THE GREEN SEA TURTLE, *CHELONIA MYDAS* (LINN.) IN MALAYA AND SARAWAK

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(With 10 plates and 15 figures in the text)

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INTRODUCTION

The Green Sea Turtle, *Chelonia mydas*, is one of the few reptiles of economic importance. Throughout its circumglobal range in tropical and subtropical waters it has long received the attention of human beings. While it is probably most widely known for the Green Turtle soup made from its fat, the species usually assumes local importance wherever it occurs because of the edibility of its flesh and eggs.

In Malaya and Sarawak, some millions of *Chelonia mydas* eggs are marketed each year, contributing valuable fats and proteins to the local diet. The present study has been carried out in an effort to contribute to a better understanding of the animals which, it is hoped, can be applied to improved management of the wild populations and the food industry based on them.

Chelonia mydas is reported to be mainly vegetarian, feeding principally in shallow waters. While migrations apparently occur from grazing to breeding areas, there is as yet no proof that the populations concerned here range over great distances. It seems likely that the entire area associated with the shallow waters over the Sunda Shelf (the Gulf of Siam and the southern portion of the South China Sea) could profitably be studied as a distributional unit for *Chelonia mydas*. Possibly the findings from the East Coast of Malaya and from Sarawak, where the present study was carried out, may be taken to represent the entire area. It is hoped that other workers, to whom the remainder of the outlined area is more accessible, will carry out comparable investigations to extend our knowledge of this " most valuable reptile in the world " (Carr, 1952, p. 349). No attempt was made to include the West Coast of the Malay Peninsula in this study. The southern and central portions of the West Coast, facing the Straits of Malacca, are in general flat and muddy, with much mangrove frontage and few sandy beaches suitable for Green Turtle nesting. Relatively few turtles are reported from these waters and there seems to be little nesting in this area. The Malayan and Siamese islands at the north end of the Straits of Malacca are reported to have nesting beaches. Few turtle eggs, however, appear to be marketed from these islands as compared with the large numbers from the East Coast. Because of their apparently minor economic importance and because the populations concerned appear to belong with Indian Ocean complexes rather than with the South China Sea turtles, the northern islands on the West Coast of the Malay Peninsula were not included in this study.

Fig. 1 indicates the principal sites concerned in this study. All are on islands ; all are separated from the adjacent major land masses by water less than 30 fathoms deep.

The details of the taxonomy of the genetic entities within the genus *Chelonia* remain somewhat obscure. The writer follows Carr (1952) in considering that there is a single world-wide species, *mydas*. Further following Carr, the subspecific name *japonica* Schweigger could be used for all Pacific populations. However, as that author points out, there are probably several recognizable forms in the Indo-Pacific area, in which case any present subspecific designation for the turtles concerned in this report is likely to be changed. Taxonomic investigation was not undertaken during the course of this work,

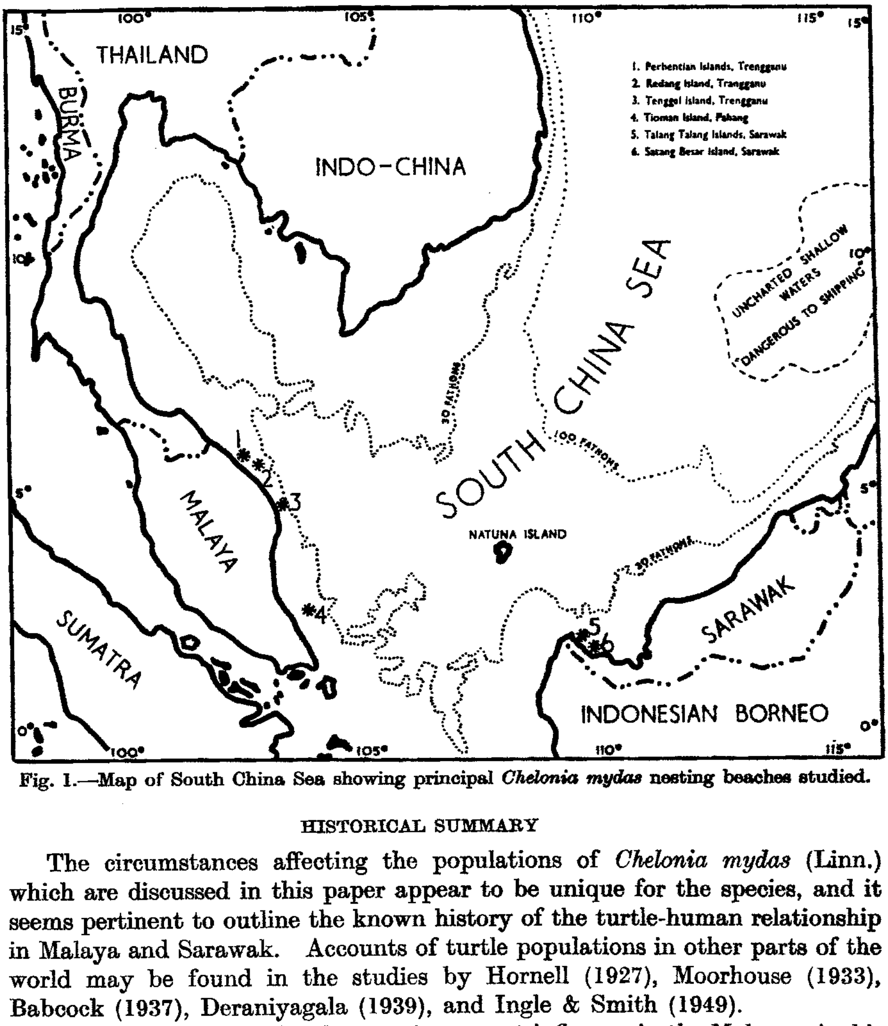

Fig. 1.—Map of South China Sea showing principal *Chelonia mydas* nesting beaches studied.

HISTORICAL SUMMARY

The circumstances affecting the populations of *Chelonia mydas* (Linn.) which are discussed in this paper appear to be unique for the species, and it seems pertinent to outline the known history of the turtle-human relationship in Malaya and Sarawak. Accounts of turtle populations in other parts of the world may be found in the studies by Hornell (1927), Moorhouse (1933), Babcock (1937), Deraniyagala (1939), and Ingle & Smith (1949).

The Muslim religion has been an important influence in the Malayan Archipelago for more than 500 years. For reasons which are not clearly defined, local Muslim custom seems to include a definite prejudice against the eating of turtle flesh, and this semi-religious attitude does not appear to be of recent origin.* It seems reasonable to suppose that in pagan times turtles were

* Careful study of the religious thought followed in Malaya and Sarawak has convinced the writer that, popular opinion notwithstanding, there is no clear religious basis for this belief. The human consumption of Green Turtle flesh is apparently to be considered neither forbidden, nor undesirable on religious grounds. Consultation with the foremost religious authority available has indicated that there is nothing in the Holy Koran which forbids the eating of sea turtles.

The Malay peoples of the areas concerned are mainly followers of the Shafi'i School of Islam. Al-Begermi, an authority of the Shafi'i School, comments as follows regarding human consumption of turtle flesh: "Turtles, if sea turtles, are permissible as food. As for land turtles, they are prohibited..." (Al-Begermi, 1929–30, Vol. 4, p. 260).

killed for food in Malaya and Borneo, and that with the spread of Islam the eating of turtle flesh was virtually stopped. Thus, during the past five centuries there must have been little killing of adult turtles in Malaya and Sarawak. This is in marked contrast to almost all other parts of the range of *Chelonia mydas*, where the animals have been and still are much sought after for flesh and fat, the eggs being of secondary importance. What little slaughter of adult turtles has occurred in Malaya and Sarawak, mostly by immigrant non-Muslim peoples, has been frowned upon or actively punished.

Muslim custom does not prohibit or recommend against the eating of turtle eggs, and these are much sought after as food by the majority of Malaysian peoples. As a result of the exclusive importance of the eggs, a natural conservation policy has developed in which not only are turtles not eaten, but they are protected in varying degree as the providers of food for men. A loose group of folkways has arisen protecting the adult turtles, and nowadays any plans for working with the living animals must be considered in the light of " adat lama " (ancient custom) to avoid giving offence to the local people. The popular attitude against killing of adult animals made it impossible to study food habits, list internal parasites, or carry out other projects which demanded sacrifice and dissection of animals.

In the earliest precise account of Malaysian sea turtles consulted during the compilation of this paper, James Brooke, later Rajah Brooke I of Sarawak, referring to the Sarawak turtle islands, writes on 7th August 1839 :

> " Morning calm. In the afternoon got under weigh, and anchored again near the islands of Talang Talang ; . . . The Bandar of the place came off in his canoe to make us welcome. He is a young man sent by the Rajah Muda Hassim to collect turtles' eggs, which abound in this vicinity, especially on the larger island. The turtles are never molested, for fear of their deserting the spot ; and their eggs, to the amount of five or six thousand, are collected every morning, and forwarded at intervals to Sarawak as articles of food." (Keppel, 1847).

In 1842 Brooke again visited Talang Talang Besar Island while in pursuit of pirates. A journal entry dated 4th May reads :

> " The islands of Talang Talang are two in number, both small and hilly, covered with vegetation, each having a narrow sandy beach. On this sand the turtles, in large numbers, deposit their eggs, which are a source of revenue and profit,... The turtle is the common green species, and a few of the kind which produce the tortoise-shell. They commence laying about the middle of May, a stray one only making its appearance at this season. From the middle of June and July they come up ninety and a hundred of a night ; and as each female, at a fair calculation, deposits 200 eggs (*sic*), there may be reckoned 20,000 eggs nightly, for two or three months. These eggs are exported to Sambas and Pontiana, and along the S.W. coast.... From twenty to forty men live on the island, and it is just the life they like. On the sand they have a small watch house ; and halfway up the hill their dwelling-house, defended by a palisade and guarded by two guns ; and on the hill-top another house, which may be called a place of refuge. From the number of pirates, they are obliged to take these precautions....
>
> I had here an opportunity of seeing a turtle deposit its eggs,... The Malays on watch have small sticks with flags on them, and as each turtle deposits its eggs, they mark the spot with one of these, and the following morning take the eggs, and store them ready for sale. With all their vigilance, however, numbers escape their observation, and some nests they purposely spare. When the young come forth, the sand (which is small) is said to be literally covered with them, and as they make directly for the sea, the sharks and other fish devour great numbers." (Mundy, 1848).

Brooke's description of the egg collection methods on the Talang Talang Islands might be taken as the essence of the methods used there at the present time.* The Rajah Muda Hassim replaced the first and only governor sent to Sarawak by the Sultan of Brunei. It may be that prior to this stage of political organisation, egg collection on the islands did not occur regularly because of domination of the area by pirates. Many of these pirates were non-Muslims and on occasion may have slaughtered turtles. It seems unlikely, however, that such killing could have been systematic or continuous enough to have reduced seriously the turtle population. Brooke rid the area of pirates, and the islands are reported to have been administered for some years by an enterprising Malay, apparently as a private business. In 1875 the Rajah pre-empted the rights of turtle egg collection and allotted them among the leading Malay Chiefs of Sarawak (Banks, 1937). In 1941 the third Rajah Brooke took over control of the turtle egg collecting industry from the Malay families who had inherited it from the original Chiefs. At this time a Turtle Trust Ordinance† was enacted ; except for the period of the Japanese Occupation of Sarawak during World War II, this law has governed the exploitation of sea turtles as a government monopoly from 1941 to the present time.

In Malaya the collection of turtle eggs on the various breeding beaches was apparently controlled in earlier times by the Chief holding sway in the immediate vicinity. During evolution toward a smaller number of autonomous political units, with the minor chiefs acknowledging allegiance to a few powerful Sultans or otherwise-designated rulers of large areas, rights of turtle egg collection came to be considered as a royal prerogative in most parts of the Peninsula. In the late nineteenth and early twentieth centuries, with the extension of British political influence throughout the Peninsula, the various States developed written codes of law and systems of taxation in the Western fashion. Laws were enacted to control the exploitation of turtles and to utilize the turtle egg industries as sources of government revenue.

The Federated Malay States (Perak, Selangor, Negri Sembilan, and Pahang) Fisheries Ordinance (No. 20, of 1937), still in operation, forbids capture, injury, or possession of turtles except with authorisation, and provides for State Rulers' private preserves and for exclusive rights of collection of eggs on specified beaches. Such licenses to collect turtles' eggs are customarily let out to the

* The statements as to the nesting season and the productivity of individual female turtles are open to question. The nesting season at present extends throughout the year, with a definite heavy period beginning about May ; the average clutch size is nearer 100 than 200 eggs (see " Studies on the Sarawak Populations "). The writer is aware of no reason for believing that laying season or individual clutch size have changed markedly since the Rajah's time.

† This law (Chapter 40 of the Laws of Sarawak, Vol. I, revised edition) declares the monopoly of the Government of Sarawak over rights of collection of sea turtles and their eggs within the territorial waters of Sarawak, and provides for a corporate body of trustees to manage the industry. The trustees, comprising a "Turtle Board of Management", operate the industry as a Government business and the profits are used towards financing Malay charities. Unlike the Malayan laws mentioned later, the collection of eggs is not let out on tender to private parties, but is administered directly by the Board. Infringement of the law is punishable by a heavy fine, or imprisonment, or both. Abuses of the law are practically non-existent. So far as this writer is aware, the Board has never sanctioned the killing of turtles, but has confined the industry solely to collection of the eggs.

highest bidders at yearly intervals, the competitive bidding for permits ensuring the governments of the maximum practicable revenue from the turtle egg industries in their States.

The Unfederated States (Kelantan, Trengganu, Johore, Kedah and Perlis) have various laws controlling the taking of turtles and their eggs. Like the Federated States law, these provide for the licensing of the highest bidders to enjoy exclusive rights to collect turtles' eggs from specified areas for a year at a time. In Kelantan, one of the more important states for sea turtles, the law (Enactment No. 2 of 1932) is considerably more elaborate than the Federated States Ordinance. It provides specifically for the setting up of sanctuary areas, adjustments in management policies, protection of adult turtles and the setting up of licensing machinery.

In view of the foregoing, the turtle populations discussed here must always be considered in the light of this background of active and increasing protection of the adult turtles, and the equally active and increasingly complete collection of their eggs for human consumption. Comparison with the histories of decreasing populations in other parts of the world would indicate that the form of exploitation carried on in Malaya and Sarawak is less disastrous for the turtle populations than is the treatment afforded elsewhere. The Malayan and Sarawak turtles do seem liable to suffer in the long run from the degree of exploitation to which they are subjected. However, the industry is peculiarly amenable to adjustments which should ensure continued profitable management on a large scale. The initial stages of conservation measures already exist in the hatchery procedures followed in Sarawak and in the legal provisions for sanctuaries in some Malayan states. It is therefore possible to sound a note of optimism with regard to the future of a wild species which is being exploited at considerable profit to mankind.

DESCRIPTION OF HABITAT

While the populations of turtles under discussion may be resident in the shallow Sunda seas and the Gulf of Siam, it must be stressed that the present investigation failed to demonstrate the existence of extensive areas of marine vegetation which were obviously feeding grounds for *Chelonia mydas*. In the absence of fuller information, it is necessary to confine the present discussion to the general aspects of the entire region and the specific characters of the breeding beaches.

The areas studied lie between 1° and 6° north of the equator, in the shallow seas of the Sunda Shelf, close to the large land masses of the Malay Peninsula and the Island of Borneo. The changing inclination of the sun in its annual cycle has little direct effect on the climate of this area because of its nearness to the equator, and seasons as experienced in temperate climates are here practically non-existent. The major climatic event of the year is the attenuated effect of the Northeast Monsoon, which brings with it a season of heavy winds and rain from beyond the Philippines and Formosa. The monsoon reaches the East Coast of Malaya and the coast of Sarawak in October or early November. It continues to modify the local climate until about March. This period of increased wind and rain with slightly depressed temperatures, mainly due to decreased insolation during overcast weather, is known among English-speaking people in Malaya simply as " The Northeast Monsoon ". In Sarawak the Malay name, " Landas ", is more commonly heard. For graphic presentations of the annual cycles of precipitation and temperature see Figs. 5 and 6.

A large expanse of shallow, heavily insolated water of the Sunda Shelf separates the nesting sites studied from the deep sea (see Fig. 1). This eliminates massive local effects such as cold upwellings, and the incoming marine currents are sufficiently tempered to produce a warm, relatively constant sea temperature comparable with the air temperature.

The waters of the region are generally clear and continually circulating according to an annual cyclical pattern which is strongly influenced by the Northeast Monsoon. There is extensive coral growth in all suitable locations, and most of the islands have fringing reefs.

The coasts of the eastern side of the Malay Peninsula and of Sarawak are not, in the main, deeply dissected or steep. In the vicinity of river mouths, particularly in the south of Malaya and along most of the Sarawak coast, there is considerable pioneering mangrove, pushing seaward and holding silt to produce extensive areas of swamp. The shores of all the islands, except for the southernmost Malayan islands off Johore and Singapore, are predominantly rocky with sandy beaches. The beaches are located mainly on the south and west sides, that is, leeward in relation to the main monsoon winds. Some of the southernmost islands support extensive areas of flat mangrove growth comparable to that on the mainland.

Most of the sizeable breeding concentrations of *Chelonia mydas* observed during the survey in Malaya and Sarawak have been on islands. Some Malayan mainland beaches are used intensively by *Dermochelys coriacea* for nesting, and many others in both Malaya and Sarawak are used by *Lepidochelys olivacea*, but these beaches which seem to suit the other genera are used only infrequently by Green Turtles.

It is possible to describe a particular type of beach characteristic of those used by the main breeding concentrations of *Chelonia mydas* studied. Such nesting as does occur on " atypical " beaches in this region is sparse and irregular. It may possibly be accounted for entirely by stray females which have hauled out to nest on whatever beach happened to be available when oviposition became necessary. A later section of this report will, it is hoped, demonstrate fully that such a random procedure is quite irregular for the species as a whole.

While it is impossible at the present time to provide satisfactory supporting figures, it is believed that the majority of turtles nesting on atypical beaches are smaller in size than the average for females nesting on the principal *Chelonia mydas* beaches. It is suggested that they are newly-matured individuals.

There appears to be a definite tendency for adult Green Turtles to return to the same beaches during successive breeding periods (see "Frequency of Breeding Periods "). In the complete absence of evidence for the existence of an inborn homing instinct in sea turtles, the writer is inclined to attribute the observed homing pattern to experience-memory more than to an innate drive. It seems possible that homing patterns related to particular beaches may be fixed by " satisfactory " nesting experience (accumulation of appropriate physico-chemical stimuli from sea and beach, and failure of disturbing factors to exceed a particular threshold). Except for possible herd tendencies which are at present difficult to demonstrate, newly-matured females without memory associations for any particular beach would appear to have little specific directive influence on their wanderings. They might be expected to range widely over the general area, nesting where they could. Such a group would constitute a sort of pioneering fringe for the main population, continually sampling the available beaches of the region. If, during the passage of time, a change in environmental factors should create a new beach which was particularly suitable for *Chelonia* nesting (creating " satisfactory " memory stimuli in those wandering individuals which happened to nest on the beach from time to time), a new breeding concentration of turtles might be built up, recruited largely from these young adults.

The sandy beaches observed during the course of this study appeared to be separable into three major types, each used principally by a different genus of sea turtles.

Most of the beaches on the Malay Peninsula and the Island of Borneo at Sarawak face long reaches of open sea and experience the full force of the principal weather from the north and east. They tend to have a low profile above high tide mark and to slope very gradually into deep water. They are composed mainly of fine sands, apparently originating from slates and shales, and containing varying amounts of silt. They are usually rather hard-packed. The distance a female sea turtle must crawl overland to deposit her eggs above high tide line is comparatively great. The densely-packed, fine sand is more resistant to digging than are other types. *Lepidochelys olivacea* is the only marine turtle making extensive use of such beaches. Of all the sea turtles occurring in the region, this species is the smallest in size and the lightest in weight. It experiences less difficulty with terrestrial locomotion than do the other species. *Lepidochelys olivacea* does not excavate an extensive body hole for nesting—relatively small amounts of digging are necessary in the hard-packed sand.

In the state of Trengganu on the East Coast of Malaya there is a limited number of high, steep beaches of conspicuously coarse sand which appears to be of granitic origin. The distance a sea turtle must crawl from the water to lay eggs well above high tide line is very short compared with the preceding beach type. An impressive concentration of *Dermochelys coriacea* nests here, while appearances of *Chelonia* are infrequent and unpredictable. Inquiries among egg collectors on these beaches indicate that about five *Chelonia* nests may be made in a year on a one mile length of this type of beach.

The island beaches used for nesting by *Chelonia mydas* are of medium-coarse sand, apparently of coral origin. This sand is light in weight and the grains do not pack easily into a hard surface. The beaches slope steeply and the crawl from the water to nesting sites, well above high tide line, is not a long one. Characteristic of these beaches, used by significant concentrations of *Chelonia mydas*, is a " high beach platform " on which most of the nesting is done. Figure 2 is a diagrammatic profile of a characteristic undisturbed *Chelonia mydas* nesting beach in Malaya. Nesting is almost wholly confined to the high beach platform. Most of the nests observed were well back on the platform and in some cases were located in the jungle fringe. All beaches vary from time to time according to the influence of wind and waves on the sand, but the general pattern depicted, at least for the *Chelonia* beaches, appears to be constant.

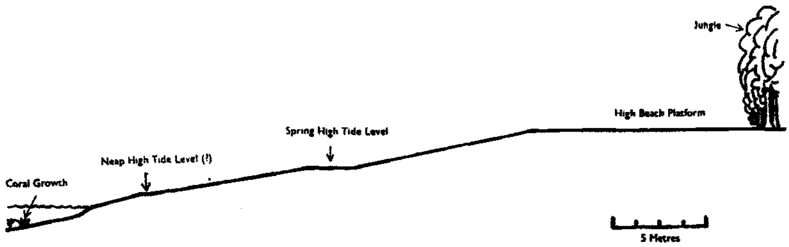

Fig. 2.—Profile of beach at Chagar Hutan, Redang Island, Trengganu, Malaya.

All the *Chelonia* beaches, on islands, are in locations where they are protected from the northeast weather and the long reaches of sea in that direction. Most of them are on the south and west sides of the islands, in lee situations; some are on more exposed sides of the islands, but are at the back of protected coves and bays. The breeding beaches do not appear to have been produced so much by ordinary surf as by sets of marine currents which have piled up the sand at certain spots. This process would presumably allow the piling up of quantities of light coral sand with minimal erosion of the soft material to small grain size. The sand is very porous and loose. Rain water percolates downward rapidly and the subsurface strata of the higher levels of the beach where nesting occurs are at the same time continually moist and comparatively well aerated. The sulphurous odours or black colours characteristic of anaerobic bacterial action were never detected during excavations on these beaches.

The Talang Talang Besar Island beach in Sarawak differs from the rest by being a spit formation. Strong currents flowing from the north around each side of the island pile up sand in an elongated triangle on the southern aspect of the island (see Fig. 4A). The spit form of the beach provides maximum access to the sea and it is believed that this beach may be considered almost an ideal breeding beach for *Chelonia mydas*. It is the most intensively used nesting beach known to the writer. It seems likely that it might be the most intensively used in the world.

At several of the localities investigated there are stream beds leading out on to the beaches and portions of the expanse which might otherwise be suitable for turtle nesting are water-logged. On the Talang Talang Islands in Sarawak the rear margins of the beaches, near the line of contact with the island soil, receive very heavy run-off from the island slopes. They show some silting and water-logging. This is particularly true of Talang Talang Kechil Island. In such portions of the beach the concentration of nesting is diminished, and it is doubtful whether nests left undisturbed there would hatch successfully.

The principal *Chelonia* nesting beaches investigated have fringing coral reefs below mean low tide line. At most low water periods the coral interferes with access to the beach sand from the water, and at spring lows it may become temporarily impossible for individual turtles to reach or to leave the beach. It is not uncommon on nights with low tides to hear the thudding sounds made by turtles left stranded on the reefs by the receding water.

The islands where the breeding beaches are found are of basaltic and granitic rock with a poor soil cover. They support a thick jungle growth, which has often been partially cleared and planted in the vicinity of the beaches with coconut palms. There commonly are small cleared areas of cultivation on the islands, usually well back from the beaches.

The land at the back of the beaches on the three Sarawak turtle islands is heavily used by the islanders and there is little natural vegetation bordering the beaches. The sand remains almost completely sterile throughout its expanse, and there is no real problem of encroachment of the jungle on to the beach. On the other hand, on almost all the Malayan turtle island beaches, the vegetation at the back of the beaches is undisturbed jungle. The potential expanse of suitable nesting sand is greatly reduced by the encroachment of pioneering plants. The activities of the turtles, churning up large areas of sand during and after nesting, probably play a part in limiting the colonisation of the sand by plants, but the presence of roots and stems which hinder digging also limits the areas where turtles successfully complete their nests (see " Wandering on the High Beach "). On several occasions turtles have been observed to wander far back beyond the vegetational border, sometimes laying eggs in what closely approached deeply shaded jungle. It seems doubtful that such nests could successfully develop and, if young emerged, that the hatchlings could find their way to the sea before they were all taken by predators (see " Movement of Hatchlings to the Sea ").

Plate I shows the vegetational facies of the back-beach on Talang Talang Besar Island, Sarawak, and at Tiga Ruang Menangis Beach on Perhentian Besar Island, Malaya. The predominance of cultivated coconut palm growth at Talang Talang Island, and the extensive evidence of human alteration of the beach-jungle contact are clear. Tiga Ruang Menangis Beach is virtually an undisturbed area, without habitation or significant cultivation near the beach. The principal plant visible in the close-up of the Tiga Ruang Menangis vegetation front is a species of *Barringtonia*. This dominant tree, along with *Cycas* and *Pandanus*, makes up the major portion of the jungle front which encroaches on the beach.

