that an increase in water uptake toward the end of incubation aided in rupturing turtle eggs.

#### Salinity and the Effect of Rollers

In the present study a significant positive correlation was found between sand salinity levels and the percentage of unhatched eggs, and between salinity levels and the percentage of eggs which died intact at

a late stage of development. Similarly, Bustard and Greenham (1968) and McGehee (1979) found that hatching success decreased as salinity increased. McGehee also found that embryos were least tolerant of high salinity during the latter half of the incubation period. In my study the highest levels of salinity were found in the most poorly sorted sands, which also happened to be those with the lowest rates of hatching success (Tables 12 and 13). Therefore, it is difficult to distinguish between the deleterious effects of high salinity and the effects of low rates of gas diffusion.

It is generally assumed that nests subjected to regular inundation by tides probably suffer high mortality (Hildebrand and Hatsel, 1927; Moorhouse, 1933; Carr, 1967b; Bustard and Greenham, 1968). Ragotzkie (1959) and Plummer (1976) found that inundation by fresh water can drown turtle eggs. However, what effect an occasional dousing by sea water may have on the hatching success of eggs is not well documented. McGehee (1979) found that even a single dousing by sea water causes considerable damage (up to 100% mortality) to the eggs of artificially incubated Florida loggerhead nests. She suspects that the mortality is caused partly by temperature change associated with inundation, and partly by desiccation caused by the high salinity levels.

The beaches at Ascension Island are seasonally subjected to huge waves, locally called *rollers*, which are believed to be generated independently of local weather conditions, by storms in the North Atlantic (Cartwright, 1971; Cartwright *et al.*, 1977). Rollers may occur singly or they may come as a continuous series and pound the shoreline for days at a time. They arrive without warning, and their

impact is magnified by Ascension's lack of a continental shelf. The roller season coincides with the turtle nesting season, and a bout of rollers can devastate large portions of a nesting beach, leaving thousands of eggs strewn over the surface. Entire clutches are also probably drowned when the rollers leave pools of standing sea water on poorly drained portions of a beach. However, it is difficult to ascertain the extent of the damage incurred by egg clutches located in well drained sand and doused by waves.

Long Beach is the beach most seriously affected by rollers. During 1978, I excavated four nests there, all of which were known to have been subjected to two bouts of roller activity, each lasting two days. The rollers arrived during the sixth and ninth weeks of incubation of two of the nests, during the second and fifth week of another, and during the fourth and seventh week of the other. The hatching success ratio of these nests was high, 80.9% to 92.2%. These values are probably inflated, since my sample only includes emerged nests, but these data make it clear that at Ascension dousing by sea water does not necessarily lead to loss of the complete clutch. The fact that the electrical conductivity of sand samples collected at nest level near these clutches was about two to three times the overall average for Long Beach (Table 13) indicates that the salt water probably did reach nest level. Possibly the coarse sand of Long Beach drains water fast enough to minimize the damage. However, the fact that a strong correlation was found between hatching success and distance from the sea at Long Beach suggests that at least some damage may occur.

### Organic Matter, Calcium Carbonate and pH

My measurements of percent organic matter, using acid dichromate digestion, are significantly lower than those obtained by Stancyk and Ross (1978) who used combustion. Paine's (1971) observation that calcium carbonate decomposes at elevated temperatures, probably accounts for their inflated values. Because so little variation among beaches was measured for both the pH levels (which in all cases were 7.0 or slightly higher) and the percent organic matter in the sands (Table 13) it seems that these factors probably do not account for differences in the levels of hatching and emergence success of nests at Ascension Island. It is plausible, however, that if there are nesting beaches elsewhere with very low pH levels, some shell disintegration might occur.

Although Simkiss (1962) theorized that the embryo may obtain some ions, including calcium, from a source external to the eggshell, subsequent studies by Bustard *et al.* (1969) discount this hypothesis. It seems, therefore, that levels of calcium carbonate *per se* probably do not influence hatching success directly.