So far as is known, none of the turtle islands visited supports carnivores larger than Civets (*Paradoxurus*). Sambar Deer (*Cervus unicolor*), Barking Deer (*Muntiakus muntjak*), Mouse Deer (*Tragulus* spp.), and Wild Pig (*Sus scrofa*) are variously reported as present or formerly present on the larger islands. Monkeys (*Macaca irus*) occur on the larger Malayan islands. Monitor Lizards (*Varanus salvator*) and the Reticulated Python (*Python reticulatus*) occur on all the turtle islands. There are no nesting colonies of sea birds, except for small numbers of terns on barren rocks off the Malayan turtle islands.

All three Sarawak islands are inhabited the year around. The inhabitants are nearly all associated with the turtle egg industry and all live in close proximity to the turtle beaches (Plate I). There are villages on Perhentian Kechil Island and on an islet near Redang Island in Malaya ; a small group of copra workers out of the latter village have established a settlement on the north side of Redang Island. Malayan islanders do not live in close proximity to the turtle beaches, and most of the beaches are a mile or more from the nearest habitation.

REPRODUCTIVE PATTERNS—THE INDIVIDUAL FEMALE TURTLE

Many accounts of the nesting of *Chelonia* have been published (see especially Catesby, 1730–1748 ; Musgrave & Whitley, 1926 ; Deraniyagala, 1932 and 1939 ; Moorhouse, 1933 ; Banks, 1937 ; Cozzolino, 1938), apparently showing that there are real differences in the nesting habits of the genus in different parts of the world. The account which follows attempts to bring together the observations of this writer with other published observations on Malaysian turtles (Mundy, 1848 ; Banks, 1937 ; and Harrisson, 1951 and 1954).

Approach to the beach

At sunset, female turtles begin to enter the beach shallows and individuals may be seen moving along the beach in from two to four feet of water. During the short tropical twilight period the animals are better able to detect objects and movements on the land than later in the night, and the first turtles appearing each evening are excessively shy.

The earliest hour at which females have been observed to show clear signs of intent to ascend the beach generally coincides with the time of Nautical Twilight: " Sun 12° below horizon ; general outlines still visible, although horizon probably indistinguishable ; all detailed operations impossible ; all brightest stars can be seen." (from " The Abridged Nautical Almanac for 1949 ", published by H.M. Stationery Office, London, 1948). The field journals kept on the Sarawak turtle islands contained approximately 100 entries recording the time at which the first turtle of an evening was noted to have ascended the beach as far as the high tide line (completely clear of the water and committed to a period on the dry beach). The earliest of these records were obtained at 1820 hours on 14th September 1952 and at 1825 hours on 10th September 1953.

Incoming turtles spend a variable amount of time in the shallow water of the beach, resting in a few centimetres of water with the plastron in contact with the sand and bearing part of the weight. During this time, the head is commonly allowed to droop low so that the water washes over the eyes ; it is raised from time to time while the turtle inspects its surroundings (Plate 2 a). The flight reaction is most easily and most strongly initiated during this inspection period ; if alarmed, the turtles turn and flee precipitately back to deep water. The amount of time spent on the preliminary patrol of the shallows and the period of inspection when partly awash at the edge of the beach appears to vary according to the illumination. During early dusk and in bright moonlight this preliminary to an ascent of the beach takes longer than in conditions of less illumination.

Night vision on the beach appears to be roughly equivalent to human vision under the same lighting conditions. There is an awareness of large masses, which appear to be seen mainly as silhouettes. Moving masses are detected much more readily than are stationary ones. Concentrated spot-sources of light such as lanterns, hand torches, moon, and lightning, appear to be detected with considerable acuity. Any continuous lighting of the beach in excess of the natural limits which are reached from time to time by the moon and stars inhibits turtles from coming ashore. Sporadic illumination from brilliant sources such as hand torches is usually possible without frightening off incoming turtles, provided the flashes of light are of short duration and are separated by periods of complete non-illumination. Very roughly, such flashes may be compared with the illumination of lightning to which the turtles are presumably accustomed. On very dark nights turtle watchers who patrol the beaches marking the sites of nests for collection on the morrow (Sarawak) or digging the nests on the spot (Malaya) carry hand torches. When in use, these are flicked on for brief glimpses only, the watcher spending most of his time in the dark. It seems quite possible that the Sarawak turtles have become increasingly adapted to tolerate temporary illumination by a hand torch through years of experience on those beaches. They show far less marked flight reactions when spotlighted than do the Malayan turtles, and the period of flight following disturbance is much shorter than in the Malayan animals.

Ordinary non-luminous objects on the beach, which are viewed only by reflected light from the sky, must be approached more closely than self-luminous objects before they provide any particular visual stimulus to the turtles. Objects of roughly the size and the shape of another turtle appear to be ignored, even if they move slightly; incoming turtles have never been observed to show any flight reaction toward other turtles which have finished nesting and are returning to the sea. Large-sized objects which do not approach the size and shape of another turtle when perceived in outline usually provoke a marked flight reaction. Detection is quicker and flight more violent if the "foreign" object moves.

On a number of occasions observations have been made on the reaction of incoming turtles to canoes which were left pulled up on turtle beaches just above high tide line. In the half-light before full night had fallen, or during periods of bright lunar illumination, turtles ascended the beach only at a distance of 10 to 15 metres from a canoe. When there was less illumination and vision was poorer, turtles were observed to pass nearer to the canoes; on occasional very black nights, tracks showed that turtles had actually blundered into them.

The following extract from the writer's field notes may help to describe the relative acuity of vision of *Chelonia mydas* and the shyness demonstrated during the initial period of inspection before actual ascent of the beach.

The account refers to the photograph in Plate 2 a :

26th August, **1953**, *Talang Talang Besar Island, Sarawak.*

Devoted the better part of the night to attempts to photograph a female turtle still in the wash of the water, just about to ascend the beach. Night was dimly moonlit; I could just make out the bulk of a turtle in 30 cm. of water from a distance of about 8 metres. At that depth of water, the turtles still keep the head below the surface much of the time and, while the head was submerged, I could move about without being detected. The method tried was to select a subject which had just lowered her head into the water and to walk quickly to a point about 4·5 metres from her. I then lay prone with camera at the ready, prepared to take a flash picture when she had advanced to a point about 3 metres away, where she could be expected to spend her final period of inspection in from 5 to 10 cm. of water before ascending the beach. On seventeen consecutive trials, the approach and preparation were possible before the turtle (often having advanced a short distance) again raised its head above water. On fifteen of the seventeen trials, the subject whirled and churned off to deep water almost immediately after raising its head again. All of these appeared to have clearly detected my motionless shape from a distance of from about 4·5 metres to about 3·5 metres. On two occasions a second advance was made after a period of inspection; both of these subjects whirled and fled almost immediately when they again raised their heads for inspection (perhaps 3·5 metres away from me).

I obtained the desired photograph on the second attempt at approaching the subject by doing a flat crawl while remaining hidden behind an exhausted female which was returning to the sea after having completed her nest. Upon reaching a pre-determined point, I was able to rear up suddenly and fire the flash before the subject reacted to flee.

I later tried to obtain a second photograph by hiding in a shallow pit dug just above the water line, moulding the excavated sand into a crude " turtle dummy ". Crouching in the pit behind the " dummy ", I waited about 30 minutes but no turtles approached close enough for a picture. It is impossible to say whether this was mere chance or was due to shyness at approaching the sand " dummy ".

There are indications that the flight response to " foreign " objects on the beach may be tempered by learning processes. On one occasion a drift log about 2·4 metres long and 60 cm. in diameter was cast up on a turtle beach and remained there for some weeks. During the first week, the pattern of fresh tracks each morning showed a tendency to avoid the log by a distance which appeared to be related to the amount of illumination on the preceding night. During the second week there appeared to be less marked avoidance of the log ; other observers during the following weeks reported that avoidance of the log became less and less marked until eventually the tracks virtually touched the log and individual turtles were observed to pass very near it, even on bright moonlit nights. It would appear that the large object had come to be accepted in the same way as the large rocks located at the ends of the beach.

Sequence of events during nesting

The hundreds of individual female turtles observed during the course of this study showed almost every conceivable variation in activities, but taken as a whole, a definite pattern of action was clearly distinguishable. The following account is a composite study representing this observer's subjective impression of the " average " or " normal " nesting pattern of female Green Turtles in Malaya and Sarawak. Field notes on twenty-seven separate female turtles have been drawn on in the course of compiling the account. All the notes were written on the spot simultaneously with the actual observations.

Generally they were rewritten on the morning following the observation. Observations on three particular turtles have been selected from among the twenty-seven chosen accounts, as representative of the "average" pattern. One of the three accounts is from the field notes of Mr Antony Santiago, the other two are from the writer's own field notes.

Ascent of the beach

Following the period of patrol and inspection already described, and provided that alarming stimuli are not received, each female turtle advances to the water line and begins to heave its bulk toward the higher levels of the beach. Ordinary forward progression is achieved by simultaneous movement of the limbs on either side of the body rather than by the alternate use of limbs practised by most limbed reptiles. With the plastron resting on the sand and bearing the full weight of the body, the front and hind limbs are moved anteriorly preparatory to the next forward shift of the body. The hind limbs are rotated laterally and somewhat forward and placed with the flipper surface broadly in contact with the sand. The fore flippers are moved first with the elbow joint flexed so that the main length of the flipper trails behind the distal end of the humerus as it is moved anteriorly and somewhat dorsally. At the end of the forward arc of the humerus, the elbow joint is straightened and the main portion of the flipper is brought forward so that when it is lowered into contact with the substratum the flipper is extended more or less straight, pointing antero-laterally at an angle of less than 60° with the body axis.

With both sets of limbs placed anteriorly, the body is swung up and forward in a short arc. The main weight is borne anteriorly by the elbow joint and the antibrachium ; the lesser posterior weight is borne mainly on the tarsal and metatarsal surfaces of the hind flipper. The arc through which the body moves ends with the plastron again bearing the weight of the animal, between 10 and 20 centimetres ahead of its former position. The usual progression of the turtle is thus in a series of short lurches, all four limbs operating at the same time to bear the main weight while the body is moved forward, then the plastron bearing the weight while the limbs are again moved forward, prior to re-assuming the weight of the body.

When partially buoyed up by water, or when under great stress, adult turtles occasionally move with alternating action of the flippers, but this mode of progression is not continued for long. Presumably the ability to move rapidly by alternate use of limbs in lizard fashion is a function of weight. Young *Chelonia mydas* characteristically progress by active alternate movement of the limbs.

The massive tracks left in the sand by sea turtles are conspicuous on all nesting beaches. By the direction in which sand has been pushed, that is, posteriorly during the forward lurches, it is easy to distinguish incoming trails from returning trails. If the beach is not too heavily interlaced with trails, a daylight survey in the morning can reveal many details of the previous night's activities. The photographs in Plate 2 b and c show characteristic trails in the beach sand. The observer is kneeling beside a " down " track in b ; the " up " track of the same turtle shows on the right-hand side of the picture. If the sand surface is damp and firm, holding a cast well, the track has more the appearance shown in Plate 2 c. Here the impression made by the animal's tail can be clearly seen. When the support of the limbs is lost, the tail tip is stubbed down into the sand at the end of each forward movement. This action takes place as the weight settles on the plastron and the flexible body expands slightly in all directions along its sand contact. Relevant to the previous discussion of avoidance of large foreign objects on the beach is the fact that the track in c is a " down " track, made after the animal had completed nesting and long after it had lost the extreme sensitivity to visual alarm stimuli already discussed.

Progression between the water and the high tide line is characteristically slow and cautious compared with the later rate of movement when the turtle is high on the beach. At this early stage, the turtle is still near enough to the water to have at least a chance of rapid retreat in case of alarm. The distance back to the water is usually relatively short and the sand is firm and provides good traction compared to the loose sand above the high tide line. There are frequent stops for rest and for observation of the animal's surroundings. The average rate of forward progression may be as little as 60 cm. per minute or as much as three metres per minute. At very low tides the turtles on some beaches may have to travel from 12 to 15 metres between the water line and the high tide line.

Turtles may begin to dig nesting sites anywhere above high tide line, where the sand changes from being hard, smooth, and packed to loose and disturbed. The great majority of turtles continue moving up the slope of the beach well above the high tide line to the level area which is here called the high beach platform (see Fig. 2). The distance between the high tide line and the edge of the high beach platform varies a great deal on different beaches and on different portions of the same beach. It may be as little as 3 to 4·5 metres of fairly steep slope, or as much as 12 to 15 metres of gentle slope.

Despite the poorer traction afforded by the loose sand on the portion of the beach above high tide line, the turtles' progression is here usually at least as fast as previously. This is mainly because there are fewer long stops, the frequency and length of pauses for inspection of the beach diminishing with the possibilities for rapid flight back to the water. Pausing to breathe after every few lurches forward, the female turtle moves steadily along. Most of the individuals observed reached the high beach platform within 25 minutes of the time they had left the water.

With progression farther from the water, most individuals become less liable to be precipitated into flight by mild alarm stimuli. Upon detection of an observer who has approached closely, they will commonly whirl quickly back to face the sea, and may make a few rapid movements towards the water, but they soon stop to rest and breathe. Thereafter, if left unmolested, most turtles will lose the temporary inhibition of the nesting pattern which had been caused by the flight reflex and will turn back and continue as before. Commonly, the flight reflex is replaced completely by a general temporary withdrawal action ; head and limbs are drawn up close and the turtle remains motionless until breathing becomes necessary. Breathing appears to be difficult for the turtles when out of water, and apparently it cannot be accomplished without ending the withdrawal state. After a short period of withdrawal, the limbs are re-extended to bear part of the weight and the head and neck are extended and raised during the laborious process of breathing. Failing further stimulation, the turtle rarely returns to a pronounced withdrawal posture.

Wandering on the high beach

On the high beach platform, where most turtles nest, the sand is remarkably soft and light, almost meriting the adjective " fluffy " by comparison with the sand at lower levels. The surface of the high beach is continually disturbed by wandering and nesting turtles. There is a multiplicity of criss-crossing trails and there are many pits in the sand where nests have been completed or abandoned. Individuals newly arrived for purposes of nesting wander over this area apparently at random. The length of time spent in wandering before beginning to dig a nest is highly variable. Individuals were observed to wander for periods of from 2 minutes to 3·5 hours before beginning to dig nests. Of 18 selected records where evidence of abnormality of the turtle or interference by humans was not apparent, the shortest period of wandering was 2 minutes and the longest was 45 minutes ; the average wandering time prior to nest excavation was 14 minutes.

All observers contributing to this survey agreed that the reflexive pattern of digging seemed to be initiated only after a short period of complete freedom from alarm stimuli and all but one set of tactile stimuli—that provided by the soft, loose sand of the high beach. Contact with all manner of foreign materials, such as stones embedded in the beach, hard soil-sand mixtures at the back of the beach, roots, and drift wood, apparently reinforced the wandering pattern and inhibited the digging pattern of activity. Even contacts with the light wands used to mark nests on Sarawak beaches commonly caused wandering females to change direction and continue moving. Contact with other turtles had the same effect.

The female turtle, wandering more or less at random, but prevented from stopping on unfavourable substrates or in the near vicinity of other turtles, sooner or later reaches a point where the various inhibitory stimuli playing on her senses are at a low ebb in relation to the strength of the stimulus to nest. At this point she begins to dig in the sand.

Female turtles often first begin to dig after blundering into an old pit left by some previous turtle. It appears as if digging reflexes are stimulated by the sense of being in a depression, whether the turtle has itself created that depression or not. It is possible to postulate adaptive advantage in an instinctual pattern such as this : each nest is associated with a " leaving pit " some distance away from the site of the eggs (see Plate 5 a and the section entitled " Covering the Nest "). Any positive guidance of other females into the " leaving pit " will reduce the chances of accidental excavation of the original nest by later turtles.

Digging the body pit

When the digging reflex pattern replaces the wandering pattern, the turtle ceases to lift its weight off the sand onto its limbs during progression forward and begins to " swim " into the sand. The plastron now remains in full contact with the substrate, serving as an anchor against the movements of the limbs. Powerful movements of the flippers throw sand well up and back, gradually producing a depression in front of the turtle. From time to time the animal moves forward into the depression, continually digging away the front wall and bottom of the pit and moving at a gradual angle down below general beach level. The photograph in Plate 3 a shows an action shot where the sand is being thrown posteriorly by the fore flippers. The pit can be seen to slope gradually downward to the front wall, which is about 45 cm. high.

Following is an analysis of the process of excavation of the body pit from the writer's field notes :

The front flippers are used simultaneously (most commonly) or singly ; if used singly, they are ordinarily used in alternation, although usually one appears to be used more strongly than the other, gripping more sand and throwing it much farther. It would appear that the single use of flippers mainly functions to trim the symmetry of the pit where either extra resistance to digging or cave-ins tended to make it uneven. The flipper is brought forward by the humerus with the elbow joint flexed, the distal end of the humerus being raised sufficiently to allow the flipper to clear the sand during its forward motion. At the limit of the forward movement of the humerus, the elbow is extended, straightening the flipper and resulting in a final position (preparatory to scooping sand) with the flipper straight and pointing almost directly forward and twisted so that the dorsal surface is either near or touching the side of the head and neck, and the leading (anterior) edge is downward, preparatory to ploughing into the sand. The extended flipper is then brought posteriorly by flexing of the shoulder joint with the elbow joint at first kept extended. As the shoulder motion continues to draw the flipper backward and downward, the elbow joint begins to flex as well, giving ever-increasing momentum to the portion beyond the elbow. The large swimming surface has by this time formed a good pile of sand behind it and, with the increasing velocity, the flipper below the elbow joint begins to rotate so that the anterior (now ventral) edge of the flipper is moving in advance of the trailing (now dorsal) edge, and is cutting under the accumulated ridge of sand in a manner analogous to the cutting edge of a plough or scraper. A little beyond the half-way point of its swing, the humerus begins to elevate the elbow joint somewhat and the increasing flexure and rotation of this joint results in the scooping up of a rapidly-moving load of sand (several pounds) ; as the flipper finishes its rapid postero-dorsal arc, this load of sand is thrown with considerable force out behind the turtle. The sand is commonly thrown backward at an angle of about 20° with the horizontal and the resultant spray of sand usually travels from 1·2 to 3·7 metres behind the turtle. The heretofore clean, shiny carapace of the turtle soon becomes heaped with as much sand as can cling to the smooth surface and a wide zone behind the turtle becomes covered with soft, disturbed sand.

The fore-flippers end their powerful backward swing on a cushion of spilled sand which usually builds up along the sides of the carapace. If for any reason the flippers spill their loads or fail to accumulate loads of sand for a few cycles, the accumulated cushion along the sides of the carapace is removed by the hind flippers or left behind by a lurch forward of the body, leaving the relatively clean carapace to take the full force of the backward momentum of the flippers. In this event the rapidly-moving, heavy flippers hit the carapace with a resounding " Thwack ! " which is audible for as much as 45 metres and is a characteristic sound on the active nesting beach.

At this initial stage in digging the body pit, the hind flippers throw sand in a series of movements roughly comparable with the action of the front flippers. They are picking up much of the spilt and lightly-thrown sand left by the fore flippers, as well as some of the undisturbed substrate, and are forcefully moving it posteriorly. The hind flippers work singly rather than in unison, almost always in alternation. While one flipper rests firmly on the sand (presumably to provide anchorage against rotation of the posterior end of the carapace), the other is brought forward as far as possible, usually touching the side of the carapace. The flipper is then rotated backward with the anterior edge in forceful contact with the sand; this edge is soon cutting under in advance of the posterior edge, and a load of sand accumulates on the ventral surface as the flipper moves back with increasing speed. Continuing its arc of movement, the digging flipper throws the accumulated sand backward and upward, as do the front flippers. The shower of sand from the rear flippers rarely travels more than a maximum of about 1·2 metres behind the turtle, much of the load falling only a few centimetres behind the arc of movement of the flipper. In its " follow through " the hind flipper crosses slightly over the median line of the animal before movement ceases. It is then brought forward to an anchoring position while the other flipper repeats the digging action.

As digging progresses, the turtle lurches forward from time to time, bringing new sand within reach of its fore flippers and providing clearance from the disturbed sand which is accumulating behind it. The fore flippers excavate a great deal more sand than do the hind flippers, and the forming pit slants gently downward. As the pit deepens, accumulated loose sand behind the animal tends to keep spilling back and after a few minutes the action of the hind flippers no longer produces showers of sand, but is reduced to simple pushing back of the sand against the posterior wall of the pit. During the digging process, the turtles breathe every 20 to 45 seconds; roughly two times per minute for most of the animals observed. The very powerful action of the fore flippers is carried on in short series of strokes, 1½ and 2 seconds between strokes for from a few to as many as 13 or 14 strokes (averaging 5 to 7 strokes in a series). A period of digging activity is followed by a rest period of anywhere from about 15 seconds to a minute or more.

Depending upon whether digging commenced in a preformed shallow pit or on the undisturbed beach surface, by the time about 10 to 30 minutes have been spent in excavation, a turtle is usually fully sunken below general beach level in a pit of its own construction. The head rests against a nearly perpendicular wall of moist sub-surface sand (the dry surface sand which will not hold a steep gradient slopes off to beach level higher up the wall).

The bottom of the pit at the head end is from 38 cm. to 76 cm. below the general beach level; the pit still slants upward posteriorly, commonly being about 25 cm. to 60 cm. deep at the posterior end of the turtle. The anterior wall of the pit consists of naturally compacted, undisturbed sand; the posterior wall is composed of moist sand packed into position by the action of the rear flippers.

After some time (whether due to time sense, sense of position, or exhaustion is not clear) excavation by the fore flippers is stopped. In the three sets of field observations selected as the principal models for this account, the turtles stopped digging with the front flippers after 13, 14 and 20 minutes. The last case was the only one of the three in which the turtle concerned did not commence digging in a ready-made partial pit left by a former turtle.

Digging the egg hole

With cessation of the use of the fore flippers, these are placed at rest in a flexed position, partially embedded in the sand at the bottom of the pit. They apparently provide anchorage against marked shifting of the body during the later activity of the hind limbs. For the next 5 to 15 minutes the hind flippers alone are active, vigorously pushing sand posteriorly and packing it against the rear wall of the pit. From time to time, the turtle may swing the posterior portion of its body from side to side, pushing some of the sand out from underneath the rear portion of the plastron and contributing to a levelling of the floor of the pit. While marked forward movements were not noted in the field observations, it seems likely that the activities of this period may gradually shift the turtle a short distance forward.

When the turtle appears to be resting almost horizontally with the posterior end lowered to approximately the same level as the head, there is a marked change in the action of the hind limbs. Following one of the frequent rest periods, the rear flippers commence activity in an entirely new pattern. The following description continues from field notes transcribed above:

. . . A radical change has now occurred in the action of the hind flippers (front limbs remain quiet). Instead of pushing sand posteriorly, the hind flippers begin to *scoop* sand and to deposit it laterally. One at a time, the hind flippers are used slowly and deliberately to scoop up an estimated half to one cupful of sand, carry it to one side, and deposit it. While the body is held somewhat raised on the three other limbs, the distal edge of one hind flipper is introduced to the sand; with the edge held stiff and pressed into the sand, the flipper is rotated in a steady, continuous motion. The distal and posterior edges of the stiffened flipper cut into the sand as a result of this action. After an estimated 20° of rotation (with the postero-distal edge leading) the cutting edges are well embedded in the sand. The terminal edge of the flipper now begins to flex, undercutting a small quantity of sand. As the rotation continues, the terminal flexion increases so that by the time the flipper has rotated through an estimated 60° to 80°, a quantity of sand is held in the scoop-shaped ventral surface of the flipper. Still without a pause, the flipper is flexed further into an even deeper scoop and is raised with its load of sand. The upward motion continues into lateral movement, still keeping the scoop facing upwards and spilling little or no sand (the other three limbs have raised the entire body sufficiently to allow clearance for this action). As the flipper moves out with its load of sand, the motion is speeded up and, at the end of the movement, when the limb is extended almost straight, the flexed terminal portion of the flipper suddenly straightens, dumping its load of sand at the instant of maximum velocity. A fraction of a second after dumping its load, the flipper comes to rest rather heavily over the sand just dumped.

The posterior end of the body now swings over this flipper. As the turtle's weight shifts, the flipper commonly slips a few centimetres medially.

The flipper of the opposite side is now moved through the same pattern, scooping up a quantity of sand and dumping it off to the side, then bearing the weight of the posterior end while the first flipper repeats the action, etc. At the time each flipper is freed from the weight of the body and becomes available for digging, it rests mostly medial to its previously-dumped load of sand, having slipped medially when assuming the support of the body. Before beginning the above-described scooping action, the flipper (held stiff) is flicked sharply forward and upward a short distance, scooping a small load of sand on its dorsal surface and throwing it forward along the side of the carapace. Thus, the sand being brought from the hole which is developing posteriorly is first deposited laterally, then part is again moved anteriorly, further preventing any build-up of excavated sand around the edges of the hole which is being made. The hind flipper, in clearing the deposited sand, may actually dig somewhat ventrally before flipping forward. The movement forward is accompanied by a raising of the body on the three supporting limbs; after the short forward flip, the digging limb continues without pause into the movement posteriorly while the body is held raised by the other limbs.