### Predation

The subject of non-human predation on sea turtle eggs and hatchlings is reviewed by Stancyk (in press). Ascension hatchlings and nests are less subject to natural predation than are those of most other populations.

### Terrestrial and aerial predators

There are no mammals endemic on the island. Domestic cats, introduced to the island by the British in 1815 to control rats, and

again in the 1940's by the U.S. Air Force to control sooty terns (Hart-Davis, 1972), are the most significant terrestrial predators. Officially, the British maintain a cat eradication program, but it is pursued erratically. Some people kill cats, others feed them. Near the beach I have found piles of dead hatchlings killed by cats, with only their carapaces, plastrons and rear flippers remaining. Feral cats detect hatchlings when they are still below the surface of the sand, and dig down and kill most of the clutch by biting their heads (Jimmy Young, pers. comm.). In the Galapagos Islands, Dagmar Werner (pers. comm.) observed similar destruction of hatchling iguanas by feral cats.

Before the introduction of cats, large numbers of seabirds nested on Ascension and at that time may have posed a more serious threat to the hatchlings. Today, the seabird rookeries are mostly restricted to tiny Boatswainbird Island, located just north east of the main island. In the early morning, Frigate birds (*Fregata aquila*) take advantage of the fact that hatchlings usually emerge from the nest only at night when the surface of the sand is cool. While moving upward through the sand from the nest, the hatchlings become inactive near the surface when they encounter sand temperatures higher than about 33°C (Hendrickson, 1958). Later, when the temperature drops, they resume their efforts to reach the surface. At North East Bay, I regularly found comatose hatchlings at the very surface of the sand with their head and sometimes the anterior portion of the carapace exposed. In this position they are able to survive the heat of the day, even though the surface sand exceeds temperatures of 43°C, which would be fatal to them if they were fully exposed above the surface of the sand. Bustard (1967)

described a similar occurrence at Heron Island, Australia. Each morning, frigate birds fly back and forth over North East Bay beach searching for hatchlings, which they pluck out of the sand. They are able to discern a turtle at the surface of the dark sand, even though it is immobile, and no more than the top of its head is exposed. Possibly this behavior in the hatchlings is more likely to be induced by the thermal properties of the dark North East Bay sand than by those of the lighter-colored sands of other Ascension beaches. On only one occasion have I seen Frigate birds which appeared to be hunting in this manner at any other beach.

Dorward (1962) did not record hatchlings as part of the diet of either the White or Brown Booby (*Sula* spp.) at Ascension. These birds rarely forage near shore, but, in view of their large size they certainly seem capable of capturing hatchlings.

In some parts of the world, burrowing ghost crabs (*Ocypode* spp.) do great damage to incubating nests and hatchlings (Stancyk, in press). Ascension has no ghost crabs. Neither the non-burrowing shore crab (*Grapsis grapsis*) which frequents beach rocks at the water line, nor the land crab (*Gecarcinus lagostoma*) found mostly near the northern beaches, preys on hatchlings regularly, and their impact on the turtles is minimal. Although both species readily consume the broken eggs and embryos exposed when nesting females destroy incubating nests, only rarely does *Gecarcinus* burrow in the beaches.

#### Marine predators

The marine environment near Ascension is also relatively devoid of hatchling predators. The diurnal queen triggerfish (*Balistes vetula*),

a species active over sandy bottoms, consumed many of the hatchlings released either singly or in pairs in the daytime. Often two fish would synchronously rise from the bottom, bite the hatchling with their chisel-like incisors and then each swim away with half of the turtle. Octopuses also take hatchlings (Chris Royal, pers. comm).

Local people usually assume that the voracious blackfish (*Melichthys niger*)--abundant in the shallow waters around the island--eat most of the hatchlings that enter the sea during daylight hours. Indeed, from shore one can see the waters churn as these fish swarm around the departing hatchlings. However, during my underwater observations, even in the water most heavily infested with blackfish, I never saw the fish kill or even injure the turtles.

At night, *Epinephelus adscensionis*, a grouper of rocky reefs, is the most important hatchling predator in the littoral zone. Up to eight hatchlings have been found in the gut of a single grouper (Ulas Brown, pers. comm.), and some insensitive fishermen even use live hatchlings as grouper bait. The pierhead workers who clean the fish brought in from deep sea fishing trips--tuna, wahoo and black jack (*Caranx* sp.)--claim they never see hatchlings in the guts of any of them.

Hatchlings departing from beaches with a sandy offshore approach probably are relatively immune from nocturnal predation, which occurs most commonly near rocky reefs. I observed no nocturnal nor diurnal predation after turtles had entered water deeper than about nine meters. Ascension lacks a wide submarine shelf, so that depth is usually reached within a few hundred meters of shore. Dalton (1979) provides evidence that the swimming frenzy of Ascension turtles is shorter in

duration that that of Tortuguero (Costa Rica) hatchlings. These results may be related to the fact that Ascension turtles only need to swim a short distance to escape most inshore predators and to reach the mid-Equatorial current that passes near the island. Tortuguero turtles, on the other hand, would benefit by a longer swimming frenzy, which would carry them beyond the wide continental shelf and the predators inhabiting it.

#### Evolutionary Response to Edaphic Stress and Predation

Ascension's most obvious asset to turtles nesting there is the small numbers of natural predators on hatchlings. At the same time, however, the turtles seem to suffer high clutch mortality induced by beach erosion and inundation by rollers. Egg clutches incubating in the coarse, dry sand risk desiccation and problems associated with cave-ins caused by slippage. Nesting females often destroy previously laid clutches of eggs while digging their own egg chambers. This density-dependent problem is aggravated by sand slippage which forces the turtles to dig multiple pits before successfully laying eggs (see Chapter 2).

Another less obvious benefit that Ascension turtles enjoy is the rapid gas diffusion that occurs, at least in the sands of the biogenic beaches. The average Ascension nest contains 120.9 eggs (see Chapter 2), as compared to an average of 112.2 ( $N = 2,040$ ) at Tortuguero (Bjorndal, 1980). Ascension eggs are also larger; the average Ascension hatchling weighs 30 g while Tortuguero hatchlings only weight 22 g (Ackerman, 1975). Ackerman (1975) found evidence that the weight-specific metabolic rate of incubating Ascension eggs is similar to that of Tortuguero eggs,

but, because both the eggs and the clutches are larger, an Ascension nest would require more oxygen. The hydraulic conductivity (used in the present study as an index for comparing the rates of gas diffusion in the sands) that I measured for the volcanic Tortuguero beach sand (1.91 cm/min) is low compared to the rates for the biogenic beach sands of Ascension (Table 13). If the average sorting coefficient (0.7124) and mean particle diameter (2.1015) of Tortuguero's beach sand were plotted in Figure 30, its position would be outside the region of optimum emergence success recorded at Ascension. Thus, it seems likely that Ascension eggs laid in Tortuguero beach sand would fare poorly.

The reproductive strategy of the Ascension population seems to have evolved in response to a complex interplay between the edaphic conditions on the nesting beach and a low level of predation pressure. The larger size and number of eggs per clutch at Ascension are probably possible because the Ascension sand is generally coarser and better aerated than Tortuguero sand. Larger-sized hatchlings enjoy an added degree of immunity from predation, and larger clutches mean more offspring. Possibly the larger size of Ascension hatchlings may also help them survive for a longer period of time without food, after entering the open sea. Furthermore, no one knows when, or what, Ascension hatchlings first eat; I saw no evidence near Ascension of *Sargassum* rafts, or of any other drifting weed or wrack, generally considered to be the habitat of hatchlings during their first year in the Caribbean (Carr and Meylan, 1980).