The sequence of events, then, is: right hind flipper scoops, carries sand laterally, dumps sand, rests on dumped sand (body having been lowered with the flipper); right hind and both fore flippers raise the body and swing posterior end to the right (right hind flipper slipping medially in the process); left hind limb flicks sand forward, continuing the motion into movement posteriorly and medially to scooping position; turtle rests (plastron lowered back onto the sand); left flipper scoops and raises load (three limbs again raise the body to give clearance), carries load laterally, dumps, rests on dumped load; posterior body swings to the left (left hind flipper slipping medially in the process); right hind flipper flicks sand forward and moves back into scooping position; turtle rests with plastron on sand. . .

At first the scooping action of the hind flippers produces a shallow basin about 30 cm. to 40 cm. in diameter and up to a maximum of 15 cm. deep at the centre, a point approximately under the posterior end of the carapace. After the first few minutes, however, the action becomes more localized and the excavation of the egg hole itself begins. Working in the manner described, the turtle excavates a neat, deep hole which is more or less centred beneath its cloacal region. Viewed from above, the hole presents a roughly circular opening except at its posterior-most point where a nick is formed by the contact of the posterior margins of the flippers as they are withdrawn with loads of sand. The egg hole is usually about 20 cm. in average diameter, its size being determined by the width of the turtle's hind flipper (small females, with small flippers, digging egg holes of smaller diameter). Plate 3 b is a view of a turtle in the act of excavating its egg hole.

The egg hole grows steadily deeper, and in most instances at the end of about 8 to 10 minutes of digging the turtle can be observed to rear up on the front flippers during each scooping action, thus tilting the rear end downward and allowing a greater reach down into the hole. As the hole is deepened, the tail and cloacal region droop into it and rest periods are spent with one rear flipper dangling into the cavity. The turtle continues to dig until, despite pronounced rearing of the front end to tilt down the posterior body and allow maximum downward extension of the digging limbs, the fully extended flippers are unable to scoop more sand from the bottom of the cavity. This stage is usually reached about 9 to 15 minutes after the egg hole was first commenced.

Upon completion, the egg hole averages about 38 cm. deep (30 cm. to 45 cm.) from the rim of the opening at the bottom of the body pit. This level is, in turn, about 50 cm. (from 20 cm. to 75 cm.) below the general beach surface. The finished egg hole is usually somewhat larger at the bottom than

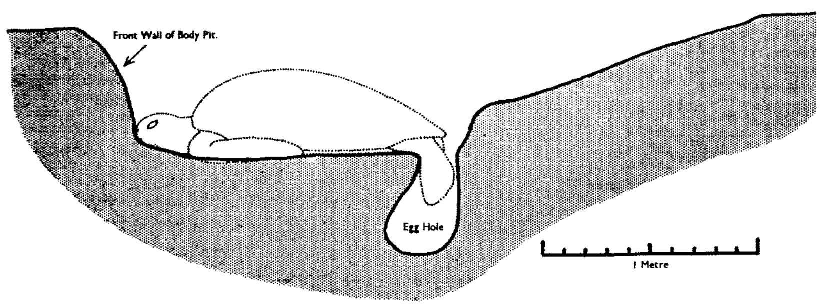

Fig. 3.—*Chelonia mydas* nest excavation, in profile.

at the top. Its axis usually curves slightly forward in the deeper portions due to the tilting of the body which is resorted to in order to extend the downward reach of the hind flippers. The enlarged bottom chamber is oval in horizontal section, averaging roughly 20 cm. to 23 cm. across by 25 cm. to 30 cm. long. Figure 3 is a diagram made from rough field sketches selected to represent an average nest.

During the process of digging the egg hole, turtles appear to become less sensitive to visual stimuli than formerly. They become, at the same time, more obviously sensitive to other stimuli such as vibrations in the substrate and shifting of the sand in the sculptured egg hole.

Watchers moving on patrol around the beach commonly flash their hand torches into the egg holes to see if laying has yet begun. The turtles usually stop all activity when the sand around them is illuminated during the brief inspection, but they usually resume the digging pattern a minute or so after being left in darkness again.

On a number of occasions turtles have been observed to stop digging well-advanced egg holes and to move up out of their pits to start other nests elsewhere. The only observable stimulus in each case was vibration in the substrate caused by other turtles which were digging body pits nearby. Similar desertions of otherwise satisfactory nests have been recorded where attempts were being made by observers to dig body trenches behind the turtles in order to allow close observation of the egg laying process. In most of the cases where the observer had apparently frightened off a turtle, he was out of sight behind the dome of the turtle's carapace and no artificial light had been used. Examination showed that no sand slides had occurred into the egg hole (see following account). Except for the undoubted presence of vibrations in the substrate caused by the observer in his digging, there was no indication of what had caused the turtle to leave her nearly completed nest.

In order to test the effectiveness of foreign vibrations in causing a turtle to change its nesting site, the writer chose three nesting females which could be approached without any possible chance of visual detection. After the vigorous activity of digging the body pit was over and the quieter excavation of the egg hole had begun, the observer attempted to duplicate the sand vibrations which might be produced by another turtle digging nearby. Using a wooden paddle, he beat the sand about 1·5 metres behind the subject, at irregular intervals producing emphatic "thuds" which were not unlike the occasional percussions produced by a turtle's powerful fore flippers during the digging of the body pit. All three females abandoned their nests and moved off, completing their nests in a normal manner elsewhere.

There would appear to be adaptive advantage in this intolerance toward other turtles digging nearby in that it would induce a nightly spacing of nests over all the suitable beach area. This would, of course, tend to reduce the chances of one female digging up or seriously disturbing the completed nest of another during the process of making her own nest. Plate 3 c showing local overcrowding on one bit of Sarawak beach on a night at the peak of the nesting season, would indicate that the use of some beaches is intensive enough to make crowding a real factor. In the case illustrated, the female beneath the wandering individual which is crawling toward the camera was already laying eggs when blundered upon. She had passed the sensitive stage at which she could have been stimulated to leave that spot to make a nest elsewhere. The third female in the background had been disturbed by the same wandering individual shown here. She had left a nearly-completed egg hole and had begun to wander in search of a new site.

Small amounts of slippage of the moist, packed sand forming the walls of the egg hole will frequently cause abandonment of a nest if the dislodged sand should be detected as it falls on a hind flipper which is extended down into the hole. It is common to find abandoned nests with open, well-formed egg holes, apparently abandoned because of minor slips of sand during excavation. A handful of sand tossed gently into the egg hole so as to hit a digging flipper was often sufficient to cause a turtle to halt in the middle of the scooping operation, pause for a few seconds, then withdraw the flipper and leave the pit. Such disturbed individuals normally wandered off to other parts of the beach and went through the entire process of nesting again from the beginning, usually completing successful nests in the normal manner on the second attempt.

The co-ordinated pattern of motor activity which results in the excavation of the egg hole eventually stops and is replaced by the completely different pattern of oviposition. The stimulus producing this radical change is apparently the negative one of failure to make good digging contact between the extremity of the hind flippers and the bottom of the egg hole—a hollow now excavated to the full limit of the flippers' reach.

Numerous observations were made on turtles which had hind flippers mutilated and shorter than normal. If only one hind flipper was shortened, digging went on in the same rhythmic cycle of alternation described previously, but only one flipper effectively excavated sand during the final stages of the work. The pattern was continued until this single normal flipper could no longer effectively reach the bottom of the pit. The time occupied in digging an egg hole by turtles which were thus handicapped was variably longer than the 9 to 15 minutes used by completely normal turtles.

Animals which had suffered damage to both hind flippers necessarily made shallower egg holes. In examples where the mutilation was not severe enough to impair seriously the digging mechanism, so that sand was excavated at about the normal rate, the shallower pit was completed in less than the usual time for normal turtles. One severely mutilated turtle had both hind limbs reduced to mere knobs. This animal was unable to excavate even enough sand to allow the cloaca and tail to droop free into a cavity. It made four successive body pits at different places, each time spending from 10 to 20 minutes in rhythmic alternate movements of the amputated stumps before moving off to dig another body pit with the unimpaired front flippers. Eventually it appeared as if oviducal contractions forced the eggs out despite absence of the appropriate trigger stimulus. The turtle moved off back to the sea, dropping eggs along its trail as it went.

In a number of instances trenches have been successfully excavated behind turtles' nests and it has been possible for an observer to lie prone immediately behind undisturbed individuals while they dug their egg holes. Once achieving a satisfactory location, working carefully during the brief intervals between insertions of the hind flippers into the egg hole, it was possible to excavate a posterior extension to the cavity which would allow cautious access to the hole without disturbing the turtle. Working in the brief period immediately after one flipper had been withdrawn with its load of sand, and before the alternate flipper was inserted for digging, sand could be added at a sufficient rate virtually to negate the efforts of the turtle to deepen the pit. In such cases the ending stimulus for the digging pattern and the starting stimulus for oviposition (no more sand within effective reach at the bottom of the hole) is never obtained. Animals have been induced to continue digging for as long as 20 minutes. In every case, however, the subjects eventually stopped digging and left the site to make another nest elsewhere. Sometimes this could be attributed to sand slips or other accidents. In some cases where obvious disturbing accidents did not occur, it is postulated that the prolonged sensation of digging in soft (added) sand instead of firmly packed residual sand was sufficiently close to the circumstances of a cave-in to cause removal of the turtle to a new site.

In similar circumstances to those previously described, female turtles were " helped " on several occasions by removing sand from the bottom of the egg hole. Such experiments, by hastening the deepening of the cavity down to the limits of the turtle's reach, encouraged oviposition in less time than normal. A similar practice is followed by impatient egg collectors in Malaya. The egg collector may then lie prone with his hand at the bottom of the pit, catching the eggs and removing them as they fall from the turtle's cloaca, thus saving himself the considerable work of excavating the nest after the turtle covered it. Turtles whose nests have been thus robbed go through the complete pattern of covering and disguising the empty nest in a normal manner.

Egg laying

After a few unsuccessful attempts to reach and scoop out more sand from the bottom of the egg hole, the turtle arranges its hind flippers on either side of the tail so as to shield the opening of the egg hole. It then begins to lay eggs. Both rear flippers may dangle into the cavity, or one or both may rest partly on the rim of the hole (see Plate 4 a).

The eggs are dropped one, two, or three at a time with short intervals between detectable contraction waves. Turtles were never observed to inspire air during the actual time of extrusion, but occasionally expired a small amount of air under pressure, producing a muffled grunt. The general impression is that the female actively exerts coelomic pressure during extrusion of the eggs, and that the lungs are kept inflated as fully as possible to aid in this process. The pink mucosa of the cloaca is extruded between 7·5 cm. and about 12·5 cm. during the laying process ; it drips quantities of clear mucus. The eggs, well bathed in mucus, drop to the bottom of the egg hole with audible impacts. At any point of contact with the sand, the mucus covering the eggs gathers a layer of adhering sand grains. The three sets of field observations selected as principal models for this account record 9, 10 and 11 minutes as the total time occupied in extruding 102, 109 and 120 eggs, respectively (see " Studies on the Sarawak Populations " for data on average clutch size). Plate 4 a shows the approximate termination of oviposition, when the egg hole is almost filled with eggs (note the bubbles in the mucous coating of the eggs).

The new-laid eggs are firm to the touch, but not completely turgid. Most of those observed showed small, shallow dimples 6 mm. to 12 mm. in diameter. The eggs are usually almost spherical, averaging about 40 mm. in diameter at the time of laying.

Samples of ten eggs each were caught as they fell from the cloacae of laying turtles. These eggs, wiped free of excess mucus, were then weighed within 15 minutes of the time of extrusion of the last egg in each sample. The freshly laid eggs averaged 36 gm. in weight, varying from a minimum of 28·6 gm. to a maximum of 44·7 gm.

The turtles providing the above samples were allowed to complete nesting undisturbed and further samples of ten eggs were taken from each nest approximately 8 hours after laying. The eggs of the second set of samples were dipped quickly in water and wiped dry to remove adhering sand, then were weighed. They showed an average weight gain of about 4 per cent of the original weight (from 0 per cent to 9 per cent). Controls left standing in water for 5 minutes after washing showed no particular weight gain over the eggs which were quickly dipped for cleaning. It was concluded that the measured weight increase was due essentially to water absorbed from the moist sand of the egg chamber during the 8 hours since oviposition.

In the thousands of clutches of eggs observed, abnormal eggs were frequently noted. Size variations were the most common ; some of the extremes found are shown in Plate 4 b.

Two of the abnormal varieties are common enough to have been given particular names by the islanders. " Telor muda " (young eggs) are abnormally small in size and in some cases they contain albumen only. " Telor putat " have abnormal shells. They seem to lack the normal content of calcium and they feel soft to the touch. " Telor putat " are often non-spherical and commonly the shell bears grooves and folds ; the name " putat " presumably refers to the resemblance of these eggs to the fruits of a species of tree (*Barringtonia*) which, according to Corner (1940), bears the Malay name " putat ". While one or two abnormal eggs frequently are found in otherwise normal clutches, whole clutches may be of consistently small size, and numbers of clutches were seen which were completely composed of abnormal eggs of all sizes and forms, indicating a general malfunction of the female genital tract. Evidence of continued malfunction over several layings is scarce. Of seven instances where females with multiple records of egg laying produced distinctly abnormal clutches, only one showed more than a single abnormal clutch, namely, forty-five " telor putat " laid on 18th July 1953, ninety normal eggs on 29th July 1953 and fifty-five "telor muda" on 8th August 1953. Plate 4 b shows a number of abnormal specimens collected. The egg at the right hand end of the centimetre scale is normal except for the small knob on its surface. The five eggs on the left hand side of the picture are " telor putat " ; the abnormally small specimens above the right hand end of the centimetre scale are " telor muda ". The thin strings appear to consist of shell substance only. The group in the upper right of the photo contained albumen only.

Throughout the period of laying, the turtle lies almost motionless. By the time laying has begun, sensitivity to external stimuli appears to have been almost completely lost. A brilliant light may be shone in the turtle's face, causing withdrawal of the head and closure of the eyes, but no cessation of laying. An observer can sit on the turtle's back—a process which one would think likely to cause the greatest distress to these animals so handicapped in breathing while on land—without obvious inhibition of the laying process. This virtually unbreakable fixation of the reproductive action pattern continues through the first part of the action pattern involved in covering the nest.

Covering the nest

After the last egg has dropped, there is only a short pause before the hind limbs begin to shift somewhat fitfully and soon begin to operate rhythmically in alternation, gathering sand and pushing it into the egg hole. Commonly the turtle shifts forward about 15 cm. at this time. The hind flippers are raised clear of the substrate and are brought anteriorly until they lie next to the sides of the carapace. They are then moved posteriorly in sweeping arcs, gathering sand and pushing it into the egg hole over the eggs. The eggs usually fill all but about the upper 12 cm. to 20 cm. of the hole. This remaining space soon fills with sand and a quantity of sand accumulates over the former mouth of the hole. This heap of moist sand is subjected to a kneading action by the hind flippers and is compacted into a low mound. The three turtles providing the principal observations used for this account spent 7, 8 and 10 minutes filling and covering the egg hole. Plate 4 c shows a female gathering and padding sand onto its egg hole. The left flipper is extended laterally prior to gathering more sand and pushing it into place over the filled egg hole.

After filling the egg hole and compacting a pile of sand over its mouth, the turtle resumes a pattern of activity similar to that followed in excavating the body pit. The fore flippers again begin to throw sand backward with powerful strokes, the hind flippers also contributing to this action by pushing backward much of the spillage from the fore flippers. For a period of from about 15 minutes to more than an hour, the turtle now "swims" through the sand, removing sand from the front edge of its body pit and piling it up behind. In effect, the depression in which the turtle lies (body pit) is moved horizontally away from the spot where the eggs were laid, leaving behind an extensive area of disturbed sand built up to a level which is often slightly above the general beach level. It would appear that the average inclination of the digging stroke of the fore flippers in this covering operation is different from the inclination followed during the original excavation, for the body pit, as it is moved along, becomes progressively shallower instead of deeper. Eventually, when anywhere from 1·2 metres to 3·7 metres away from the site where the eggs were laid, either the turtle has arrived at the level of the general beach surface or it simply stops digging further and crawls up out of the remaining shallow pit. The three turtles providing the basic notes for this account had moved about 1·5, 2·7 and 3·4 metres from the eggs when they stopped digging. Plate 5 a shows a completed nest; the stick bearing a slip of white paper marks the location of the eggs ; the observer is standing in the pit left at the time when the turtle stopped digging.

Return to the sea

Upon completion of the long process of covering the nest, the turtles appeared to regain some of the sensitivity to visual stimuli which had been temporarily lost, and individuals were again easily alarmed. The rate at which individuals crawled across the beach during the return trip appeared to be more rapid than it had been when wandering about the beach prior to nesting. Returning turtles moved along at an average speed of about 2 metres per minute on the high beach.

Memory seemed to play no part in turtles finding their way back to the sea. They neither consistently followed their incoming paths back to the water nor necessarily made off in straight lines for the nearest water. When out of a direct line of sight to the water, individuals usually wandered somewhat erratically, but once reaching the crest of the high beach platform where the sea was in sight, they usually followed a straight route to the water. On the packed sand of the lower portion of the beach they moved about twice as fast as had been done on the loose sand of the high beach platform, often reaching the water in a few minutes even at low tide periods when the water was far out.

Table I shows the timing of the beach activities of the three female turtles providing the principal observations used in the foregoing account. It is believed that the timing of these three individuals may be considered as representative of the nesting Green Turtles studied in Malaya and Sarawak.

TABLE I

Timing of activities of individual female *Chelonia mydas*

Stage of Process	Turtle " A "	Turtle " B "	Turtle " C "
Turtle mostly awash, just visible	0(–0035 hrs.)	0(–2020 hrs.)	0(–2225 hrs.)
Reached high tide line	15 min.	20 min.	—
Reached margin of high beach platform	20 min.	25 min.	—
Commenced to dig body pit	28 min.	27 min.	35 min.
Changed digging activity to rear flippers only (beginning posterior shallow basin)	42 min.	50 min.	—
Actual egg hole begun (rear flippers first began to *lift* sand)	60 min.	65 min.	—
Egg hole completed, first egg dropped	72 min.	75 min.	83 min.
Laying completed, first began to push sand over eggs	82 min.	86 min.	92 min.
Egg hole covered and packed, first began to to flip sand with fore flippers	92 min.	94 min.	99 min.
Had moved 1·5 metres away from nest ; still digging strongly	148 min.	—	—
2·7 metres away from nest (immediately after this, began to move back to sea)	—	—	159 min.
Reached high tide line on way back to the sea	176 min.	145 min.	170 min. (22·6 metres in 11 min.)
Reached water's edge	177 min. (4 metres in 1 min.)	—	172 min. (9·6 metres in 2 min.)

OBSERVATIONS ON MALE TURTLES AND ON MATING

The male of *Chelonia mydas* is easily distinguishable from the more commonly seen female. Its two most obvious distinguishing characters are the long, heavy, prehensile tail (see Plate 5 b; compare tail length with that of the females in Plate 6 c and Plate 8 c) and the prominent, recurved spurs on the fore flippers (Plate 5 c).

Male turtles were never found out of the water except for rare instances where copulating pairs were stranded on the beach at night by a rapidly receding spring tide. Except for the rare stranded individuals, the only males which could be identified and observed as such were those seen in the sea, engaged in some sort of overt mating behaviour. When in copula, the male is frequently exposed above the water and is conspicuous at some distance. Moorhouse (1933) provides an excellent photograph of a pair of turtles in copula. During the period March to July, copulating turtles were commonly seen in the waters around the turtle islands throughout the daylight hours, and courting or copulating turtles could be seen almost any night in shallow water just off the beaches. In March, when the heavy laying season was just beginning, copulating pairs were recorded with the greatest frequency; not uncommonly two or three pairs were noted at one time, more commonly in the morning than in the afternoon or evening. In July, the usual peak month for egg production by the industry, there began to be a reduction in the numbers of copulating pairs noted. By the end of August, sightings of copulating pairs were rare. Mr. Alfred's journal entry for 22nd August includes the following observation: " For the first time in many days saw two pairs of turtles mating off beach in morning. The heavy season is now definitely coming to a close—fewer turtles coming up now each night ". Harrisson (1954) states, " It is believed that copulation only occurs close to the breeding beaches . . . it has not been seen more than half a mile offshore ". While the writer has on several occasions seen copulating turtles considerably more than half a mile from shore, he agrees that there appears to be pronounced concentration of breeding activity, as indicated by sightings of copulating pairs on the surface, in the immediate vicinity of the islands. Field records of daytime sightings of copulating pairs on six different days show a total of forty-two copulating pairs noted nearer than an estimated 230 metres from the coast of Talang Talang Besar Island, as compared with fifteen pairs noted more than an estimated 230 metres offshore. These records were made both from boats and from land, in the latter case using powerful binoculars from a raised verandah offering a good view of a large area of sea. All six selected days were calm, with good possibilities of viewing copulating pairs as far off as 0·5 kilometre.

It seems possible that breeding females do not wander any great distance from the islands during the intervals between nestings. It is believed that there is a continual concentration of reproductively active females in the waters around the small breeding islands, and that the breeding males are similarly drawn into a concentrated area by the numbers of females encountered near the islands.

Under the shelter of darkness, this zone of concentration of females is apparently narrowed down considerably and extreme concentration occurs at the margins of the nesting beach itself, with females continually moving to and from the land. With the aid of a bright moon an observer can stand up to his knees in water on a calm night in the heavy laying season and observe almost continuous mating activity near his station. While standing in waist-deep water, the writer has twice experienced mild collisions with male turtles who were milling around a female.

Observations to date indicate a general interest in any female on the part of breeding males. They have been seen to attempt copulation at all times of the day and night, choosing females on their way to the beach to lay as well as females returning to the sea after oviposition. There is insufficient evidence at this time to indicate clearly any period in which the female is more receptive to the male than at other times. The field journals on which this report is based contain more observations of " stable, apparently successful " connections in the hours from 0300 hours to 1000 hours than during the remaining 17 hours of the day. The daylight hours after 1000 hours contribute the majority of records of attempted, but apparently unsuccessful, copulations. Possibly this indicates a greater receptivity on the part of the female in the period following a nesting. Seven clear records of attempts by males to copulate with females just prior to nesting (the females observed to lay eggs that night) all indicate failure to achieve actual connection.

While a fairly definite pattern of courtship behaviour apparently does exist, close observation proved to be almost impossible. Observations through binoculars from an elevated point on shore gave only vague information on activities carried out beneath the surface of the water, and early attempts to observe at close quarters with mask and swimming flippers were given up after it was decided that such activities entailed a certain degree of real danger. At night, when the observer had to approach very closely to a female turtle and attendant males in order to see anything clearly, the males showed a certain amount of aggressiveness. During the day, when all mating activities were removed to deeper water, attempts to approach animals by swimming out beyond the reef edge were discouraged by sharks. There appeared to be a feeding concentration of Tiger Sharks (*Galeocerdo*) in the near vicinity of the islands (see " Predation ").

On numerous occasions observations through binoculars showed one turtle (presumably a female) receiving the attentions of several other turtles (presumably all males). Whenever approached closely the presumed female apparently attempted to turn rapidly so as to face the approaching individual. However, with from two to five turtles milling about, the central animal could not avoid being approached from behind. From time to time one of the encircling turtles was observed to swim rapidly forward, riding up over the posterior carapace of the presumed female, sometimes remaining in position there for a short period. At no time, however, was this copulatory position observed to be held for a long period after it had been assumed ; in all cases the uppermost turtle slid off the back of the female (?) again after a minute or less. In view of the frequent observations of pairs remaining in copula for extended periods of time, it is believed that none of the observed short-term mountings marked successful copulations.

Most of the information on courtship behaviour was provided by occasional fortunate observations very close inshore on bright moonlit nights or at dawn. The following extract from this writer's field journal for 13th March 1953, includes almost all the details noted at other times and may be taken as a summary of such observations made during the work reported on here :

13th March, 1953. Just before daylight, near the tip of the beach at Talang Talang Besar, I observed a large female *Chelonia* attended by four males. She was in about three feet of water, and the males were milling about her in confused fashion ; it was possible to see the difference in tail length between the sexes. At about daylight the group moved into shallower water and I retreated to hide behind a large drift log about 20 ft. away. The steep incline of the beach at this season and the size of the log enabled me to view the turtles from a high angle and I could see what went on more clearly than at any time previously.

When any male was seen to approach within two or three feet, or upon being touched from behind, the female made vigorous attempts to turn to face the male concerned. Because of the number of males around her, however, she was frequently unable to avoid contact from behind. The males engaged in numerous quick head movements toward the female whenever they were near her, both when she was facing them and when she was facing elsewhere. Whether these movements by the males were biting or butting motions I could not tell. At no time did they elicit any violent response from the female at the moment of contact, and at no time did the male's head appear to remain in contact with the body of the female ; for these reasons I suspect that they were butting her with closed mouths (analogous to the shoulder " nudging " in courting land tortoises ?).

Although it is possible that the impression was due to confusion on my part during several periods of great activity, one particular male appeared to be dominant over the others. It is possible that I lost track of individuals at one time or another, so I can only say that this condition of dominance appeared to be quite clear to me at the time. The only male to mount the female appeared to be this dominant male ; this occurred several (five ?) times, each time sustained for a period of less than a minute (estimated time). Upon sliding off the female's carapace the (apparent) dominant male swam rapidly toward one or another of the attendant males which each time appeared to give way to him after a fashion. Having chased one male for perhaps four metres, the dominant male returned in a tight circle to the female and mixed in somewhat confused fashion with the other males which had crowded in during the interval. After from one to ten minutes (estimated time), copulation with the female would again be attempted.