CHAPTER 6  
SUMMARY AND CONCLUSIONS

1. The nesting season of the green turtle (*Chelonia mydas*) at Ascension Island runs from December through June, peaking during the months of February, March and April. This period coincides with the wettest and warmest time of the year. The higher levels of rainfall would facilitate nest construction, since the turtles have difficulty digging egg chambers in the coarse, dry Ascension sand. Females usually emerge on two or three successive nights and construct multiple trial nest holes before successful egg laying occurs. While attempting to lay a clutch of eggs, turtles made more emergences and dug more nest holes on beaches with coarser grained sand.
2. Each female lays between one and seven clutches during the season ( $\bar{x} = 2.2$ ), separated by mean intervals of 14.0 days (range seven to 20 days). The average clutch size of Ascension turtles is 120.9 eggs ( $N = 548$ ; S.D. = 26.8). During renesting emergences, the females show a tendency to emerge at the same beach, often to within a few meters of previous nestings, or to an adjacent beach. Stronger site tenacity was evident in renestings separated by less than seven days (assumed to be repeated attempts to lay the same clutch of eggs), than in those separated by longer time intervals. Higher levels of philopatry (return to the same beach or cluster of beaches) were recorded for turtles nesting on longer beaches than on shorter ones.

3. Predictable behavior patterns were observed in females tracked during the interesting interval. There is evidence that after laying eggs females travel to a shallow area off the north west coast of the island. Turtles tracked after frustrated nesting attempts remained within the vicinity of the beach that they had just abandoned. These differences in observed behavior may account for the higher levels of site tenacity observed in nesting emergences separated by less than seven days. Similarly, there were higher levels of site fidelity in turtles nesting at South West Bay beach than at North East Bay beach, and the movements of turtles tracked after frustrated nesting attempts at South West Bay beach were more restricted than those of turtles that had abandoned nesting attempts at North East Bay beach.
4. There have been a total of 64 long distance tag recoveries of turtles tagged at Ascension, all from the coast of Brazil between latitudes  $3^{\circ}$  and  $22^{\circ}$ S. There are 68 records of tagged turtles remigrating to Ascension. The predominant remigratory intervals are four years and three years. Tag loss in remigrant turtles is high at Ascension-- 78%.
5. The physical characteristics of the 32 cove-head nesting beaches of Ascension differ with respect to the following parameters: size and shape; offshore approach configuration (depth, topography); and beach sand type. The nature of the offshore approach exerts more influence on beach selection by nesting females than do features above the high tide line. Nesting is most dense on beaches with unobstructed sandy offshore approaches. The turtles avoid beaches with rock-strewn foreshore, or with artificial lighting nearby. Surprisingly, levels

of nesting density are not correlated with characteristics of the beach sand. Approximately 50% of all nesting activity occurs on three of the 32 beaches--South West Bay beach, Long Beach and North East Bay beach. These beaches should be designated as sanctuaries, and restrictions should be placed on mining of sand there and on construction of beach huts or other lighted buildings in the vicinity.

6. Nesting occurs on all beaches even though on some, hatching success approaches zero. Reproductive success is correlated with characteristics of the beach sand, especially particle size distribution. Sand that is too fine or too poorly sorted probably inhibits gas diffusion. Coarse sand encourages cave-ins. There is evidence that desiccation also reduces hatching success at Ascension. Positive correlation between hatching success and depth of the nest was observed, probably because higher moisture levels occur at greater depths. Elevated levels of salinity, most frequently seen in poorly sorted sand, may induce desiccation through osmotic stress. The positive correlation between hatching success and distance from the sea may be related to inundation by rollers. There is a relative dearth of both terrestrial and offshore predation upon the eggs and hatchlings. Heavy mortality is caused by beach erosion and inundation. Density-dependent mortality occurs when females destroy previously laid clutches while digging multiple trial nest holes.
7. An estimated 2,600 females nested at Ascension during the 1976-77 season, and 1,800 during the 1977-78 season.

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#### BIOGRAPHICAL SKETCH

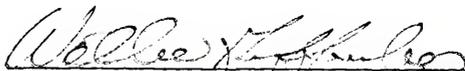
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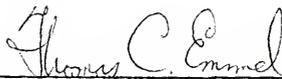
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This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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