The male, about to mount, makes a rush towards the female from a few feet behind her, gaining momentum as he approaches. Approaching at considerable speed, he makes one or two very powerful sweeps downward with his fore flippers and at the instant of contact between her carapace and his plastron he is about half out of water. His momentum carries him up onto her shell into mounting position and he lays his fore flippers down and antero-laterally over her shell, usually hooking his recurved flipper spurs on the edge of the female's carapace just over the bases of the female's front limbs. Apparently the hind flippers are manipulated so as to engage their spurs after the front spurs are engaged. The spurs of the hind flippers appear to be hooked under the postero-lateral edges of the female's carapace, approximately over the bases of her hind limbs.

Once securely engaged, the front flippers are relaxed while the rear flippers pull the male as far back and down as the passive engagement of the anterior flippers will allow. The portions of the male's hind flippers distal to the spur are bent down and forward under the female's carapace, more or less incapacitating action of the female's hind limbs. The male's long tail is bent down along one side of the female's tail and then forward, placing his cloaca in position for copulation.

Even when apparently firmly engaged in appropriate copulatory position, the observed male several times disengaged and left the female for short rushes at other attendant males.

I can only assume that the close proximity of other sexually aggressive males could not be tolerated by the mounted male, and recall another observation at a distance in bright daylight when I saw a second male mount and successfully engage a mounted male, both males then separating from the female.

After approximately 45 minutes of observation, there was full daylight and I felt almost certain that the turtles would soon move out to deeper water. I waited until all the individuals immediately inshore had their heads under water and approached to within about 2 metres of the female. Upon putting up her head to breathe, she saw me and left with a great rush and foaming of water, followed by two attendant (minor) males. This occurred just after the dominant male had left on a rush at one of the other males. He returned to the female's former location and made two six metre diameter circles at high speed, apparently trying to locate her, then went off into deep water. On one of these circles he passed within about four feet of me (I was standing in about 20 cm. of water), churning up the sandy bottom with each stroke of his flippers.

Plate 6 a and b show a copulating pair which were stranded on the beach by a rapidly receding spring tide. Presumably the male had mounted a female which was coming up to nest. Hampered by the firmly attached male, the female nevertheless continued to try to make her way up the beach. In Plate 6 a, note that the male's strong, recurved spurs are hooked under the edge of the female's carapace. It will be seen that, in this case, the male is slightly smaller than the female.

Once fully engaged in copula, the male appears to become quiescent, allowing its head and neck to droop except for periodic elevation for breathing. Many females seemed to be continually engaged in minor movements, turning this way and that and swimming short distances on erratic courses. In many cases this activity was thought to be related to the presence of attendant males, whose shapes could be seen in the water near the copulating pair. Many of the pairs remained together for periods of observation of 20 minutes or more. Reliable records of the full duration of an average copulation could not be obtained.

During the longer copulations it would appear that the female hyperinflates her lungs, making the locked pair float much higher in the water than might be expected. Jacobs (1939) discusses buoyancy regulation in Loggerhead Turtles ; it is assumed that a similar mechanism operates in Green Turtles. Hyperinflation probably has no significance other than that it allows the female to remain near enough to the surface to breathe without pronounced swimming efforts. When stable copulating pairs were closely approached, the male usually detected the observer during one of his periods of breathing activity (raised neck and head), and disengaged from the female when the observer was from 15 to 50 metres distant. The male dived from view when this happened, but the female commonly remained conspicuous, floating high in the water with as much as 12 cm. of carapace dome projecting above the surface. After a short time the floating female usually would raise her head out of the water to breathe, detect the presence of the observer, and move vigorously away. Very often it appeared as if she had not expelled sufficient of the excess air in her lungs to dive efficiently, and she would leave a 10 to 20 foot trail of disturbed water marking the course of her progress away from the spot.

STUDIES ON THE SARAWAK POPULATIONS

The turtles nesting on the Sarawak Turtle Islands are particularly suitable for statistical studies. Large numbers of individuals are concentrated on three small beaches at the time of nesting, minimising problems of access to a large sample. Records of the turtle egg industry have been kept for a number of years and some of these have been published by Banks and by Harrisson (see Literature Cited). The particular nature of the industry as it is at present administered by the Sarawak Turtle Board of Management facilitated accumulation of data during the period of this study. As pointed out in the acknowledgements at the end of this paper, the Board of Management aided the writer's work in many ways.

In 1952 and 1953 the writer made four visits to Sarawak, spending a total of 54 working days on the turtle islands. Two student research assistants from the Department of Zoology, University of Malaya, spent a total of 106 days at work on the islands during the same two years ; Mr Santiago worked for 29 days in 1952 on the preliminary survey and Mr Alfred worked for 77 days during the main marking programme in 1953. From time to time, particularly during 1953, the Turtle Board employed local men for the particular purpose of helping in the research programme. The Turtle Board's own staff on the islands consistently supplied many hours of help besides their regular duties in the egg collection industry.

Description of the Sarawak Islands

There are only three islands off Sarawak which provide nesting beaches for large numbers of *Chelonia mydas*. All three are near the coast of the main island of Borneo, within the 10 fathom line. Satang Besar Island is located at about 110° 9′ E., 1° 47′ N., roughly 1·5 kilometres off shore and about 4 kilometres from the Santubong mouth of the Sarawak River. The two Talang Talang Islands lie less than 500 metres apart at 109° 46′ E., 1° 55′ N., roughly 2 kilometres off the mouth of the Sematan River. The Handbook of Sarawak, 1949, gives the following areas for the three islands :

Satang Besar	250 acres
Talang Talang Besar ("Big Talang Talang")	92 acres
Talang Talang Kechil ("Small Talang Talang")	29 acres

On all three islands the turtle beaches are relatively small ; while subject to changes in shape and size, they probably remain within about 10 per cent of the following areas, as read with a planimeter from copies of survey maps :

Beach at Satang Besar	11,600 sq. metres
Beach at Talang Talang Besar	8,300 sq. metres
Beach at Talang Talang Kechil	4,500 sq. metres

Figure 4 shows the shape, disposition, and comparative size of the beaches. It is worthy of note that, while the beach at Satang Besar is the largest of the three, it has the smallest nesting population of *Chelonia mydas*.

All three islands are of hard, black rock which carries a relatively thin soil cover. They support a thick jungle growth which has been partially cleared and planted with coconut palms and a few fruit trees. There are fringing coral

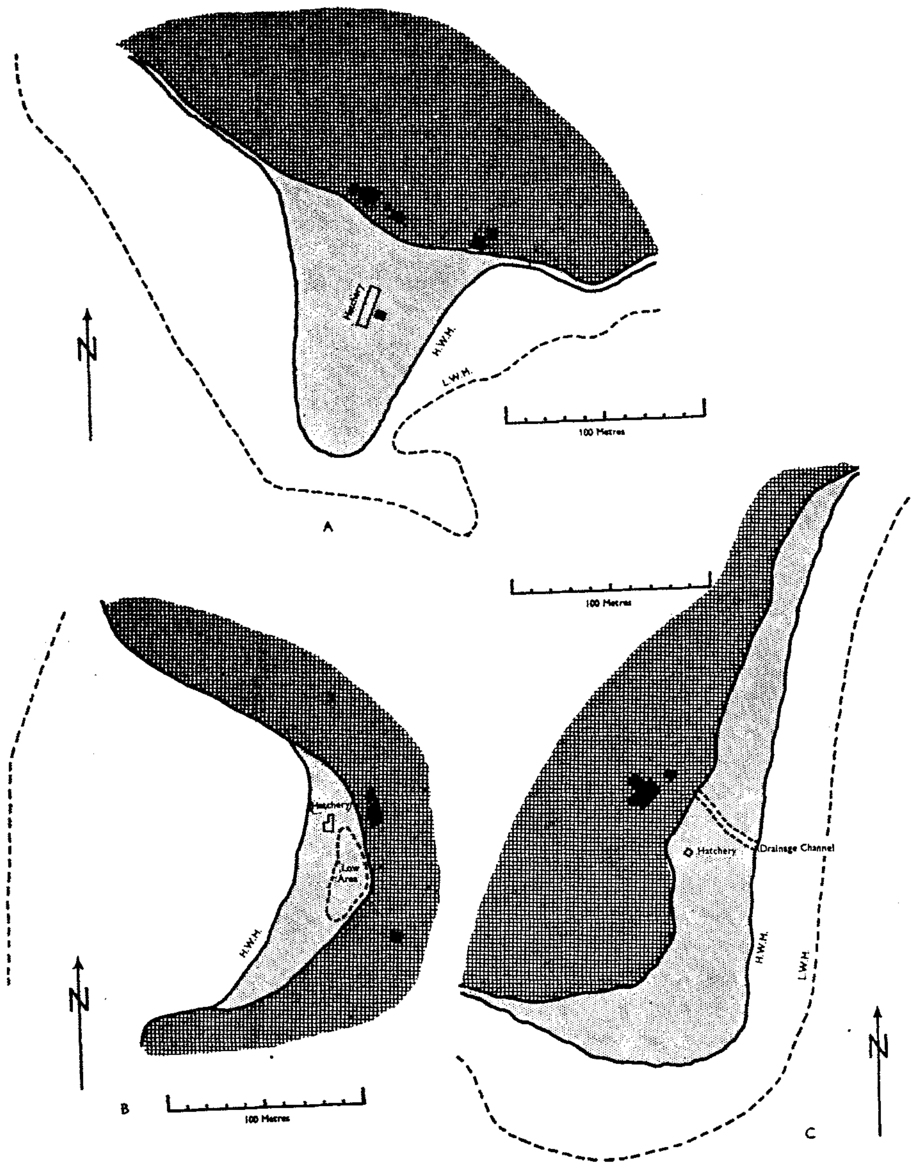

Fig. 4.—Maps of the nesting beaches on the three Sarawak turtle islands.
A.—Talang Talang Besar Island.
B.—Talang Talang Kechil Island.
C.—Satang Besar Island.

reefs on all aspects of the turtle beaches, except at the tip of the spit beach at Talang Talang Besar.

The water around the Talang Talang Islands has been impressively clear at all times when the islands were visited during the course of this study. These islands apparently receive throughout the year a continual current from the open sea to the north, preventing the silty effluent of the nearby Bornean rivers from reaching the islands. Satang Besar Island is bathed by eastward-flowing coastwise currents which have acquired silt from rivers. The major outflow of the Santubong mouth of the Sarawak River may also affect directly the waters of the island. While far from being actually muddy, the water around Satang Besar definitely carries more suspended matter than the Talang Talang waters.

To date no extensive areas of aquatic vegetation have been discovered in the vicinity of the islands. It is not possible to point to any extensive plant forage grounds available to the turtles nesting in that locality. As pointed out in the historical summary, adult animals could not be killed during the course of this study. Stomach contents, therefore, could not be analyzed, making it impossible to infer the extent to which the breeding period of the individual turtle may be a non-feeding period.

Methods of investigation

The most important single phase of the field work was the marking of adult female turtles in order that individuals could be recognised again and that their activities could be tabulated. Various methods of marking (see Moorhouse, 1933; Schmidt, 1916; Banks, 1937) were tried in 1952. A modification of the method used by Moorhouse (1933) was adopted and 250 females were marked on Talang Talang Besar Island by attaching numbered copper tags to their carapaces. To attach a tag, a twist drill was used to bore two holes through one or the other of the pygal plates of the turtle's carapace. Copper nails were inserted through holes in the tag and the carapace and were clinched on the under-surface of the carapace. Plate 6 c shows a copper tag in place on the pygal region of a turtle. Difficulty was experienced in boring the holes through the carapace to match the holes in the tags. It was felt that forcible immobilisation of the turtles during the operation, quite aside from the physical problems posed, would have had a pronounced disturbing effect on them and might have influenced their normal pattern of returning to that beach to nest. Many drill bits were broken and much time was consumed in working on the unconfined turtle as it lurched across the beach. While many records of repeated returns were obtained from this work, the copper tags did not last well. The pygal plates of the carapace are the only portion which provides a thin enough projecting shelf for attaching tags in this manner, and this portion receives severe abrasion from the plastra of male turtles during copulation. Many of the tags were loosened and lost, as demonstrated by frequent records of females with two small, appropriately-placed holes in the pygal area, but no tag. Moorhouse (1933) postulates the same reasons for loss of pygal tags which were affixed by a different method. After appraisal of the total data collected in this manner, it was decided to discard the method and in the following year to attempt another technique.

In 1953 a supply of cattle ear tags,* especially made of monel metal, was obtained. Made to be affixed with a patented applicator plier, the tags are self-piercing and self-clinching. Stamped on one surface of the tag was a code letter (" B ", " K ", or " S " for Talang Talang Besar, Talang Talang Kechil, or Satang Besar, respectively) followed by a number. All numbers were from the same non-duplicated series, irrespective of the letter prefix. On the other exposed surface of the tag (ventral, as affixed to the turtle) was the legend: SARAWAK MUSEUM REWARD.

Tags were fastened to the trailing edge of one of the front flippers, piercing the tough, thin, scaled margin of the flipper. While they were never placed on the basal part of the limb where the tissues were soft and fleshy, they were located proximally, as far as possible away from the main blade of the flipper. In this position there was minimal abrasion by sand during nest digging and the minimal arc of movement during swimming strokes decreased the potential amount of play in the attached tag. There was little evidence of sensitivity in this region, and hardly ever any external sign of blood following the operation. The tissues at the selected site gave excellent anchorage for the tags, but they were so tough that, in forcing its way through the flipper, the piercing point of the tag was often bent out of line sufficiently to cause improper clinching. Modification of one of the patented applicator pliers by fitting it with a sharpened steel chisel at the level where a tag point would be held made it possible to pierce the flipper prior to the actual tagging. In one quick operation, this tool pierced the flipper with a small slit which was in an appropriate position for the tag. With a prepared slit for the tag point to follow, the actual affixing of the tag could be quickly and easily accomplished. By dividing the tagging process into two separate, simple operations, no restraint had to be applied to the turtle. Each operation could be accomplished during the frequent short periods when the turtle was resting with its flippers virtually motionless. Turtles from Talang Talang Besar Island had their tags applied to the right fore flipper, turtles from Talang Talang Kechil Island had tags placed on the left fore limb.

Plate 7 a shows an applicator plier with tag inserted ready for use and a modified plier fitted with a piercing chisel. Plate 7 b shows a tag held so as to show the serial number on the upper surface. Plate 7 c shows a tag affixed to a turtle.

After short practice, all the men doing tagging work were able to approach a turtle, inspect the flippers to make certain that it did not already bear a tag, pierce a flipper and affix a tag, all in less than 2 minutes. Since the operations were swift and since turtles did not need to be forcibly restrained, the disturbance to the animal was very slight compared with that caused by the 1952 technique. The turtles showed little violent activity during the process and there was apparently minimal fixation of the incident in their memories.

* " Hasco " Brand Cattle Ear Tags, No. 19M, produced by the National Band & Tag Co., Newport, Kentucky, U.S.A.

Except for occasional lapses by enthusiastic helpers among the islanders, individual females were not approached until they had begun to lay eggs. By this time they were unlikely to be particularly influenced by mild disturbances. If the regular watchmen had not yet placed a numbered flag marking the position of the nest, they were asked to provide one. Approaching the subject from behind and illuminating the front flippers briefly, the worker gently brushed the critical areas of the flippers free of sand and inspected them. If a tag was found, it was inspected to see how well it was affixed and the tag number, nest flag number, time, and name of the observer were recorded in a field record book for returns. From the nest flag number, the size of the clutch was determined from the regular records of clutch size which were made when the nests were dug up the following morning. If no tag was found, the nest flag number was noted and the turtle was checked at intervals. When the turtle had finished laying eggs and had begun to cover its nest, tagging was carried out. The flipper was pierced and a tag affixed and inspected for adequacy of clinching action. The observer then retired a short distance away to record tag number, nest flag number, time, and his own name in a special field record book reserved for newly tagged turtles. Upon completion of the entries in his record book, the tagger again approached the turtle. He checked his entries, re-inspected the tag to see that it was securely attached, and noted any striking abnormalities, injuries or other features which came to his attention.

Frequently turtles continued the process of covering and hiding the nest all through the tagging operation. Often, an individual would "freeze" temporarily or lurch forward once or twice during the process, but by the time the observer had finished recording his data and flicked his light on the turtle for the final check, most turtles had resumed normal activities in covering the nest. It was found that the easiest working period, with the least observable residual effect on the turtle, was during the time when the female was still filling in the egg hole, before she had begun to throw sand with the fore flippers to cover and disguise the body hole (see description of the nesting process).

Animals were marked primarily for short-term study during one breeding season. However, it was hoped that over the long term some knowledge might be gained concerning migrations, the timing of the breeding periods of individual females, homing to particular beaches each breeding period, and other activities. Up to the present, so far as the writer is aware, the only record of wanderings is an unconfirmed report of the 1952 (copper-tagged) turtles being seen at the Natunas Islands (see Fig. 1). Return of females to the same breeding beaches in later years, and the period of absence between breeding periods are briefly discussed in another section of this paper.

The research party concentrated mainly on Talang Talang Besar Island, which has the largest population of turtles nesting on its beach. Throughout the most intensively worked period from June to October, 1953, there was continuous patrol of the beach on Talang Talang Besar throughout the dark hours of each night by both research workers and regular watchmen. The regular watchers were instructed in the techniques of examining for old tags, and the more literate men were taught to record the essential data in the field book for returns. After the research party left, the regular staff continued to accummulate data on returning, marked turtles.

On Talang Talang Kechil Island the foreman of the regular island staff, a man who had received training as a ship's engineer and who was fairly sophisticated along mechanical lines and in the keeping of records, did most of the tagging. While some features of the work on Talang Talang Kechil did not compare favourably with the severe standards maintained on the larger island, discipline among the general staff was very good and there is reason to believe that the records kept after the research party had left were more accurate than on Talang Talang Besar.

Tagging was not begun on Satang Besar until the middle of September 1953. At this time an able young man from the Satang staff returned after two months' training under the research staff on Talang Talang Besar and began a tagging programme on his home island. Rigorous analysis did not demonstrate any clear faults with either the tagging or the collection and recording of data on Satang Besar.

2,720 female turtles were tagged on the three Sarawak islands, 1,798 on Talang Talang Besar, 750 on Talang Talang Kechil, and 172 on Satang Besar. Most of the tagging (2,404 turtles) was done during the period March to October, 1953, which included the peak of the breeding season. The remaining 316 tags were affixed by workers as other duties permitted during the remainder of 1953 and the first four months of 1954.

8,468 standard observations were made on tagged turtles at the time of tagging and upon subsequent returns to the beaches. Each observation included code letter and number of the turtle's tag, hour and date of the record, number of eggs in the clutch, or failure to lay, as the case might be, name of the observer, and miscellaneous remarks as indicated by the turtle's actions or appearance.

Data were entered on punched cards, double-punched for verification and machine-sorted for the analyses presented in this paper. Further exhaustive sortings were made as part of a programme of checking on the reliability of each of the eighteen persons who contributed to the body of data.

Potential sources of statistical error

Throughout the period in which statistical data were collected, every effort was made to ensure the reliability of the information gathered. An attempt was made to comment in each day's field notes on possible sources of error in method or interpretation which had been brought to mind by that day's activities. Certain of the real or potential sources of error which, by the nature of the programme itself, could not be obviated were noted fully and were kept in mind throughout the course of the work. Since it has appeared impossible to provide numerical indices of reliability for the statistical results presented here, a general discussion seems to be called for in order to clarify some of the factors which may have had, or did have, an effect on the data.

All persons concerned in data collection except for the writer and three research assistants were non-English speaking. All but a few of the regular island workers were virtually illiterate in Roman letters. On the other hand, the writer and the student assistants from the University of Malaya were illiterate in the Jawi script which was understood by most of the islanders. Problems of communication, particularly of written communication, were ubiquitous.

Every attempt was made to prevent the participation in data gathering of the totally illiterate men who could not even read simple numbers. Despite all precautions, however, errors were to be expected in data recorded by non-scientific workers lacking the sophistication brought by years of constant use of written numbers in everyday life. Furthermore, such persons could not in all fairness be expected to appreciate the stringent self-imposed discipline for absolute accuracy which the ordinary scientist applies almost automatically to his work. It is therefore reasonable to expect more errors in data recorded by the regular staff on the three islands than in data recorded by the more highly trained workers.

While less confidence can be placed in the data collected by the islanders, in the writer's opinion they did an exceedingly good job. Statistically-contrived " traps " set for them, with token rewards for the cleanest records, stimulated considerable friendly competition. They enjoyed this partly-mysterious lottery and teased each other about being caught out on mistakes. Comparative sorting did not demonstrate any particular unreliability in the recording of data on the part of any one of the eighteen individuals concerned. In every case where statistical analyses presented here could be broken into two appropriate bodies of data, the records contributed by the writer and his two university student assistants were compared with those contributed by the other workers. None of the comparisons showed a significant difference in results.

As far as possible within the limits of human endurance, the writer and his research assistants collected all data during the periods they were active on the islands. The sheer physical work involved was, however, considerable. Fatigue must undoubtedly be considered as an ever-present source of observational error. Working night after night under tiring conditions called for extreme care and great effort on the part of the research assistants. It is to their great credit that none of many cross-checks revealed any glaring errors in the recording of data.

The method of counting the eggs dug up from each nest resulted in manifold minor inaccuracies in the records of the number of eggs per clutch. Eggs excavated by the men unable to count were counted by the island foreman or his delegate, so no particular inaccuracies are to be expected from this source. However, the common pattern of action used by most of the men in handling the eggs does appear to be a continual source of error. The usual method observed in use by the island workers was to handle the eggs five at a time, counting by fives. Theoretically, odd numbers left at the last would be appropriately added on, but analyses of several thousand egg counts show about twenty times the expected frequency of zeros and fives as last digits of recorded egg numbers. It is assumed that this is referable to the method of counting, and that all figures on numbers of eggs per clutch must be considered as plus-or-minus at least four. Two different research workers ran test checks on 100 nests on two different occasions. These checks on the accuracy of islanders' egg counts were done without warning and were successfully disguised as investigations on the sizes of eggs. The last digits of the research workers' test counts did not show a particular preponderance of zeros and fives. The two double-checked test counts were later compared with the figures recorded in the industry's record books. There was no particular tendency for the islanders' counts to be either consistently above or consistently below the exact numbers of the test counts. Accordingly, when included in this paper, figures on clutch size from the records kept by the industry have not been adjusted.

The majority of the tags placed on turtles on Talang Talang Kechil were affixed by one man. Machine sorting of all return data according to the persons who affixed tags demonstrates a clear tendency for turtles tagged by this individual worker to fail to appear again in records of returns. Journal notes indicate a proportionally high frequency of turtles from that island with suspicious scars in the location where tags were affixed. The logical assumption is that the person concerned was not affixing the tags securely enough, and that a high proportion of his poorly clinched tags fell off soon after tagging. Comparative checking on all taggers did not reveal such inconsistencies in the work of other men.

The data show a disproportionately high number of turtles on Talang Talang Kechil recorded as visiting the beach but not nesting, and a disproportionately high number of one–, two– and three–day intervals between returns is referable to these same turtles. This was due to an unfortunate eagerness on the part of some of the Talang Talang Kechil workers during the earlier stages of the programme to inspect all turtles as soon as possible. Turtles were approached, contrary to recommendation from the research workers, before they had ascended even up to the high tide line. The men read and recorded the tag numbers correctly, but the turtles were so disturbed by the premature inspection that they returned to the water without laying. This caused the records to be distorted by numbers of " nestless " records. It would appear that most of the turtles thus disturbed returned on following nights to lay, producing a misleading frequency of one-, two- and three-day intervals between recorded returns.

On Talang Talang Besar Island, where the turtle population and the attendant industry was largest and most complex, the organisation was strained to cope with the job. On this island there was the most obvious relaxation of discipline after the research party had left. There was a pronounced fall-off in records of returning turtles in excess of that which could reasonably be attributed to the declining season. As a result of the incomplete recording which occurred on this island after the research party had left, the gross data for 1953 on the numbers of nests per turtle have needed compensatory treatment (see Figs. 9, 10 and 11, with accompanying discussion).

Productivity of the islands

Published records (Banks, 1937 ; Harrisson, 1947, 1950, 1951, 1952 a and b and 1955 a) show an annual total egg production from the three islands which averages slightly less than two million eggs per year. The variation from year to year is considerable; the lowest recorded yield is for 1947, when about 700,000 eggs were collected; 1934 and 1936 produced yields in excess of three million eggs. The latest published record at the time of writing this paper was for 1954, with a reported total of just over a million eggs.

The proportional contribution of the individual islands remains relatively constant from year to year. Talang Talang Besar regularly contributes about 50 per cent of the total eggs; Talang Talang Kechil produces from 35 per cent to 40 per cent and Satang Besar accounts for about 10 per cent or less. In the earlier records, Satang Besar accounts for 6 per cent or 7 per cent of the total eggs. In the three most recently published sets of figures which give production by islands (for 1948, 1950 and 1951), the figures for Satang Besar show an increase to between 10 per cent and 12 per cent of the total. A leper settlement was formerly maintained on Satang Besar for a number of years. It is possible that abandonment of this settlement is related to the increased production shown in the later records. Exceptionally thorough collection of eggs and extensive disturbance to nesting turtles during the time of the leper colony could have reduced the size of the population nesting on Satang Besar and the number of turtles may, now that the pressure is relieved, be slowly increasing.

Breeding season

As other workers (Banks, 1937; Harrisson, 1952 a) have pointed out, there are at least a few Sarawak turtles nesting at all times of the year. So far as the writer is aware, this is at variance with most populations which have been studied in other parts of the world. The absence of a non-breeding season in Sarawak appears to correlate with the absence of any gross annual temperature cycle such as occurs in the areas where there is a pronounced non-breeding season. Figure 5 contrasts the approximate mean temperature curve of the Sarawak turtle islands, where breeding occurs the year around, with the curve for Brisbane, Australia, about 257 kilometres south of Heron Island, where Moorhouse (1933) reports a definite non-breeding period of more than 7 months.

It is noteworthy that the only records of year-round breeding mentioned by Carr (1952) in his comprehensive treatment of Green Turtles are for the Seychelles and the Gulf of Siam. Both these localities have annual temperature cycles more closely comparable to the Sarawak curve in Fig. 5 than to the Brisbane curve.

Like populations elsewhere, the Sarawak turtles have a definite peak season of nesting activity. It would appear that the adaptive advantages of synchronised aggregation for mating are sufficient to account for the existence of a peak season. The particular placement of the Sarawak peak season in the annual cycle (regularly every July–August) would appear to correlate with the monsoon cycle. The curve of egg production on the Sarawak islands appears to be in negative relationship to the Northeast Monsoon, with the lowest egg production when the monsoon is in force and vice versa.

It seems likely that the monsoon is the least favourable period for turtle breeding because of the increased winds and rain and the decreased insolation which occur at that time. Winds, by their effect on the state of the sea surface, may cause minor inconvenience to the turtles, principally by increasing the violence of the surf through which females must pass on their way to and from the breeding beaches. Violent storms during the monsoon period may produce waves of such size that large parts of the beaches, including the high beach platforms, are repeatedly flooded. Previous discussion has pointed out that females are guided in selecting sites for nesting by the softness and lightness of the sand. With an increased frequency of rainy weather during

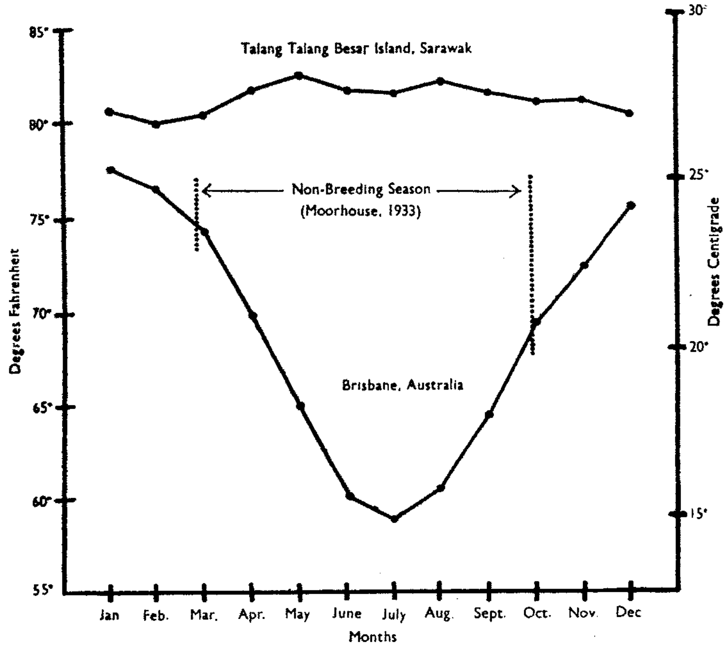

Fig. 5.—Graph showing mean monthly air temperatures for Brisbane, Australia (nearest available station to Heron Island, Great Barrier Reef), and Talang Talang Besar Island, Sarawak. Heron Island turtles show a definite non-breeding season; at least some nesting occurs in Sarawak in all months.
(*Brisbane data for* 1931–1940 : *means of* 1/2 (*daily maximum plus daily minimum*), *from Clayton & Clayton*, 1947. *Talang Talang Besar data for* 1950–1955 : *means of* 1/2 (*mean monthly maximum plus mean monthly minimum*), *from records kept by Sarawak Dept. of Civil Aviation.*)

the monsoon, the sand surface on the high beach will be wet and compact much of the time, and it is believed that the absence of the ideal stimuli provided by a soft sand surface may hinder normal progression of the instinctual nesting pattern. The effects of increased rain and decreased insolation on the incubation of eggs are discussed in the section entitled " Early Development of the Young ".

It is impossible to demonstrate precisely the relationship between the monsoon period and the cycle of turtle nesting because of the difficulty in treating a general phenomenon such as a monsoon in terms of units. Of the various measurable weather components which go to make up a " monsoon ", precipitation appears to vary in closest relationship to the trends of the total complex. Figure 6 shows the curve of egg production on the combined Sarawak turtle islands during the years 1950 and 1951. Superimposed on this curve is the curve of mean monthly rainfall on Talang Talang Besar Island for the years 1950–1955 (same data repeated to cover the two-year span). Rainfall peaks may be taken to correspond roughly with " monsoon peaks ", etc.

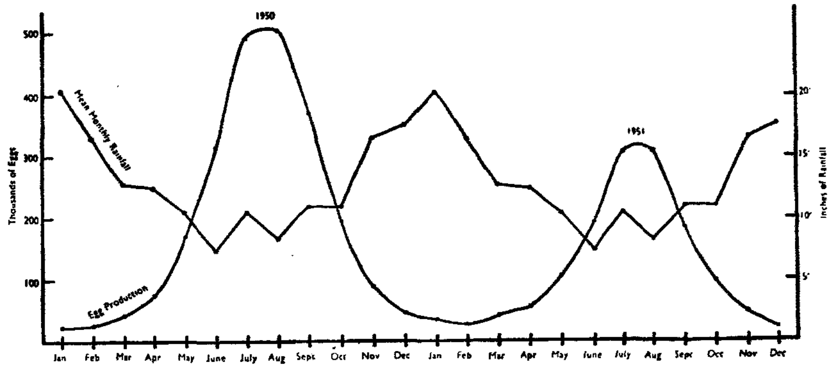

Fig. 6.—Graph showing egg production and rainfall on the Sarawak turtle islands. (*Egg production data from Harrisson*, 1951, 1952. *Rainfall data from records kept for Talang Talang Besar Island by the Sarawak Dept. of Civil Aviation.*)

Banks (1933) suggests that there is a correlation between the severity of the monsoon and the numbers of turtles nesting in the season following the monsoon —a " good " season following a mild monsoon, and vice versa. It is difficult to substantiate this situation as a simple relationship. However, observation over a number of years may provide evidence of the influence of rainfall on the number of turtles nesting each season.

Inspection of the egg production curves in Figure 6 reveals that 1950 was a " good " year in comparison with 1951. Yet one can hardly help noting the symmetry of the curves for both years. The differences between the curves for the two years are almost solely differences of magnitude. In studying all the published statistics of egg production on the Sarawak turtle islands, one is impressed by the cyclic regularity of the nesting season despite variations in the magnitude of the annual yields. The per cent contribution of each calendar month to the annual total tends to be the same whether the year is a " good " one or a " bad " one in terms of numbers of eggs produced.

Figure 7 shows the seasonal distribution of egg production on each of the three islands for the years from which monthly figures are available. Talang Talang Besar Island has the largest egg production and shows the most constant curves from year to year. Satang Besar, with the smallest production, shows the greatest variation from year to year.

The published figures for egg production on the Sarawak turtle islands include small numbers of eggs laid by *Lepidochelys olivacea* (estimated at less than 2 per cent of the annual total eggs). It has been impossible to eliminate the *Lepidochelys* figures from the data used in drawing the curves in Figure 7. Records of *Lepidochelys* nestings are scattered irregularly throughout the year, with a distinct small peak in March. At no other time of the year was it possible to demonstrate a significant effect on the general figures, but the seasonal influx of *Lepidochelys* in March when relatively few *Chelonia* were nesting tends to produce small secondary peaks on the curves in Figure 7. Approximately the same finite number of *Lepidochelys* nest on each of the three islands. Satang Besar, with the smallest numbers of *Chelonia*, has the

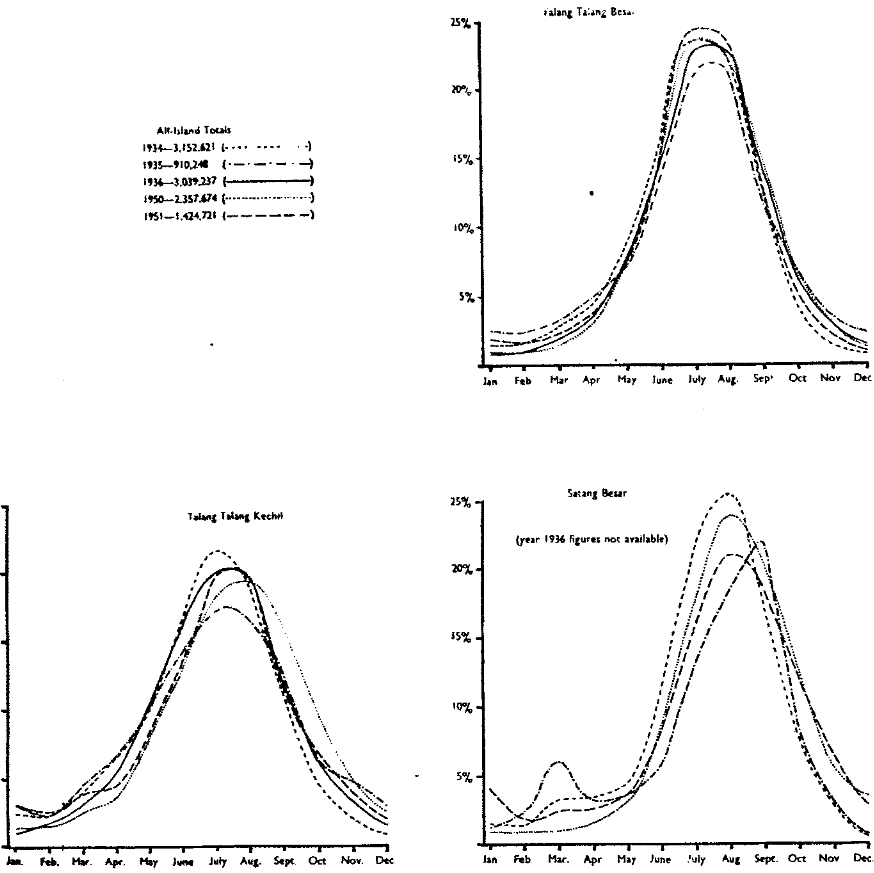

Fig. 7.—Graphs showing seasonal distribution of egg production on the three Sarawak turtle islands. Monthly egg totals are expressed as percentages of the annual totals.

most pronounced secondary peaks. On Talang Talang Besar the number of *Chelonia*, even in March, is so large relative to the numbers of *Lepidochelys* that there is little or no perceptible effect on the curves. Since the curves express monthly egg production as percentages of the annual total, the major peaks are skewed in proportion to the heights of the secondary peaks produced by *Lepidochelys* nestings.

Selection of particular beaches for nesting

Records of returning tagged turtles showed a decided individual preference for particular islands, coupled with a distinct homing ability which enabled individuals to return again and again for nesting purposes to the same island. Of the 5,748 records made on female turtles returning to the beach to lay after an average absence of about 10 days at sea, only 215 (3·7 per cent) showed a change of islands from the previous records for those individuals. Since the two Talang Talang Islands are less than 500 metres apart, and the great majority of records concerned these turtles, this low rate of change of islands would appear to demonstrate a remarkable selectivity on the part of the individual female *Chelonia mydas*. So far as known, the channel between the two islands is nowhere more than about eight fathoms deep. It presents no known remarkable features which could possibly provide a good boundary for isolation of the populations of the two islands. Many of the matings observed were in mid-channel, and it is inconceivable to the writer that turtles restrict their wanderings during the interval between nestings sufficiently so as not to cross the channel. It is concluded that the average female Green Turtle has a strong sense of location and the ability to remember and differentiate between different beaches, returning by choice to the beach selected for the first nesting of her breeding period. An error of the magnitude of 3·7 per cent seems plausible in selection between two islands so close together as are the two Talang Talang Islands. There is some reason to believe, however, that the normal error is much less than this and that many of the turtles recorded as changing islands during this study did so in an attempt to escape the disturbance of being tagged or examined for tags. The following is a breakdown schedule of the records of change of islands which were made during this study :

96 individuals changed once, from Talang Talang Besar to Talang Talang Kechil.

29 individuals changed once, from Talang Talang Kechil to Talang Talang Besar.

21 Talang Talang Besar-tagged individuals changed to Talang Talang Kechil, then back to Talang Talang Besar.

9 Talang Talang Kechil-tagged individuals changed to Talang Talang Besar, then back to Talang Talang Kechil.

8 individuals changed between Talang Talang Islands more than twice (five changed three times ; two, four times ; one, five times).

A single individual each from Talang Talang Besar and Talang Talang Kechil appeared on Satang Besar.

The larger number of Talang Talang Besar-tagged turtles in the above schedule is consistent with the larger size of the population using the beach at Talang Talang Besar. Satang Besar is approximately 45 kilometres distant from the Talang Talang Islands and presumably is well beyond the normal cruising radius of the female turtles during the interval between nestings. The two individuals which appeared on Satang Besar are therefore considered as probable strays.

The high degree of restriction of individual females to particular beaches has considerable bearing on the evaluation of other portions of the work reported here, since it gives some assurance that the Sarawak data presents a true picture of the turtles' breeding behaviour.

Interval between nests

It has long been recognized that females of *Chelonia mydas* and other marine turtles nest more than once per breeding period. The nestings are normally separated by intervals of some days spent at sea, presumably in the general vicinity of the chosen nesting beach. The length of the interval between nestings has been stated in most reports to be in the vicinity of 2 weeks.

The 5,748 records of returning, tagged females on the Sarawak turtle islands show intervals of from zero to 118 days between nestings. Eliminating all records for which no eggs were reported and all records showing intervals of more than 35 days, Figure 8 shows the distribution of intervals which preceded each of 5,566 returns.

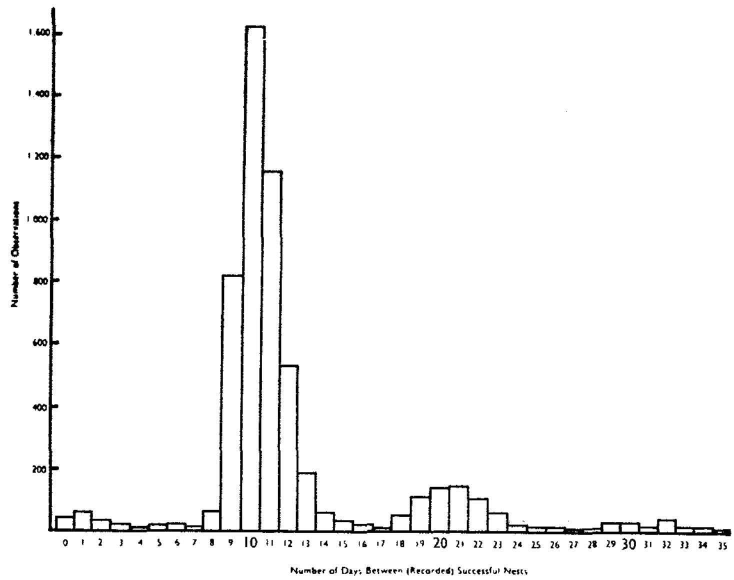

Fig. 8.—Histogram showing number of days interval between nestings by marked female *Chelonia mydas*.

The pronounced mode at ten days is presumed to represent the most common interval between nestings. The smaller peaks around multiples of ten are taken to represent those individuals who were not seen and recorded on all their nestings. They are thought to have kept more or less to the ten-day rhythm, but to have missed tabulation on one (twenty-day group) or two (thirty-day group) occasions. If the arithmetic mean is calculated for the major peak (including those intervals from eight to seventeen days), 4,493 records show an average interval of 10·5 days. In the second peak, 672 records (eighteen to twenty-seven days) show an average interval of 20·9 days, very close to being exactly double the first mean. In the third group (intervals of twenty-eight to thirty-seven days), 191 records show a mean of 32·1 days.

The small peak around one day deserves some attention. Throughout the period of study there was a continual sprinkling of records showing two nests by the same turtle in the same night, or return for nesting after only one or two days' absence. Some of these cases may be due to confusion in the records, but most are well authenticated. This writer observed the entire process of double-nesting of an individual selected for measurement of the time spent covering its nest and returning to the water. Observation began during the act of oviposition, and the observer remained near the turtle constantly. Covering its nest in an unusually short time, it moved about 15 metres across the beach and began anew to dig and to lay eggs. Many of the nests separated by these abnormally short intervals contained smaller numbers of eggs than the majority of nests which are made at intervals of about ten days.

Number of nests per female

Moorhouse (1933) gives the only report known to this writer recording extended observation of numbers of nesting *Chelonia mydas* females. His turtles were tagged and individuals could be accurately identified, giving particular authenticity to his statement that many of the individuals he observed in Australia laid eggs as many as seven times. Work on the Sarawak turtles has done little more than extend Moorhouse's data, as could be expected when applied to a larger number of tagged individuals under the conditions operative in this area.

Moorhouse began marking turtles under circumstances which almost guaranteed that his marked individuals would be marked and observed from the very beginning of their nesting period. The marking was done at the beginning of a clear-cut season and turtles coming up prior to the marking campaign were removed for slaughter. These circumstances do not apply on the Sarawak Islands, where there is no definite beginning to the season and where turtles are never killed. Beyond doubt, a great many of the Sarawak tags were applied to turtles which had already nested a variable number of times. Therefore, the records of returning turtles in Sarawak cannot show a clear mean of the total number of nests laid per turtle. Figure 9 shows the numbers of nests per individual female as recorded from 2,702 marked Sarawak turtles.

Besides the fact that the Sarawak turtles were tagged at unknown stages in their breeding periods, the confused, crowded conditions on the beaches and the variable quality of the watching for tagged animals undoubtedly allowed some returns to go unnoticed. It may be valid to select out a portion of the Sarawak data in which the above factors appear to have had minimal influence. Although tagging operations had begun in March 1953, the intensive period of tagging began on 29th June, when the fully staffed research team began

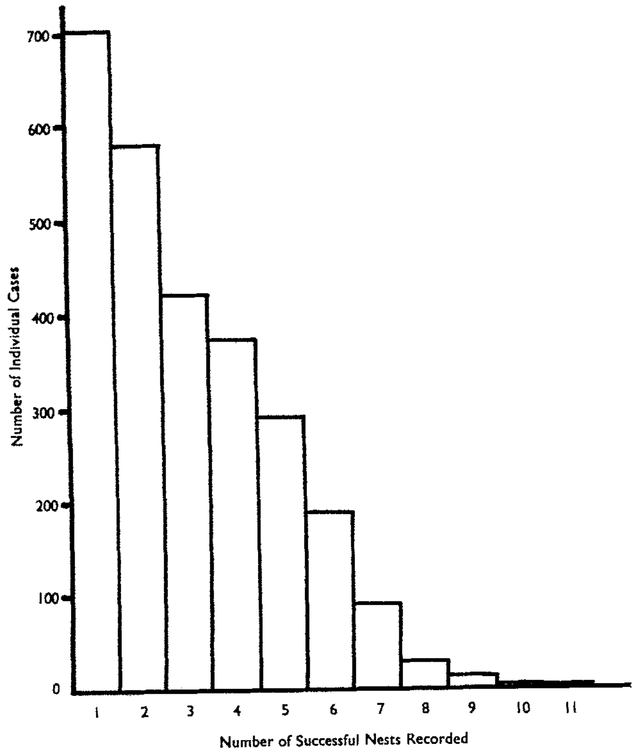

Fig. 9.—Histogram showing numbers of nests recorded for individual marked female turtles—*Gross Sarawak Records.*

work on the islands. From 29th June to 6th July, 447 tags were applied to female turtles on the beach at Talang Talang Besar. This group of females, of all the animals tagged, probably received the most careful watching over the longest period. The research group remained active on Talang Talang Besar until the end of September, approximately 90 days of well-disciplined watching activity. Figure 10 shows the records of this group of tagged females. Similarly to the other Sarawak turtles, members of this group were tagged at all stages in the breeding period, and therefore a meaningful peak cannot be expected in the graph of their records. There is, however, an obvious sudden fall-off in the numbers of turtles laying more than six or seven times. As in the case of the Barrier Reef population described by Moorhouse, Sarawak turtles do not appear, on the average, to lay eggs more than about seven times in a breeding period. The Sarawak records of eight, nine, ten and eleven nests are probably to be considered as extremes.

Further analyses failed to demonstrate any clear correlation between number of clutches laid and season of the year or size of the female turtle.

Another approach to the problem of determining the number of nestings in a season may be made through the records indicating the total span of time

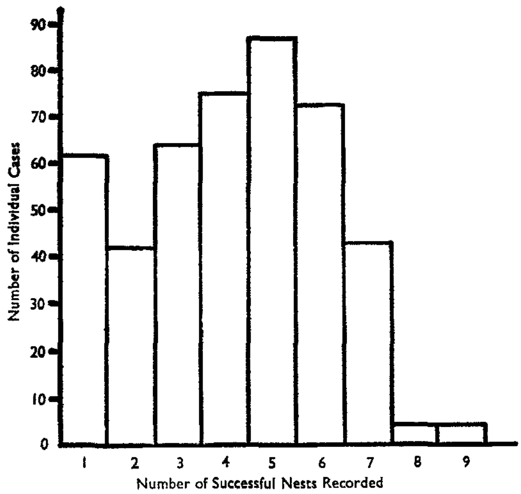

Fig. 10.—Histogram showing numbers of nests recorded for individual marked female turtles—*Optimal Sarawak Records*, comprising those turtles marked during the period 29th June to 6th July 1953.

each turtle was under observation (from the date of tagging to the last recorded observation). If the interval between nestings can be assumed from the foregoing evidence to be generally constant around ten days, the total time under observation divided by ten should indicate the approximate number of times each marked turtle nested, irrespective of whether or not it happened to be seen and recorded each time it nested. Figure 11 shows the number of days between the first and last observations on 2,025 turtles which were seen at least once again after tagging. The time-scale on the abcissa of the graph is arranged so as to divide the records into groups which correspond roughly with the number of nestings which would be expected to have occurred. This treatment of the total data, by eliminating the many instances in which nests were probably missed, may come nearer to representing the true situation than does the graph of actual, observed nest records in Figure 9. It will be noted that the first five columns of the graph in Figure 11 are nearer equal height than the comparable columns in Figure 9. It would appear that, by applying the tags to each and every untagged turtle encountered, as chance and labour time dictated, the workers on this project tagged roughly as many turtles which were on the beach for the first time that season as they tagged turtles which were on the beach for the second, third, fourth and fifth time. The marked fall-off in numbers of cases after six assumed nestings is taken to indicate that nearly all the turtles nested six times, many turtles nested seven times, and a significant number nested eight times. Small numbers produced more nests, up to at least eleven nests, as indicated by actual observation. In view of the fact that Figure 11 is an extrapolation which should be expected to indicate trends but not precise numbers, the column representing periods sufficient for twelve or more nests (up to 149 days) is here not given any weight.

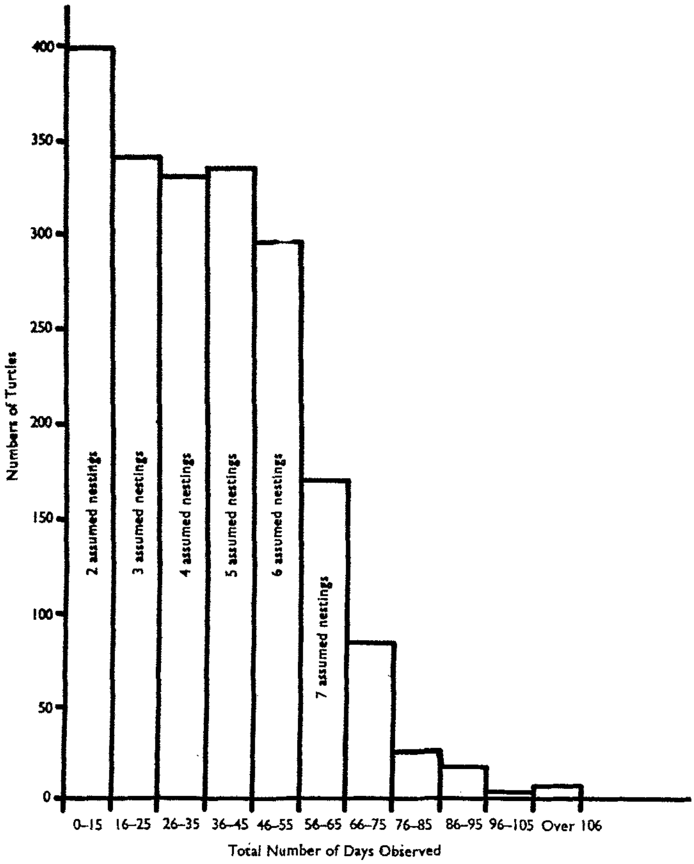

Fig. 11.—Histogram showing total periods of observation on marked female turtles in Sarawak. The length of time between first and last observations is assumed to indicate the number of nestings which occurred during the observation period.

Clutch size

The numbers of eggs per clutch observed during the course of this study varied from a minimum of three eggs to a maximum of 184 eggs. Records of 8,147 clutches laid during a fourteen month period in 1953 and 1954 showed a mean clutch size of 104·7 eggs (Standard Deviation of 1·31). While statistical analysis of the above eight thousand records does not reveal any significant differences in clutch size between different islands or between different parts of the yearly cycle, it is felt that the data was not spread evenly enough over the year to warrant firm conclusions as to the absence of differences.

Frequency of breeding periods

So far as this writer is aware, published accounts of *Chelonia mydas* to date have not provided accurate information on how often individual females become reproductively active or whether they show any tendency to return to the same beach during each breeding period.

The Sarawak turtles tagged during 1953 were not seen again until 1956. Harrisson (1956 b) reports that the first return was on 4th July 1956—a turtle which had been tagged on 30th July 1953. By the end of July 1956, Harrisson reports records of fourteen returning turtles which had been tagged during July and August of 1953, and he states (Harrisson, 1956 b) that . . . "This trend has continued increasingly to date". One turtle with five recorded returns in 1953 was recorded six times in 1956.

While information is not yet complete, the results to date indicate that:

(a) The Sarawak *Chelonia mydas* probably follow a triennial cycle of breeding. Further records from the Sarawak islands should indicate whether three years is the usual cycle or whether this is the minimal length of cycle. It remains to be proved whether or not the Sarawak animals are a circulating population, breeding every year and returning to Sarawak only every third year, but this possibility seems to be remote.

(b) At least a proportion of the Sarawak animals appears to demonstrate a homing instinct which brings them back to the same place to breed after two years' absence. A breeding migration is assumed to occur. Hornell (1927) speculates on a comparable migration from Madagascan and African waters to the Seychelles Islands; Carr (1952) suggests that mass seasonal movements occur in the Caribbean area, but states that there is almost complete ignorance regarding them. It remains to be proved that all the Sarawak turtles do not remain in the vicinity of the islands all the time, in which case there would not be occasion for migration. However, the rarity with which Green Turtles are sighted or taken in fishing operations in Sarawak coastal waters indicates against the likelihood of there being any such large population of permanent residents.

It is not yet known whether the individual female turtle consistently returns to the same island previously used for nesting, or whether she returns to the general area and selects any one of the available nesting beaches. This problem of the relative specificity of the homing instinct over the long term may be solved as more data on returning Sarawak turtles are accumulated.

EARLY DEVELOPMENT OF THE YOUNG

The completed natural nest

The completed natural nest consists of a more or less spherical mass of eggs—a clutch of 100 eggs forms a mass roughly 25 cm. in diameter—covered by 45 cm. to 90 cm. of sand. The chamber in which the eggs lie has been excavated from the permanently moist, residual sand well below the beach surface and its walls are therefore relatively firm. The fresh eggs falling into the chamber are fairly turgid and do not compress together to any great extent. There are, therefore, many air-filled interstices throughout the egg mass. Upon completion of laying, the female turtle pushes loose masses of moist sand into the egg hole on top of the eggs. This falling moist sand does not appear to infiltrate extensively into the interstices of the egg mass, and soon piles up to the top of the egg hole. When the female forcefully kneads more moist sand into place over the filled egg hole, she builds a slightly dome-shaped mass of packed moist sand without, apparently, transmitting extensive pressures to the lower levels of looser sand in contact with the eggs. The packed sand at the entrance of the egg hole appears to resist the pressure of the loose sand thrown over it during the later stages of disguising the nest. The eggs, except the few uppermost ones, must not be thought of as literally embedded in sand, but as resting in a firm-walled subterranean chamber with most of their surfaces in contact with air. The considerable volume of air filling the interstices of the mass is presumably at a continual high relative humidity, making water loss from the eggs by evaporation a negligible factor. The walls of the chamber are kept continually moist by capillary water from rains or from the deeper layers of sand ; there is no evidence to date that even heavy showers are manifest at this depth in the sand except as capillary flow along grain surfaces and, conversely, samples at various levels during the most extreme droughts experienced during 1952 and 1953 showed continual presence of capillary water at the levels of the beach sand occupied by the turtle egg chambers.

Fewer than one hundred of some 10,000 *Chelonia mydas* nests observed in the course of this study were noted below the spring high tide levels. In no case were nests found at levels where it was clear that they would be constantly in contact with salt water. The high rate of precipitation on the breeding beaches produces a continual percolation of fresh water downward and outward, preventing saturation of most of the beach by sea water. The high precipitation produces extensive run-off onto portions of some of the beaches from the adjacent parts of the islands, and Talang Talang Kechil in particular has a portion of the beach where egg chambers would probably be flooded by fresh water much of the time (see Fig. 4, B).

Incubation was not followed in natural nests because of the difficulties inherent in this process on beaches as intensively used for nesting as those here studied. Moorhouse (1933) and Harrisson (1953) point out that previous nests are indiscriminately dug up by turtles excavating their own nesting sites. If each nesting female turtle excavates an area of, say, 5 or 6 square metres of sand each time she nests, in theory the turtles using the beach at Talang Talang Besar Island during July and August of 1953 dug over every square centimetre of suitable nesting sand at least three times. Such concentrated stirring up of the beach results in rapid change of the minor configurations of the beach surface ; in the 45 to 60 days required for hatching, a large proportion of incubating natural nests would become vulnerable to excavation during later nest-digging activities, and many nests would be lost in this way. On the Sarawak turtle islands, where a trained staff attempts to mark and excavate 100 per cent of the nests, some are missed during the heavy laying season when there is such a confusion of females active on the beach. Approximately 120 of these so-called " wild " nests (in contradistinction to the transplanted ones in the hatchery enclosures) were noted during the investigations on the island of Talang Talang Besar. More than two-thirds of the wild nests were detected as a result of other turtles' digging through the nests, scattering partially developed eggs over the surrounding area as they excavated their own body pits prior to nesting. All such nests were presumed to have been destroyed. Less than one-third of the wild nests noted were discovered by virtue of hatchling turtles seen emerging from them and only this fraction of the nests could be considered as productive.

Hatchery methods

Since about 1947 (Harrisson, 1951), attempts have been made to hatch some of the clutches of eggs laid on the three turtle islands. Workmen on each island transplant eggs into special hatchery enclosures built on the highest portions of the beaches. The enclosures are made of strong stakes driven deep into the sand, supporting horizontal bars of bamboo, split palm logs, or coconut palm leaf midribs. These fences project from about 20 cm. to 45 cm. above the beach surface and satisfactorily keep out wandering adult female turtles in search of nesting sites. No marked differences in operating the hatcheries were noted between the different islands. The hatchery at Talang Talang Besar is the largest and the description which follows refers to the operation of this hatchery as observed during 1952–53.

Commonly the last one or two nests to be excavated in a morning were chosen for transplantation to the hatchery. Sometimes one or two of the nests nearest the hatchery fence were set aside for this purpose at an earlier stage in the morning's digging. The nests were excavated in the same manner as those harvested for eggs for market and did not receive particularly gentle treatment. After digging, the eggs of a clutch were ordinarily left exposed on the surface while the worker detailed to transplant them went to the hatchery and dug a hole for their reception. This hole varied with individual workmen and pressure of other work, but ordinarily was a vertical shaft 45 cm. to 60 cm. deep and about 20 cm. to 25 cm. in diameter at the bottom. Returning to the excavated eggs, the worker tossed them into a shallow basket, carried them to the hatchery, and poured them into the prepared hole. Sand was then pushed in on top of the clutch of eggs until the hole was filled to the general level of the beach. The worker sometimes compacted the sand over the filled hole by treading lightly over the area. By the time the eggs had been transplanted to the hatchery, the number of eggs excavated had usually been recorded in the daily record book by another man, along with the flag number and a note that those eggs had been put to hatch. The marking wand from the original nest was then used to mark the position of the eggs in the hatchery enclosure. At the men's convenience, usually within a day or two, the marking wand was replaced by a stake bearing a small metal plate on which were painted an identifying hatchery number for the nest, the date of laying and the number of eggs in the clutch. Apart from rather rare breakages during digging or handling, the clutches observed during transplantation were moved to the hatchery in their entirety. Usually at about the same time the permanent hatchery stake was placed, a circle of wire mesh fencing material about 60 cm. in diameter and 45 cm. high was placed around the area over the nest. This was embedded a short distance in the sand and, when the young turtles hatched some weeks later, served to confine them until morning, when they were collected and placed in a " nursery " tank. They were kept in the tank for about one week before being released. Plate 8 a shows an early morning view of the hatchery on Talang Talang Besar Island ; four of the wire mesh enclosures contain hatchling turtles which emerged during the preceding night.

Records of 354 clutches of eggs transplanted to the hatchery enclosures on the Sarawak islands show at least some young turtles emerging from all but 8 per cent of the nests. Most of those nests which failed to produce any young were transplanted during the period of the Northeast Monsoon. An over-all average of 47·1 per cent of the eggs transplanted produced young which emerged to the beach surface. The percentage productivity of hatchery nests varied somewhat during different seasons of the year, being usually higher during the peak breeding season and lower during the monsoon period. It is believed that increased experience and care on the part of the industry's workers may considerably raise the productivity of the hatchery nests.

For a study of embryological development, nests were especially transpplanted to the hatchery by the writer and research assistants. During one night period, fourteen turtles were watched carefully and the time at which the last egg was dropped was recorded to the nearest half hour. The time at which oviposition ended was arbitrarily considered as the zero hour for each clutch in timing developmental stages collected from that particular clutch. The clutches were selected to cover the maximum range of oviposition hours in order to facilitate later daytime collection of eggs of any desired post-ovipositional age. Zero hour for the first clutch was 2100 hours on 16th July 1953 ; for the last clutch was 0600 hours on 17th July 1953.

Transportation was carried out with great care under specified conditions in order to enable later comparisons with the percentage of young hatched from the routine hatchery nests.

All fourteen embryology study nests were transplanted between 0530 hours and 0830 hours, ensuring against any extreme temperature change during transfer of the eggs and allowing for completion of all handling within 9 hours or less from the time of oviposition. Holes to receive the eggs were dug prior to their excavation from the original nest. These holes were about 60 cm. deep by about 25 cm. in diameter at the bottom. The eggs were then dug with special care to avoid jarring. When uncovered, the eggs were picked up carefully and, without rotation in any direction, placed in a shallow basket which contained about 2·5 cm. of loose, damp sand. When placed gently down in the sand, the eggs were prevented from rolling about. As soon as all eggs had been transferred to the basket, they were carried carefully to the hatchery and lowered one or two at a time into the prepared hole, great care being taken to ensure against any marked rotation of the eggs. When all eggs, each with original upper surface still on top, were satisfactorily deposited in the hatchery hole, about 15 cm. of loose, moist sand was scattered over them. It was then pressed down firmly by hand, with an attempt to equal, but not to exceed the force exerted by a turtle's flippers in compacting the sand over the egg hole. More sand was then pushed in to fill the prepared pit.

Eight of the nests were left to hatch and emerge, completely undisturbed. Hatchling turtles emerged from all eight nests. The average time between oviposition and first emergence of hatchlings was 51·4 days (minimum 51 days, maximum 53 days). Twenty-three routine hatchery nests planted the same month averaged 54·3 days (min. 49, max. 58 days). The per cent of hatchlings emerging from the experimental nests varied from 3 per cent to 90 per cent, averaging 46·7 per cent. In the regular hatchery nests planted the same month the comparable records show from 2 per cent to 93 per cent emergence, averaging 40 per cent.

From these observations, it appears that the present techniques in transplantation of eggs to the hatchery are not causing excessive reduction in productivity of the clutches because of rough handling. Concussion and rotation of developing eggs were almost uniformly damaging at later stages when the embryonic disc and overlaying albumen had become adherent to the shell, but eggs moved on the morning after laying seem to suffer little from relatively rough handling.

Temperature relationships

Short-term constancy of sand temperatures

As pointed out in the description of "The Completed Natural Nest", the egg chambers are buried deep beneath the surface of the beach. At these levels, temperatures remain almost constant over the diurnal period, virtually independent of the extensive fluctuations which occur in the temperature of the insolated surface sand. Figure 12 shows in diagrammatic form the thermal maxima and minima recorded at various levels during a sample two-week period in August 1952. The air temperatures were taken in the shade, 1·2 metres above the sand surface. The surface temperatures were recorded from a thermometer lying on the sand with the mercury bulb approximately half covered by sand. The temperatures at 7·5 cm. and 15 cm. depths were obtained from thermometers thrust vertically into the sand for these depths and left *in situ* for the two-week period. The temperatures of depths greater than 15 cm. were obtained by burying bamboo tubes vertically to the desired depths ; thermometers were then lowered on strings until their mercury bulbs touched the sand at the open lower end of the bamboo tubes. The upper ends of the tubes were closed by corks. To read each of these deeper thermometers, the cork was removed from its tube, the thermometer was quickly pulled up by its string, and reading was accomplished as rapidly as possible. Readings of sand temperatures were made four times a day on as strict a schedule as was possible without interfering unduly with other work : in the morning before the sun began to heat the beach noticeably, usually about 0730 hours; between noon and 1400 hours ; in the late afternoon when the sun was well down, 1700 hours to 1900 hours ; and between midnight and 0200 hours. Undoubtedly periods of actual maximal and minimal temperatures, especially of the surface sand, were missed on some occasions. However, the critical levels below 45 cm. did not show temperature variations greater than the tested variation between the ordinary laboratory thermometers used (about

$\pm 2°$ C.). Air temperatures were read once a day from a permanently placed maximum-minimum thermometer.

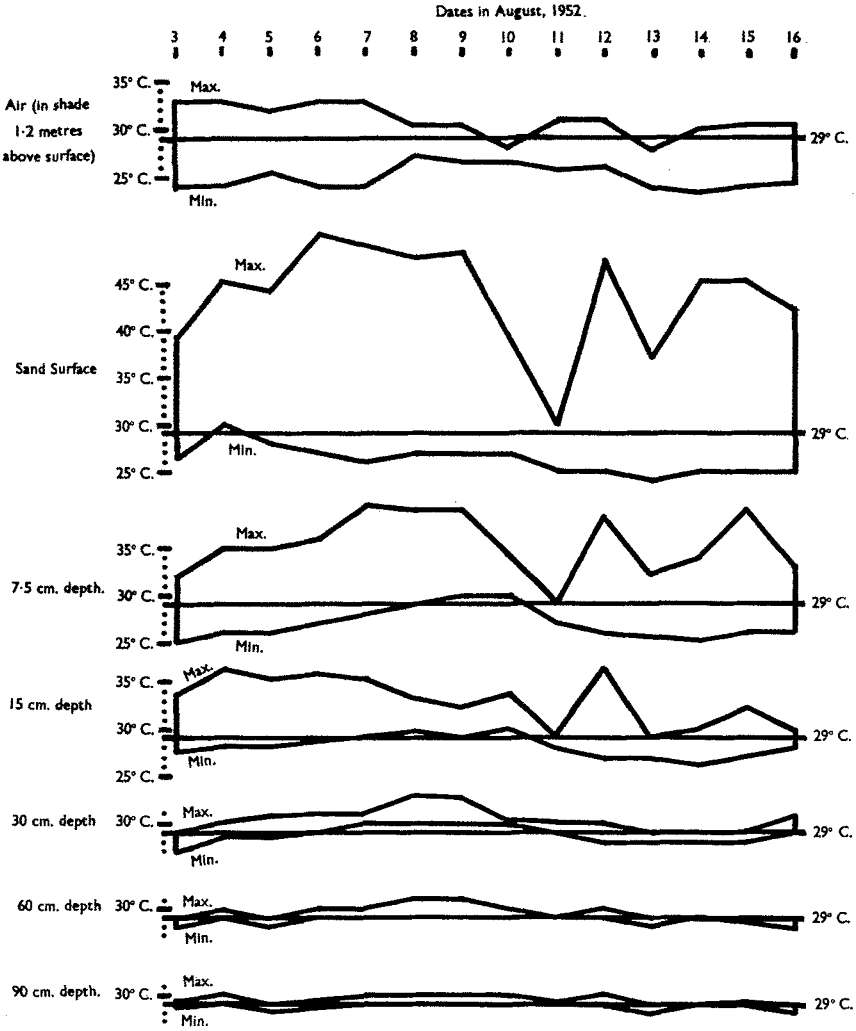

Fig. 12.—Graphs showing temperature ranges in the air and at various levels in the beach sand over a two-week period on Talang Talang Besar Island, Sarawak.

It will be noted that air temperatures, comparable to the ordinary weather bureau records of this type, have little relation to surface sand temperatures which vary sensitively with the direct radiation received from the sun. The reader is asked to note the air and sand surface maxima on 10th August, a day which had an almost continual sea breeze, and which was overcast except for a short break around noon when the sun shone brightly for about 45 minutes.

This may be compared with 11th August, which was continually overcast with some rain.

The graphs of ranges of sand temperatures demonstrate the gradual modification of surface temperature fluctuations which occurs with increasing depth. Because of widely fluctuating surface temperatures and time lag in transmission of thermal changes between layers, temporary inversions of temperature gradients do sometimes occur. These are most commonly found at depths between 15 cm. and about 40 cm. In no case have any marked changes of temperature been noted in the levels utilised for *Chelonia mydas* egg chambers, except as produced by metabolic heat from the developing eggs.

Twenty-two natural nests were tested for temperature following the removal of the eggs by the industry workers in the early morning. Immediately after the worker had removed the eggs, a Schultheis rapid reading mercury thermometer was thrust about 2·5 cm. into the sand forming the wall of the egg chamber. It was assumed that the sand of the chamber wall was at almost the same temperature as the egg mass and that, in the short time the nest had been open, no significant changes in temperature had occurred. The 22 nests measured showed a mean temperature of 29·3° C. (minimum of 28·0° C., maximum of 30·4° C.).

Five nests were measured by placing the bulb of the thermometer into the approximate centres of the egg masses while still *in situ*. These readings averaged 28·8° C. (minimum of 28·7° C., maximum of 29·2° C.).

Temperature rise due to metabolic heat

The metabolic heat produced by the developing eggs in their insulated chamber tends to raise the temperature of the egg mass significantly above

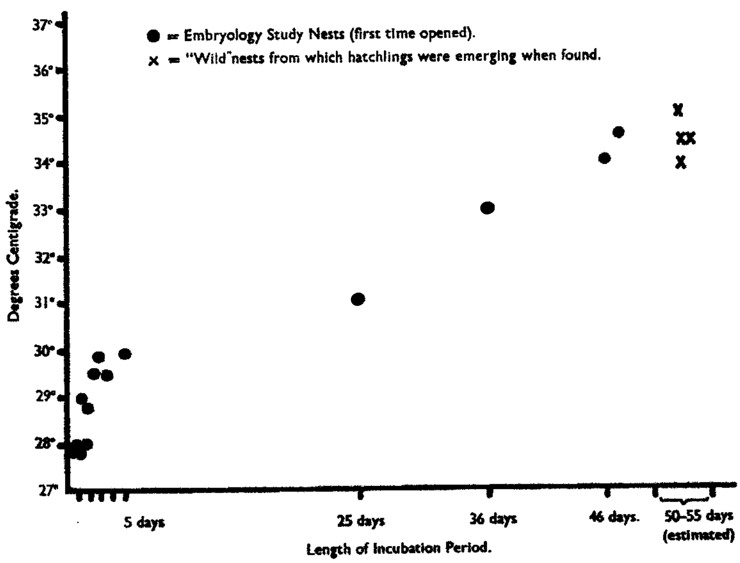

Fig. 13.—Temperatures of incubating *Chelonia mydas* nests.

the prevailing temperature of the surrounding sand. Figure 13 shows temperature readings made when nests were opened at various stages in the incubation period.

The temperatures recorded from hatchery nests, set aside for periodic collection of samples for embryological studies, represent in all cases only the temperatures at the first opening of the nest. In some cases the act of opening a nest appeared to unbalance the temperature gradients existing near the egg mass, and temperatures recorded after the original sampling were deemed insufficiently reliable for inclusion in this paper.

It seems likely that the temperature differential maintained between the developing eggs and the surrounding constant temperature sand is an important factor in the developmental process. Some embryological study nests which were repeatedly opened at 12- to 24-hour intervals showed erratic temperature curves which never rose to the higher levels seen in Figure 13. A significant increase of abnormal, retarded and dead embryos occurred in the samples from most of these nests.

It would appear from the foregoing that in natural, undisturbed nests the size of the egg mass as determined by the number of eggs contained might be an important factor in influencing the per cent hatch. Considering the clutch as a single heat-producing body, abnormally small clutches of eggs could be expected to lose their metabolic heat to the surrounding sand at a rate proportionate to their higher surface mass ratio, with resultant lower temperatures than those maintained by larger clutches. Moorhouse (1933) reports the failure of artificial small nests and postulates mechanical injury during transplantation as the principal cause of failure. It would seem that the failure of his small nests was as likely to have been due to low temperature in the egg mass as to mechanical injury.

Seasonal variation in incubation time

The term " incubation time " as used in this paper refers to the span of time elapsing between oviposition and emergence of young turtles to the beach surface. Actual hatching from the egg occurs some days before the baby turtles appear at the surface (see " Emergence From the Nest ").

Figure 14 shows the incubation times recorded for 328 hatchery nests on the Sarawak Islands. The individual records are plotted on the graph according to the dates of the first emergence of young turtles from each nest. The solid line connects the mean incubation times calculated for fortnightly groups of records.

The seasonal variation in mean incubation time is assumed to be a simple function of temperatures experienced by the developing eggs. While the deeply buried nests are effectively insulated from diurnal fluctuations in temperature (see Fig. 12) they are nevertheless in equilibrium with the long-term means of temperature at the surface and they might be expected to show annual cyclic variation in response to general changes at the surface.

As illustrated in Figure 13, metabolic heat produced in the developing eggs causes an early rise in the temperature of the nest, so that throughout almost all of the incubation period the nest is at a higher temperature than the

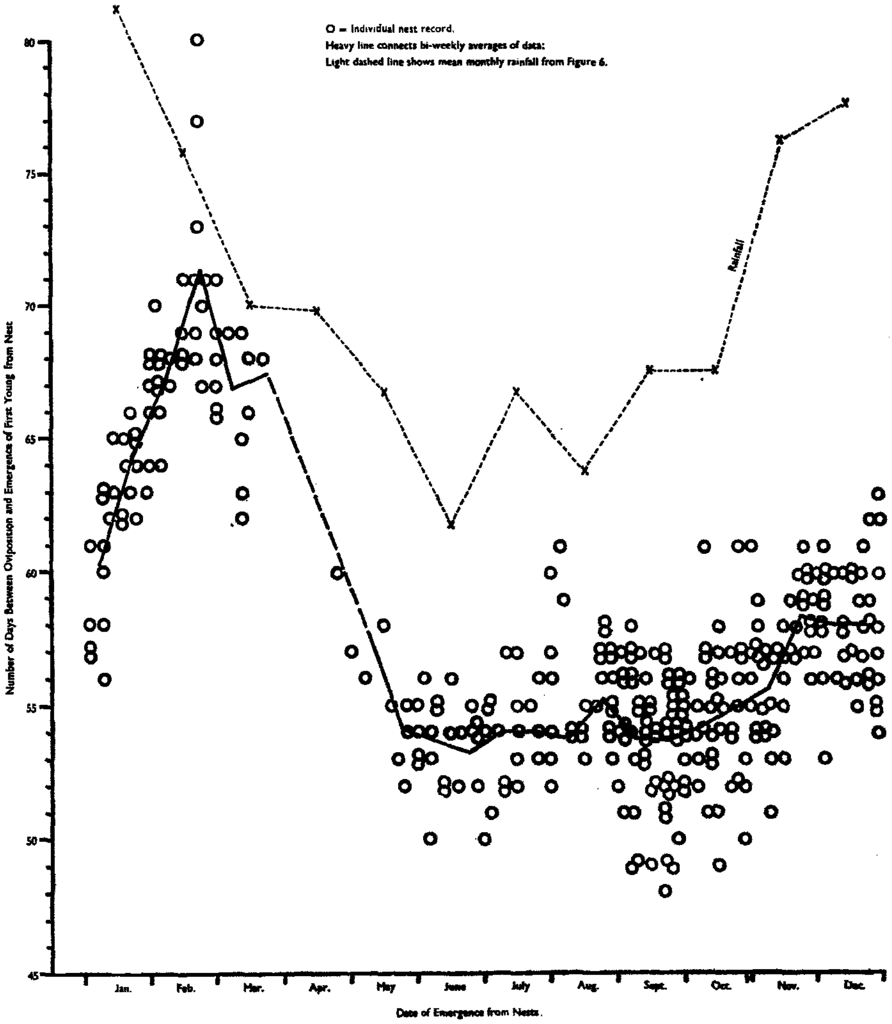

Fig. 14.—Graph showing variation in length of incubation period of *Chelonia mydas* nests at different times of the year.

surrounding sand. The incubating nest, therefore, is continually losing heat in all directions at a rate proportional to the steepness of the temperature gradients existing between eggs and sand and to the thermal conductivity of the sand. Due to the general characteristics of the heat economy of the Sarawak beaches (continual daytime input from the surface), there is presumably the least heat loss in an upward direction from the nest.

During the monsoon period, the heat input to the beach surface is considerably reduced. Even though ordinary meteorological data may not show a marked drop in mean air temperature during the monsoon (see Fig. 5), there is almost certainly a marked drop in beach temperature coincident with the cloudy weather and resultant decreased irradiation of the surface sand by the sun (see Fig. 12 and accompanying discussion). With reduced heat input at the surface, the deeper layers of sand must become cooler. Incubating nests in January must experience a more rapid upward heat loss than do July nests.

Besides the increased heat loss from incubating nests due to steepened temperature gradients during the monsoon, the increased precipitation during that period might be expected to have a further effect. In the very porous sand of the beaches concerned here, percolation downward of rain water is very rapid, and it seems doubtful that saturation of the sand could be so complete as to flood the egg chamber or to affect materially the rates of gas exchange between egg chamber and surrounding sand. However, it seems likely that there is variation in the thickness of the capillary film of water around the sand grains ; with a continued increased rate of precipitation this film might be maintained at a sufficient thickness to affect materially the thermal conductivity of the sand, producing a significant increase in the rate of heat loss from the developing egg mass.

As previously explained, the annual curve of mean monthly rainfall appears to be the simplest available referent to the state of the monsoon. The rainfall curve extracted from Figure 6 and plotted on a slightly modified scale is shown in Figure 14 as a dashed line. It will be noted that the curve of mean fortnightly incubation times corresponds roughly with the " monsoon " curve, being offset from it by units on the time-scale which roughly correspond with one-half the length of the incubation periods. It will be recalled that the data for incubation times is plotted according to the *termination* of incubation, while the weather data is plotted according to *mid-point* of each monthly period.

Emergence from the nest

Although Moorhouse (1933, p. 11) mentions opening an overdue nest and finding enmassed young in an underground cavity, he and other workers do not appear to lay stress on the difference between time of hatching from the egg and time of emergence from the deeply buried nest to the surface of the beach.

Excavation of hatchery nests at late stages indicates that a period of four to five days between hatching and emergence at the surface is minimal, and that this period of subterranean confinement may be extended for a much longer, though undetermined, time without serious mortality among the brood of hatching turtles. Heavy rains, packing the upper layers of beach sand, are believed to be the main factor prolonging the period of underground confinement (see also Moorhouse, 1933, p. 11).

In visualising the conditions in a hatching nest and the sequence of events which occurs during hatching, it is important to bear in mind the concept of the egg chamber as a stable subterranean cavity with well-defined walls, containing a considerable quantity of air in the interspaces of the egg mass. The young turtle emerging from the egg does not meet resistance from sand pressing in on all sides, but emerges into an irregular space equal to the former volume of the unhatched egg, plus the interstitial spaces adjacent to that egg. In the process of hatching, other eggs lying above the hatching egg and supported by it may move downward as the shape and resistance of the supporting egg changes during the struggles of the hatchling turtle. The overhead eggs eventually come to lie on the collapsed empty shell of the hatched egg while the baby turtle rests in a new location nearer the top of the egg mass. With every hatching, there is an increase in the available free space for movement within the egg chamber as the shape of each unit changes from spherical egg to hatchling turtle.

The change in shape of the units of the mass, altering the supports of unhatched eggs on each other, plus the movements of the baby turtles, results in a sorting out of the contents of the nest chamber. Hatchling turtles congregate at the top, while unhatched eggs move downward. A definite negative geotropism in the baby turtles, coupled with their sporadic movements, causes the domed sand roof of the nest chamber to be continually eroded away. The loosened sand falling from the roof is packed beneath the active hatchlings, and a cavity containing the hatchlings slowly progresses upward through the sand as the material of its roof is dug away and is compacted into the floor of the cell.

The following extract from field notes is representative of the observations made on the early stages of the process of emergence of hatchlings from the nest:

> 28th August, 1952: I dug into the oldest unhatched nest in the hatchery (56 days since oviposition) . . . a group of already hatched baby turtles was uncovered. These were about 44 cm. below the surface, in a cluster. They were quite immobile at first, but upon being freed from the sand, they became as active as others newly arrived at the surface. The cavity in which they were found was lens-shaped with arched roof and fairly flat floor, about 15 cm. in diameter and about 9 cm. high at the centre. There were 23 baby turtles in this space. Below it, and separated from it by from 1 to 5 cm. of sand were 39 unhatched eggs. By no means all the shells of the hatched eggs were at the top of the egg mass, and no hatched baby turtles were found down in the egg mass. Six of the 39 eggs in the lower mass contained baby turtles; the rest were rotten.

The young turtles in the escape chamber are heaped on each other several layers deep. The uppermost ones continually loosen sand from overhead and this sand filters down through the sporadically active mass of hatchlings until it is eventually packed under-foot by the lowermost individuals of the mass. When the cavity eventually reaches the uppermost layers of dry, loose sand (upper 2·5 cm. to 20 cm., depending on recent rain), the roof caves in and the young turtles struggle up out of the crater so formed at the surface.

There is reason to believe that a protective instinctual mechanism prevents the young turtles from emerging to the surface during the heat of the day, when the very high temperatures of the surface sand would kill them in a few minutes. It is believed that, upon encountering temperatures much above about 33° C., the hatchlings cease activity in their escape chamber, resuming active movements only when lower temperatures return with the fall of night. Most of the field records of young turtles escaping to the surface, both in the hatchery and in the so-called "wild" nests, are for hours past midnight.

None are recorded earlier than 2000 hours or later than 0700 hours. A mechanism such as this would appear to have considerable survival value for the young, not only guarding against the necessity of a long trip across a strongly irradiated beach at lethal temperatures, but also allowing protection of darkness to the majority of young during their migration to the water (see " Predation "). Moorhouse, 1933 (p. 15), states that some young turtles buried themselves again after emerging to the surface in daylight hours.

Not all the hatchlings of a nest travel to the surface in the same escape chamber. About one half of the hundreds of hatching nests observed produced young at the surface on different nights. Most commonly, a large batch one night was followed by a smaller batch the following night. Some nests were recorded as producing small batches of young on as many as five different nights, over a maximum span of eight days. It seems likely that the nest earlier described in the extract from the field notes might have been recorded as producing a second batch of six young a day or two after the original emergence of twenty-three young.

In several excavations of nests two weeks after natural emergence of large batches of young, remains of young turtles were found deep down in the sand. Some of these fatalities may have been non-viable for other reasons, but it is believed that it is not uncommon for some late-hatching young to die underground simply because there are insufficient numbers present to produce a chamber of sufficient size to allow escape to the surface under the sand conditions operating at that time, such as density and resistance to digging due to moisture content.

Movement of hatchlings to the sea

Upon emergence to the surface of the beach, the group action of the hatchling turtles ceases and they spread in all directions, each now reacting only to his own stimulus-reflex pattern. The negative geotropism which operated in the escape chamber completely disappears. So far as could be determined in the course of this work, there is no demonstrable geotaxis on the part of young wandering on the beach. It might be assumed that they would always head down any incline and thereby increase their chances of finding their way down the slope of the beach to the sea. However, the beach they must cross is usually so deeply pitted and piled up by the activities of adult females that it constitutes a series of veritable mountain ranges to the hatchlings. In finding their way to the water they must ascend almost as many slopes as they descend. A variety of tests failed to provide evidence of any particular reaction to the direction of gravity.

The young turtles move actively and almost continuously with a floundering gait in which the pairs of limbs are not used synchronously as in the heavy adult turtles, but alternately in clumsy crawling fashion.

The writer believes that the main environmental stimulus utilised in the instinctual pattern which carries the young turtle from the high beach to the sea is light (see Parker, 1922 a & b ; Moorhouse, 1933 ; Hornell, 1927 ; Daniel and Smith, 1947). The hatchlings observed on the beach invariably moved in the direction of the most intense light. By playing a torch light on the sand near them, they could be guided at will, up and down slopes, toward or away from the water. If the beam of a torch was played downward on the baby turtles, placing them in the centre of a circle of bright light of equal intensity, they wandered in a confused manner.

On all the Sarawak and Malayan beaches observed during the course of this study, there is a marked difference in intensity of illumination between the land side with its high, dark border of vegetation and the exposed seaward side of the beach. The young turtles' horizon therefore almost always shows a differential in illumination between the darker landward side and the lighter seaward side, and there is a constant tendency for ambulatory movement to carry the young turtles nearer the sea. Upon reaching the edge of the high beach platform (see Fig. 2), the white zone produced by breaking waves is ordinarily visible on a line of sight to the hatchlings and may provide additional directional photic stimulus which leads them to the sea.

Upon reaching the water, the baby turtles demonstrate a strong orientative reaction to environmental motion, aligning themselves against any water movement, whether this be continuous current or intermittent wave wash, and swimming strongly against the direction of water movement. They are commonly battered about for some time by incoming waves, being unable to resist the surf. In the areas of Malaysia studied during this survey, the surf is mild by general standards, but it is nonetheless violent for so small and light an animal as a 5 cm. hatchling turtle with a relatively low specific gravity. Eventually, after being repeatedly washed back up on the beach, each hatchling makes its way past the breaking waves and swims vigorously out to sea.

On the Sarawak islands where the majority of young turtles were observed, fairly strong currents run off the beaches, and the turtles, although oriented against the water flow and swimming actively, are carried away by the currents. Of thousands of hatchlings released near the beach or observed to enter the water by themselves, none was seen again.

From the time of entering the water, the baby turtles showed a strong avoidance reaction toward any solid mass which obscured a sizeable portion of their visual field. This did not appear to be a further manifestation of the photic response already described. Hatchlings showed a distinct negative reaction to any large, solid objects in the water near to them. On a bright moonlit night, they veered off into the blackness of the surrounding water away from the relatively light-coloured mass of the writer's body. In other observations they showed comparable avoidance of submerged black rocks at the ends of the beach. Even if carried shoreward by currents, this reaction would cause maximum possible avoidance of land in any form and would contribute toward movement into the open sea.

The newly emerged young are usually buoyant and appear to be unable to dive effectively. Continually repeated attempts result in submergence of momentary duration a few centimetres beneath the surface, the hatchling bobbing back to the surface after each attempt. The buoyancy of the newly emerged young is presumed to be due to the quantity of contained yolk of low specific gravity. Babies kept captive for a week before release show increased ability to submerge for short distances and to remain submerged for more than a few seconds at a time.

Daytime attempts to follow newly-emerged or week-old baby turtles by swimming after them or by following them in a boat gave little further information of value. When followed closely enough to ensure against losing track of them, the actions of the turtles appeared to consist mainly of avoidance reactions to the large mass of the swimmer's body or of the boat. Close approach of a large mass such as a boat stimulated diving as well as directional swimming activity. Approach of a swimmer much closer than about 2 metres to the side or 1 metre beneath the turtles stimulated increased directional swimming at the surface. Avoidance reactions appeared to depend roughly on the proportion of the field of view occupied by the foreign object. An 8 cm. disc on the end of a thin pole produced roughly equivalent reactions at about 20 cm. to 30 cm. distance to those elicited by the body of a swimmer at about 1·5 metres distance. Rapid movement on the part of the foreign object increased the distance at which it was detected and the violence of the avoidance response. So far as could be determined, the hatchling turtles showed colour responses comparable to those reported for young Loggerhead Turtles by Mayer (1909), Hooker (1911), and Parker (1922, a & b). In crude experiments which were performed, there appeared to be a positive tropic response to blues, tending to direct individuals to open, deep water ; there was a positive biting response to reds in small mass, presumably relating to feeding on animals such as some of the reddish-coloured planktonic shrimps.

GROWTH RATE AND ADULT SIZE

Despite the release of thousands of cultured young turtles each year from the hatcheries in Sarawak, and the natural hatching of uncounted wild nests throughout the area, this writer and his assistants never observed a single juvenile *Chelonia mydas* at freedom in a completely natural state despite extended efforts to find them. Moorhouse (1933) reports the release of 1,300 marked young on the Barrier Reef, none of which was seen again. None of the Malay residents in the vicinity of the turtle beaches ever made a substantiated claim to knowledge of where the young turtles went after leaving the beach. When questioned, some of the turtle egg gatherers at various places said that they thought the baby turtles lived "among the rocks" on other shores of the islands or of the mainland, but none admitted to having good evidence of other than newly-hatched young which were trapped temporarily among the rocks by waves, currents or low tides. Ignorance of the habits of wild young sea turtles has been so complete among most of the local people in Malaya and Sarawak that a somewhat mystic attitude has developed concerning this stage. On one island off the East Coast of Malaya the writer was warned that the Sea Spirit might punish too persistent an attempt to learn " his secrets ".

The only published information on rates of growth of individual immature turtles in the wild state appears to be the data obtained by Schmidt (1916) from eight recaptured tagged turtles in the West Indies. Schmidt's data dealt with individuals of unknown age, belonging to the Atlantic populations (*Chelonia mydas mydas*). His animals were all branded with a hot iron as well as being marked in other ways. It is possible that severe trauma due to branding had a retarding effect on the growth of the eight recaptured individuals during their period of freedom. There would appear to be reason to believe that the West Indian turtles reach maturity at a smaller size than the Asian stocks. From the data available to him, Schmidt attempts to estimate growth rates which, when applied to Malayan-Sarawak turtles, appear to be improbably slow. Schmidt's estimate of the probable weight of a West Indian turtle aged three to three and one-half years is about 9·1 kilos. The most rapid increase in weight recorded among his eight recaptured animals was about 431 grams per month. At this rate, the smallest individual of a sample of 200 adult females measured in Sarawak (weight 89 kilos) would be about eighteen or nineteen years old.

Lacking information on the growth of young Asian turtles in the wild state, records of the growth of captive specimens provide the only indications of the time necessary to reach maturity in the animals. It is dangerous to make assumptions of the normal state of affairs on the sole basis of results with captive animals, particularly as concerns growth rate and most especially as concerns growth rate in poikilothermic animals such as turtles. It is felt, however, that the data presented here will allow some cautious speculations on the probable rate of growth and the number of years needed to reach maturity in the Asian stocks of *Chelonia mydas*.

Hornell (1927), Moorhouse (1933), Deraniyagala (1939) and Harrisson (1955 b, 1956) give measurements of captive young *Chelonia mydas* at particular ages. This writer and others have kept hatchlings from the Sarawak turtle islands for various periods of time. When all the available information is examined, it becomes apparent that measurements of weight of captive individuals vary within wide limits at any one age level. Measurements of carapace size—the other common form of measurement—also vary, but do so less erratically than weight measurements.

Figure 15 shows the proportion of carapace length to carapace width in Asian turtles of different ages. Included in the figure are all those published measurements known to the writer giving the length and the width of the carapace at definite ages. In the upper right of the graph are plotted the proportions of 200 wild females from Sarawak which are known to be mature by virtue of having been observed to lay eggs. It will be seen that the data from young, captive turtles lie along a line which, if extended, enters the cluster of adult records.

Schmidt (1916, Table III, p. 19) gives measurements taken from a number of turtles which were brought to market in the West Indies. If the data in his table are plotted on a graph similar to that in Figure 15, it will be found that West Indian turtles show a comparable relationship between increase in length and breadth of carapace. The slope of the line in the West Indian data is slightly less than in the Asian data. This may be due to the fact that the West Indian stock tends to produce a proportionally wider shell. It may, however, be due entirely to the fact that all of Schmidt's measurements were made with a tape measure laid over the curve of the carapace, while all the measurements of the Asian turtles are straight-line distances between the

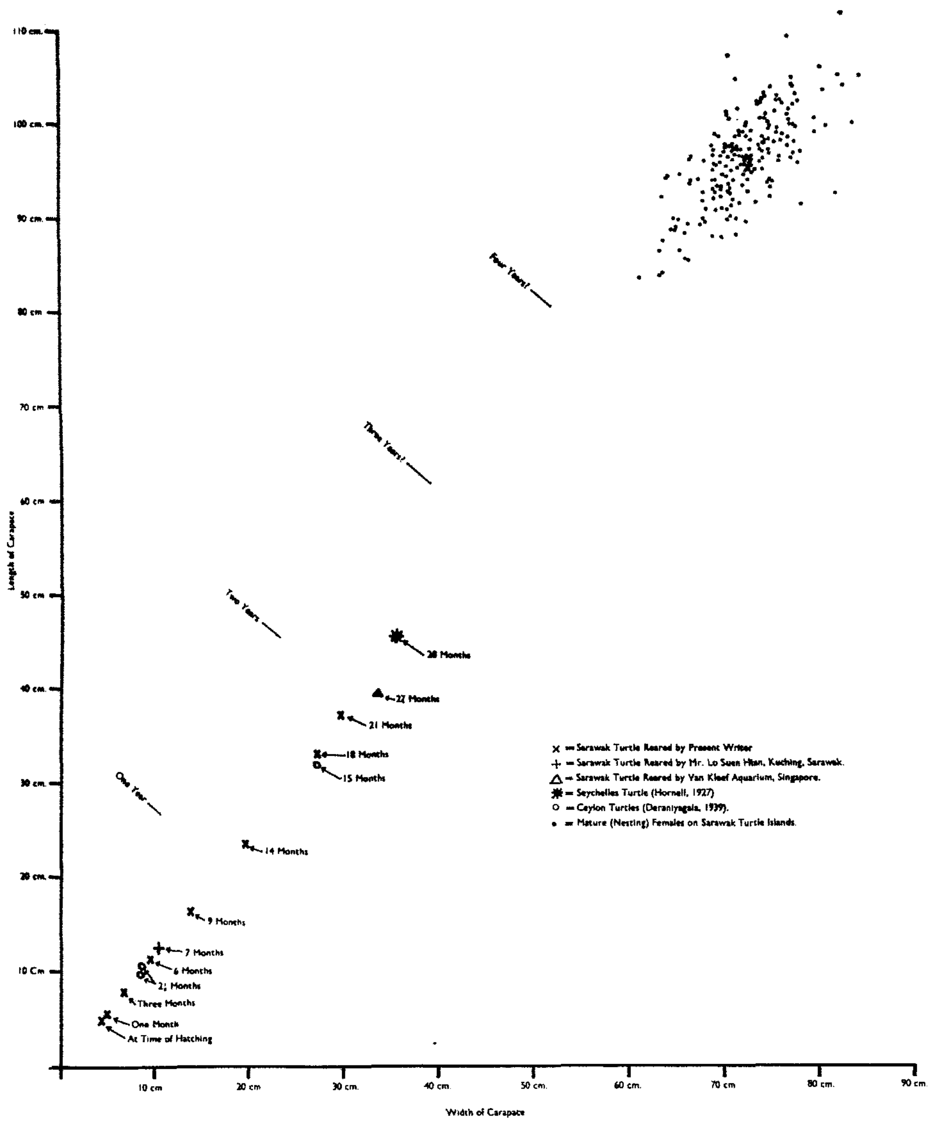

Fig. 15.—Relation of carapace length to carapace width in *Chelonia mydas*.

points measured. The West Indian turtles happened to be mostly of sizes intermediate between the two groups of Asian turtles represented. If it were not for the difference of slope in the data from the two stocks, the West Indian specimens would bridge the gap which at present exists in Figure 15.

The 200 Sarawak females were measured in two series, one group in 1952, the other in 1953. In each series of measurements samples were not consciously selected. Every turtle was measured as it was encountered in the course of routine patrols of the beach at Talang Talang Besar Island, Sarawak. It is believed that the records give a fair representation of the range of size in mature Sarawak females. Moorhouse (1933) measured fifty Barrier Reef turtles at random. Thirty-three were between 100 and 107 cm. in carapace length, five were less than 100 cm., and twelve were over 107 cm. The smallest ovipositing female measured had a carapace 87·5 cm. by 87·5 cm.

Male turtles have not been available for measurement in any numbers. Many observations from a distance have failed to indicate the existence of a size differential between the sexes.

In Figure 15 it will be noted that the increase in carapace size during the second year is virtually the same as during the first year. It is assumed that, while there may be some decrease in rate of growth with succeeding years, no marked decrease is to be expected until the animals have reached sexual maturity. It is postulated that the difference in size increase between the third and second years will not be greater than the difference between the second and first years, and that the fourth year will not vary from the third year more than the third does from the second. On this basis, postulated sizes at the end of three years and four years (with queries) are indicated on the graph.

There is little reason to doubt that varying conditions in the wild will cause different individual turtles to come to maturity after different lengths of time. However, the data in Figure 15 would appear to indicate that Asian Green Turtles do not mature in less than about four years and that there is a probability that most individuals reaching maturity do so in less than six years. If further information demonstrates that five years can be taken as a rough working figure for the length of a generation, it will have considerable

TABLE 2

Measurements of adult female *Chelonia mydas*, Talang Talang Besar Island, Sarawak, 1953

Length : Shortest linear distance between the anterior edge of the nuchal plate and the point of juncture of the two pygal plates of the carapace.

Width : Shortest linear distance between the lateral margins of the carapace at its widest point.

Weight : Determined to the nearest 1210 gm. unit (equals two of the Malayan weight units called " katis "), using a rope sling to suspend the turtles from a Chinese balance (" daching ") used for weighing copra.

Tag Number	Carapace Length	Carapace Width	Weight
194	98·6 cm.	72·5 cm.	121 kilos
196	95·2 cm.	71·6 cm.	113 kilos
198	97·2 cm.	74·9 cm.	115 kilos
199	95·5 cm.	73·0 cm.	126 kilos
201	98·3 cm.	72·9 cm.	118 kilos
203	97·8 cm.	71·0 cm.	114 kilos
204	87·8 cm.	69·9 cm.	89 kilos
205	88·0 cm.	71·4 cm.	91 kilos
206	100·0 cm.	77·2 cm.	123 kilos
207	92·4 cm.	70·8 cm.	99 kilos

value in planning further study of the dynamics of Green Turtle populations and in organising management programmes for some of the populations which are being exploited for food.

While no attempt has been made here to use weight measurements of turtles as a basis for drawing any conclusions, it is recognised that many weight records exist in the literature and that other workers may wish to analyse such data. For this reason, it is deemed worthwhile to record in Table 2 the measurements made on ten adult female *Chelonia mydas* which were weighed on the Sarawak turtle islands.

PREDATION

From the time the eggs are deposited in the sand, a wide variety of animals prey upon sea turtles. At the present time and in the area studied, man is the most important enemy of the turtles by virtue of his use of the eggs for food. Human depredations are so widespread and so thorough that other enemies are virtually excluded from having any importance. The apparently minute fraction of the total nests which are not discovered and excavated by organised human efforts remains, however, subject to exploitation by a variety of other animals.

Ghost Crabs (*Ocypoda* spp.) were numerous on all the turtle beaches visited during the course of this study. On the Sarawak turtle islands these crabs were observed to have burrows extending down into the subterranean egg chambers, both in the hatchery and in natural nests. Numerous burrows made by the crabs were excavated on all parts of the beach. It was not uncommon to find turtle eggs which had apparently been carried to the burrows from some distance.

On two occasions when crab (?) burrows leading down to turtle nests were being investigated, rats emerged from the burrows. The islands on the East Coast of Malaya have a heavy rat population. Signs of rat investigation and exploratory digging around fresh nesting sites were frequently observed. Rats caught on the Sarawak turtle islands and held captive readily accepted both turtle eggs and hatchling turtles as food, killing the hatchlings with despatch and eating the head first. On one occasion on a Malayan turtle beach a *Varanus salvator* of about 90 cm. snout-vent length was observed for about 45 minutes while it closely explored a fresh nesting site. The exact location of the egg mass of this nest had been marked during the laying process by placing a slanting wand in the sand so that the tip was directly over the eggs. The lizard correctly chose the proper location and made several small test pits before leaving the area. This action occurred at about 0200 hours, and was seen only by the illumination of the observer's headlamp. Presumably it was the lamplight that frightened the lizard away.

Although *Varanus* occurs on the Sarawak turtle islands, individuals were never seen on the beaches, probably because of the intensive local human activity there in the form of continuous night patrol during most of the year. On the more deserted Malayan beaches, however, many signs of *Varanus* were seen, and on numerous occasions there was clear evidence of close exploration of fresh turtle nesting sites, including minor excavations.

One informant told the writer that he had disturbed a Long-Tailed Macaque (*Macacus irus*) from an opened turtle nest on one of the Malayan East Coast islands. It is not clear whether the monkey had accomplished the excavation or had merely taken advantage of work done by a *Varanus* or some other agent.

Upon emerging from the nest, the hatchling turtles risk encounters with numbers of predators on their way to the water. Predation at this stage is more obvious than is nest destruction and has been repeatedly observed. Moorhouse (1933) mentions daytime capture of young turtles by gulls and herons, and nocturnal predation by Crabs (*Ocypoda*) and House Cats. The most extensive loss of hatchling turtles observed by the writer and assistants has been to the Ghost Crab (*Ocypoda ceratophthalma*). Moorhouse (1933) describes the *Ocypoda* observed by him as standing over its victim, presumably fully exposed on the beach surface, and stripping off the carapace plates. Of fourteen entries concerning crab predation in the field journals kept over the 4 years in which this study was carried out, only two indicate that the crabs observed were operating on the open sand. On the Sarawak islands it was usual to find that the crabs dragged the baby turtles to their burrows immediately after capture. Some of the crabs then began to feed on their prey at the entrance of the burrow, the walking legs of one side actually inside the opening (Plate 8 b). Commonly the crabs attempted to drag their prey out of sight down into the burrow. *Ocypoda* were never observed stripping off carapace plates from their prey. All partially consumed young turtles examined showed evidence of marked uniformity in the habit of attacking the head first. Usually the head and neck were severely mangled at an early stage, but the first conspicuous excavation (consumption ?) of tissue which occurred was the eyes, followed by the dorsal portions of the head in the general region of the brain.

Resident turtle egg collectors on the East Coast of Malaya state that, besides heavy loss to crabs and rats, there is considerable predation on migrating young turtles by *Varanus* and by snakes. On several occasions at widely separated areas the distinctively coloured Mangrove Snake, *Boiga dendrophila*, a characteristic beach forest inhabitant, was described as another snake besides the python (*Python reticulatus*) which had been observed in the act of swallowing baby turtles.

Large aggregations of sea birds do not exist in the vicinity of the turtle beaches visited during this study. Predation by sea birds on young turtles was not observed.

Those young turtles which survive the migration across the beach to the water suffer further concentrated attacks in the beach shallows by small sharks which have been seen patrolling almost every beach after dark. Attacks on young turtles by 45 cm. to 60 cm. sharks were repeatedly seen in water as shallow as 15 cm. Since such observations were always at night, and since the sharks refused to approach in the full glare of the observers' headlamps, there was originally some doubt as to whether the sharks were actually attacking the turtles or were merely making numerous passes without endeavouring to seize them. However, when baby turtles were released trailing after them fine nylon lines attached to fish hooks which were tied onto their plastra, frequent " bites " were felt and, occasionally, sharks were hooked and landed.

On Talang Talang Besar Island, when large numbers of baby turtles were released at the water's edge after dark, heavy splashing some yards out from shore indicated unusually concentrated feeding activity by large fish near the edge of the coral reef which fringed most of the beach. During the routine daytime release of large numbers of young turtles from a boat rowed well out past the reef edge, it was common to see attacks by fish on the concentrated group of baby turtles.

It seems reasonable to assume that predation pressure on *Chelonia mydas* is most extreme during the first few weeks of life in the water. After this original period has passed the young turtles have not only grown somewhat and become more vigorous and better coordinated swimmers, but they have lost the disadvantageous buoyancy which had originally prevented any effective diving, thereby severely limiting their escape activities.

With increased size and swimming power, the growing turtles find progressively increasing immunity from most of their smaller predators, but they never achieve immunity from the larger sharks. Moorhouse (1933) states that sharks appeared to have done considerable damage to some of the turtles he studied on the Barrier Reef in Australia. Norman and Fraser (1948) give an account of an attack by what was presumed to be a *Carcharodon* on a large Loggerhead Turtle. In the course of the study in Malaya and Sarawak, an estimated 4 per cent of the adult females examined on various beaches showed signs of assumed shark damage. In many cases, such damage was severe, involving amputation of limbs and loss of sizeable portions of the pygal area, including large pieces of shell. Plate 8 c is a photograph of a turned female which has suffered high amputation of a rear limb and some carapace damage. It seemed remarkable that some of the more extreme cases had survived such severe damage. Any preconceived notions the writer and his assistants may have had as to the ability of the shell of *Chelonia mydas* to resist the shearing action of the bite of a large shark were soon revised upon seeing the mutilated female turtles which came up on the beach to lay eggs. Most of the wounds were old and well healed, and it was impossible to be certain that the damage had not been suffered when the turtle was much smaller. However, some fresh and recently healed cases were also observed and there was no doubt that these wounds had been suffered by fully grown animals with carapace lengths in excess of 90 cm. Damage to the rear flippers and the pygal region was much more commonly observed than was damage to the fore flippers. This might conceivably have been due to the greater vulnerability of the posterior portions of the body to shark attacks. It was thought, however, that severe damage to the fore flippers would so hamper escape and later survival that the smaller number of anteriorly-mangled females on the beach was really an index to the greater mortality following attacks on that part of the body. Most of the animals sustaining complete or nearly-complete amputation of a limb experienced considerable difficulty in digging normal nests. Some of these turtles returned repeatedly to the beach but, so far as known, did not nest successfully.

On three occasions during 1952 and 1953 shark fishing rigs were set up in the waters near the Talang Talang Islands, Sarawak. Sharks caught were measured for length, weighed, and examined for stomach contents. Of the seven sharks caught, one was a Nurse Shark (*Ginglymostoma* sp.) measuring 2·6 metres and weighing 130 kilos and six were Tiger Sharks (*Galeocerdo* sp.) varying in length from 3 metres to 4·4 metres (193 kilos to more than 484 kilos). One of the six *Galeocerdo* had its entire abdomen ripped out by other sharks. Of the remaining five specimens, two had completely empty stomachs. One contained portions of another shark, including the complete head, about 30 cm. in breadth. Two contained identifiable turtle remains. Plate 9 a and b are photographs of the stomach contents of one of the turtle-eating Tiger Sharks.

The writer believes that *Galeocerdo* is the dominant large shark in the vicinity of the turtle islands. In the shallow seas of the Sunda Shelf, this fish is a common, fast-swimming predator of voracious habits. On several occasions when the observer attempted to swim far out from the reef edge at Talang Talang Besar Island to approach copulating turtles, fast-swimming sharks tentatively identified as *Galeocerdo* made repeated inspections of him. These inspections were sufficiently pointed that further attempts to observe turtles at sea by approaching them in the water were given up as unsafe.

Some of the islanders held the opinion that sharks are attracted to the vicinity of the islands by the concentrated " turtle smell " in the adjacent water. During the heavy nesting season up to 100 females lay each night and return to the water with mucus still exuding from their cloacae. Whatever the actual causes, the writer is inclined to agree that sharks do apparently congregate in large numbers around the turtle islands during the peak breeding season.

Large sharks appear to be the only important predators on adult turtles in the water. An early Indonesian reference (see Journal Straits Branch Royal Asiatic Society, 1885) describes extensive slaughter of adults on the breeding beaches by tigers and wild dogs (*Cuon javanicus*). The writer was told of tigers roaming the turtle beaches in Trengganu, Malaya. In one case an egg collector completely covered in a sarong and sleeping on the beach, was reported to have been seized by a shoulder and dragged for some distance by a tiger. It was concluded that the sleeping man was mistaken for a turtle, and that the tiger was almost as surprised as his victim when it discovered the error.

PARASITISM

It has been explained that, during the course of this study, it was not possible to sacrifice adult turtles for any purposes. Only external parasites were therefore recorded, since they could be collected without unduly harming the turtles.

Several times mosquitoes were observed biting nesting turtles on the beaches. Usually these were seen biting on the relatively soft skin of the upper eyelid.

The encrusting barnacle, *Chelonibia testudinaria* (Linnaeus, 1758) (Plate 9 c), occurred commonly on about one-third of the turtles seen during this study.

Although these barnacles were firmly attached and could be prised off only with difficulty, they did not cause any particular erosion of the part on which they were growing. It would appear that these barnacles caused little inconvenience to the host except in cases where encrustations on the head interfered with the action of the eyelids.

On a few occasions, small isopods (genus *Eurydice*) were found clinging to the margins of the eyelids of turtles. They were not obviously associated with lesions or other signs of pathology.

A careful inspection of the heads of turtles sometimes revealed the presence of many small leeches (*Ozobranchus branchiatus*) clinging to the softer membranes, mainly on the eyelid margins and at the mucous junctions of mouth and nostrils. These parasites varied in size up to a maximum of about 8 mm.; some individuals as small as 1 mm. were noted. Occasional turtles with raised, ulcerating growths on throat and neck had numbers of these leeches clinging to the growths. On gross examination the growths appeared to be ulcerating fibromas. They varied in size up to observed maxima of about 3·7 cm. by 7·6 cm., by about 2·5 cm. high. Nigrelli (1942) reports on the association of *Ozobranchus* with fibro-epithelial tumours on marine turtles.

The most damaging ectoparasite of *Chelonia mydas* observed during this study was the rather rare burrowing barnacle, *Stephanolepas muricata*, P. Fisher, 1886. The following two extracts from field journals describe infestations of *Stephanolepas* as observed on Sarawak turtles :

10th September, 1952 : The barnacles were deeply embedded in a sort of leathery tissue which replaced the normal hard plates over irregular areas totalling perhaps 900 square centimetres on the dorsal portion of the carapace. The barnacles lay embedded with their exposed ends approximately flush with the surface of the leathery tumour-like tissue, which in turn was raised up to about 1·5 cm. above the general carapace level. We were unable to extract any of the barnacles by more delicate means than by prising them out with a screwdriver. The longest barnacles were almost 4 cm. from end to end, and apparently had penetrated completely through the carapace to the body cavity. All holes which were left after the extraction of barnacles filled with blood, and the blood in the deeper holes moved in and out with movements of the turtle ; air sucked in and bubbled out of one hole with each breathing movement of the turtle. The barnacles had a hard cylindrical casing with numerous irregular processes projecting out at right angles from the casing; these processes were embedded in what bone remained in the area. Most of the attempts to prise out individual barnacles broke the brittle casings and severely damaged the barnacles. By dint of much force and considerable time, I was able to excise a piece of the " tumour " roughly 5 cm. in diameter. This piece contained five undamaged barnacles ; when it was placed in sea water in an aquarium, the barnacles began to sweep the water in characteristic fashion.

16th March, 1953 : Found a turtle with a large, mushroom-shaped, leathery growth on its carapace (situated roughly on the highest point of the carapace dome). This growth, measuring about 10 cm. by 15 cm., was attached by a relatively small stalk and I was able to remove the mass in its entirety. The growth was rooted very strongly through the carapace plates into the underlying bone, and the root was highly calcified. The mass contained a number of the burrowing barnacles seen before. When the mass finally came away from the turtle's carapace, it left a hole about 2·5 cm. in diameter and about 2 cm. deep. Compared to the previous experiences at prising individual barnacles out of the surrounding tissue, there was very little blood lost during this operation. Is this a sample of a relatively successful host reaction to the parasites, isolating them off in a stalked tumour where they receive minimal blood supply, etc. ?

Plate 10 a shows barnacles embedded in a turtle's carapace. Plate 10 b shows the stalked tumour mass described above and Plate 10 c shows individual barnacles dissected out from the surrounding tissue.

It would appear that severe infestations of *Stephanolepas* might be lethal to turtles. It should be recorded, however, that the second turtle described above returned to the same beach at later dates to lay eggs, and that it appeared to be in good health.

SPECIES MANAGEMENT—AN ANALYSIS

So far as the writer is aware, all Green Turtle populations throughout the world are exploited principally as a source of food. It so happens that the turtles occur mainly in areas where the human diet is notably low in high grade proteins. Therefore, the writer believes that the logical goal of management should be the production of the maximum sustained yield in kilograms of protein food per year.

To date, industries in the Muslim areas of Malaysia have tended to concentrate mainly on harvest of the turtles' eggs only, while in most other parts of the world industries have been based mainly on slaughter of the adults or near-adults for flesh and fat. The available evidence indicates that the number of turtles in Malaya and Sarawak has declined much less than elsewhere, and it seems logical to infer that exploitation for eggs has a much less adverse effect than has the slaughter of adult turtles.

The difference in the effects of the two methods of exploitation seems to relate directly to the positions of the two food forms in the life history of the animals, and to the manner in which the species is adapted to its particular environment. The individual *Chelonia mydas* female has a high reproductive potential and the species is adapted to sustain enormous losses at the very early stages of its life history. The small proportion of individuals which survive the early period of high mortality mature rather slowly and presumably remain reproductively active for a considerable number of years. In maintenance of the population, each adult female is of equal value to several thousands of eggs. The harvesting of eggs constitutes exploitation at that stage of the life cycle where the species is adapted to sustain high losses in the natural course of events. A very large portion of the eggs collected represent, not new losses to the population, but diversion of losses which would have occurred even if there had been no intervention by man. The slaughter of grown turtles, on the other hand, is a direct threat to the dynamic equilibrium of the population, and it would appear that the species is ill-adapted to sustain such losses. It is obvious that flesh and fat are the biologically more expensive food form to be obtained from Green Turtles, while eggs are biologically cheap. Given nutritional equivalence between eggs and flesh in terms of kilograms of edible protein per year, exploitation for eggs is the logical choice.

It has been demonstrated that the Sarawak Green Turtles lay, on an average, over 100 eggs at a time, and that they usually lay six or seven clutches in a breeding season. If the average female lays 600 eggs per season and experiences at least three seasons during her life (this seems minimal to the writer), then an adult turtle may be equated with 1,800 eggs or more. An estimate of double this number might be justified, but the conservative figure will serve to illustrate the desired principles. In a hypothetical population of animals with the breeding potential outlined above, the population size would remain stable if only slightly more than one-tenth of 1 per cent of the eggs laid resulted in adult turtles which lived out complete lives. 99·9 per cent of the eggs (or individuals resulting from them) could be lost from each generation.

Using the above figures in a working hypothesis, the following table gives rough estimates of losses which the writer considers to be within the range of possibility for a population using a concentrated Malaysian breeding beach in an undisturbed state.

TABLE 3

Chelonia mydas. Estimated rates of loss to various factors during early stages of life cycle

Decimating Factor	Percentage Loss	Remnant of the Hypothetical 1,800 Units after Loss	Percentage Remnant
Non-developing eggs (see p. 506)	40	1,080 Developing eggs	60
Nest destruction by turtles (p. 505)	50	540 Developing eggs	30
Predators on nests (p. 520)	25	405 Developing eggs	23
Beach predators on hatchlings (p. 521)	40	243 Hatchlings	14
Shallow water predators on hatchlings (during first hour or so in the water) (p. 521)	50	122 Hatchlings	7
Deep water predators on hatchlings (during first week of life at sea)	75(?)	31 Juveniles	1·7

During the remaining period of at least four years before maturity (see p. 519), plus (apparently) nine years before the third breeding period is finished (p. 503) and the hypothetical quota of 1,800 eggs has been laid, it is assumed that a further mortality of more than 90 per cent would occur from disease, parasites, and large predators (see pp. 522–525).

The proximity of the foregoing estimates to the true facts in any one turtle population is less important than the sequence and resultant magnitude of effect of the different decimating factors. From the listing as given it is possible to judge the relative value and estimate the necessary scope of particular management techniques. Particular techniques may be more expensive to administer in one situation than in another, and the central problem of management is usually one of getting the most results from the least expenditure of money and effort.

The percentages shown in the right hand column of the foregoing table can, in the hypothetical case under consideration, be considered as the percentage of the original units which a good management policy would allow to contribute to the population. Thus, if the beach concerned here produced a total of one million eggs per year, the annual release in deep water of 17,000 week-old baby turtles in good condition (1·7 per cent) would be inadequate replenishment for maintenance of a stable population. If hatchlings were not kept for a week, but were dumped into the sea on the same day they hatched, 140,000 individuals (14 per cent) would have to be produced annually; by merely scattering the day's production of hatchlings widely at sea in deep water after dark, this number could be cut to 70,000 (7 per cent), etc.

The most obvious managerial technique for ensuring adequate replenishment of the turtle population while obtaining the maximum harvest of eggs is a hatchery programme. Transplantation of clutches of eggs to a protected enclosure on a suitable bit of beach sand can eliminate losses caused by nesting turtles. Presence of humans harvesting eggs in the immediate vicinity will probably automatically reduce the numbers of vertebrate predators on nests and newly-emerged hatchlings; use of wire enclosures (see Plate 8 a) to prevent the newly-emerged hatchlings from wandering to the sea will further reduce predation. Poisoned baits in the hatchery enclosure might be effective against burrowing crabs. Hatchlings may be kept in tanks of clean sea water for about a week before they exhaust the yolk supply which is incorporated from the egg; there is no indication at present that any feeding is necessary during the first week in a nursery tank.

Attempts at culture of young Malaysian turtles beyond the first week have demonstrated a number of complications in proper care and feeding. While small numbers have been reared satisfactorily, there has to date been little success in developing methods for culturing large numbers of young turtles conveniently and cheaply.

As pointed out in the section entitled " Predation ", there is apparently a significant loss of prime reproducing animals to large sharks in the vicinity of the breeding beaches. It is believed that the shark population tends to build up during the heavy breeding season as wandering sharks tend to remain in the areas because of the concentration of turtles there. From the results of the shark fishing carried on by the writer in Sarawak, it seems likely that the local shark populations might be significantly reduced by planned fishing programmes. If catches on the scale experienced in 1952 could be continued indefinitely, a worthwhile industry based on fins, liver oil, and salt flesh could develop. If the catch dropped off to a low level after a while, the turtle population would be afforded the desired relief from predation during the vulnerable period of breeding concentration.

The preceding discussion of management techniques has been devoted to a consideration of the decimating factors which operate on turtle populations. The measures suggested are all intended to make possible a maximum diversion of natural losses to the harvest reaped by humans while maintaining a stable population. It may also be possible in some cases to manage certain limiting factors, thereby encouraging increase in the size of the population.

In the section entitled " Description of Habitat " it has been pointed out that *Chelonia mydas* in Malaysia restricts itself to certain types of beaches for breeding purposes. The limited number of suitable beaches available constitutes a limiting factor on the potential increase in the turtle populations. While the number of separate beaches of suitable type is unalterable, the limiting factor resolves itself into the total *area* of suitable nesting sand, and in many cases individual beaches can be altered so as to increase the available nesting area.

It has been pointed out that on the Malayan beaches there is usually an encroaching jungle front which makes considerable areas of sand unsuitable because of roots and stems which hinder nest excavation. Clearing of plant growth back to beyond the sand limits could materially increase the potential nesting area of many beaches.

A high rate of precipitation causes extensive drainage onto many breeding beaches from the adjacent island soil, transporting fine material which is deposited in the beach sand, eventually making it unsuitable for nesting. Diversion of run-off from the island soil could, in some cases, increase the total area of suitable nesting sand. In some special cases, as on Talang Talang Kechil Island, Sarawak, low areas of beach which are too close to the water table to allow ideal nesting lie adjacent to high dune fronts. It might be feasible to shift quantities of sand so as to level the beach and increase the area of optimal nesting sand.

The foregoing discussion has attempted to show that, of the two methods of exploitation of Green Turtle populations, exploitation for eggs is not only the biologically practicable choice, but is also the policy likely to provide the greater management opportunities. It remains to be shown that exploitation for eggs is economically more profitable in terms of kilograms of protein food per year than is slaughter for flesh and fat. Ingle & Smith (1949) state (p. 37) that, " The flesh of the Green Turtle . . . constitutes about 40 per cent of the entire body weight ". The only mention of the relative amount of fat in this reference is in the table on page 38, where " calipee " is recorded as contributing roughly 7 per cent of the body weight. For purposes of argument here, it is assumed that flesh plus fat account for about 50 per cent of the live body-weight of Green Turtles. Again for purposes of argument, it is assumed that the average adult turtle weighs about 120 kilograms (see Table 2). Slaughter of such a turtle would then provide 60 kilograms of flesh and fat for human consumption.

If the eggs average about 35 grams each, 600 eggs laid in a breeding season by the average female turtle would weigh about 21 kilograms. Since the average number of eggs is almost certainly higher than 600 per season, it is probably fair to disregard the weight of the egg shells and to consider that the turtle produces about 20 kilograms of protein food per season. At this rate, in three breeding seasons each female will produce food in the form of eggs to equal the weight of food obtainable by slaughter of the animal. If it could be proved that, as the writer suspects, the average female Green Turtle experiences more than three breeding seasons in a lifetime, then the weight of protein available in the form of eggs would clearly exceed the weight available in the form of flesh and fat. The eggs are probably a richer source of available high energy protein than flesh and fat; they are naturally " packaged " for easy handling, long preservation, and uncomplicated marketing procedures.

In a properly managed industry, up to 96 per cent or more of the average turtle's productivity may be utilised for human consumption, without removal of the producing unit from the population and with the possible expectation of " bonus " productivity during all breeding seasons after the first three. In exploitation for flesh and fat, 100 per cent of the turtle's productivity is utilised once and for all and that particular unit ceases to confer any benefits. There is no doubt in the mind of the writer that, so far as our present knowledge goes, the exploitation of wild Green Turtle populations for eggs is more profitable in terms of nutrition than is exploitation for flesh and fat.

It is recognised that economic practices in human society do not always follow closely the nutritional criteria which have been considered above. The existence of what is often considered a luxury food—Green Turtle soup—complicates the picture in some parts of the world. The special demands for a luxury food, mostly from outside the protein-poor areas where turtles breed, may exert economic pressures on local industries to ignore the basic nutritional grounds on which good management should be based, and some areas may sell their needed protein. The writer believes that such policies will almost inevitably result in a net nutritional loss by the time the money received for turtle soup has been converted back into consumed food in the stomachs of the local people. It is suggested that no luxury demand should be allowed to produce a net nutritional loss in the areas concerned, particularly when past history indicates that the form of exploitation necessary to supply the luxury obliterates the industry concerned after a time. If Green Turtle soup is to be made available at all, it should partake in increased amount of that essential element—rarity. Such slaughter of adult turtles as occurs should be strictly limited and should be devoted entirely to money-making on the luxury food market. A significant fraction of the higher profits obtained from sale of the soup should be ploughed back into intensive management of the turtle populations.

Experience with the marked population in Sarawak suggests that intensive marking studies over a long period of years might make it possible to determine reliable criteria for identifying aged females which were unlikely to live through another non-breeding period. Such biologically exhausted females, along with severely crippled and incapacitated individuals, might conceivably provide an adequate source of flesh and fat for a subsidiary turtle soup industry.

SUMMARY

A four-year study was conducted on breeding populations of Green Sea Turtles, *Chelonia mydas* (Linn.), in Malaya and Sarawak. The area of study was confined to the South China Sea (Sunda Shelf) coasts of the two countries. The history of the exploitation of sea turtle populations for eggs in the Muslim areas of Malaysia is reviewed; compared with other parts of the world where turtles are killed for flesh and fat, the populations in Malaya and Sarawak appear to have suffered little reduction in size. The general aspects of the marine environment and the different types of sea turtle breeding beaches in the area are described. *Chelonia mydas* tends to build up large breeding concentrations around a small number of beaches, with only limited use of other beaches in the region. Possible causes and adaptive features of the observed situation are discussed. The type of beach utilised by large breeding concentrations of Green Turtles is described, and several particular beaches are described in detail.

The process of nesting is described at length, drawing on extensive field notes made over a four-year period. Particular attention is paid to behavioural aspects of the nesting process and to their possible adaptive significance. Female turtles approaching the beach for nesting are very shy while still in the water and still able to make a rapid escape ; they show a clear set of reactions to visual stimuli. With progression up onto the land and isolation from the aquatic environment, the turtles show progressively less response to alarm stimuli. The mechanics of terrestrial locomotion and of the various nesting activities are described, along with discussions of inhibitory and initiatory stimuli which appear to govern the different stages in the process. A table is presented showing the timing of the nesting process in three selected observations on individual females.

Courtship and copulation in *Chelonia mydas* are described as they were observed in Malaya and Sarawak.

2,720 adult female turtles were tagged on three islands off Sarawak, where the Sarawak Government operates a turtle egg industry. Through the cooperation of the industry, statistical studies were carried out. Methods of tagging are described and pertinent features of the statistical work are discussed The recorded annual egg production from the three islands averages slightly less than two million eggs a year, with a recorded minimum of 700,000 and a maximum in excess of three million eggs.

While there is no non-breeding season in Sarawak, there is a pronounced annual cyclical variation in the intensity of breeding, with a marked heavy season around June, July, and August. The absence of a non-breeding season is considered to be related to the virtual lack of any marked annual variation in temperature. The existence of a definite peak breeding season is thought to relate to the adaptive advantage of a habit of synchronous breeding aggregation in a widely ranging species. The timing of the peak breeding season appears to relate to the period of the Northeast Monsoon, which brings relatively inclement weather from November through February.

The development and decline of the breeding season as shown by egg production figures from the industry shows a remarkable consistency through " good " years and " bad ". While presumably located in time to occur when monsoon effects are minimal, it does not show correspondence to yearly fluctuations in the timing of the monsoon. The per cent contribution of each calendar month to the annual total egg production tends to remain constant regardless of whether the monsoon periods preceding or following are early or late.

Individual tagged turtles returned repeatedly to the same beach to nest. Of 5,748 records of returning tagged females only 3·7 per cent failed to return to the same island previously used, despite the fact that two of the islands were only about 500 metres apart.

Female turtles nested six or seven times in a season at intervals of about 10 days. Records showed a maximum of 11 successful nests made by a single individual. 8,147 clutches of eggs averaged 104·7 eggs per clutch, with a Standard Deviation of 1·31.

The return in 1956 of numbers of the turtles tagged in 1953 indicates a three-year breeding cycle in the Sarawak turtles, and provides evidence that individuals are able to make their way back to the same nesting grounds after the long absence.

The environment of the incubating nest is described and the hatchery procedures practised on the Sarawak islands are outlined. A special series of nests was transplanted to the industry's hatchery enclosure for studies on incubation. Although surface sand temperatures underwent a diurnal fluctuation of as much as 23° C., at the depths where eggs were deposited the measured temperature never fluctuated more than about 2° C. Incubating nests showed a progressive temperature rise due to the metabolic heat produced by the developing embryos, reaching temperatures as high as 35° C. by the time of hatching. Records of 354 hatchery nests showed an average of 47 per cent of the transplanted eggs resulting in hatchlings which emerged to the surface. Recorded intervals between oviposition and time of emergence of young turtles to the surface varied seasonally from an average of about 70 days during the latter part of February to an average of about 54 days during the period June to October.

The process of emergence of the hatchling turtles from their subterranean chamber and their movement to the sea is described.

The available data on growth rate and age of maturation is assembled and discussed. It is concluded that Asian Green Turtles probably mature in from four to six years. The carapace measurements of 200 adult females from Sarawak are plotted on a graph ; the weights and carapace measurements of ten females are given in a table.

Predation upon incubating nests and upon turtles at all stages is discussed. Ghost Crabs (*Ocypoda* sp.) were the most serious observed menace to incubating nests in the areas studied. The heaviest predation observed on hatchling turtles was by Ghost Crabs and small sharks. There is little predation by sea birds on the Malaysian beaches. Several large Tiger Sharks (*Galeocerdo* sp.) were caught off the Sarawak islands ; two of these had the remains of adult sea turtles in their stomachs.

The various parasites and commensals found on turtles during the study are reported ; observations are made on the burrowing parasitic barnacle, *Stephanolepas muricata*, and its apparent tumour-inducing proclivities.

The paper concludes with an analysis of the problem of scientific management of wild populations of Green Turtles. It is concluded that exploitation for eggs is more logical, more profitable, and more amenable to management techniques than is exploitation for flesh and fat.

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EXPLANATION OF THE PLATES

PLATE 1

a.—Photograph of the beach at Talang Talang Besar, Sarawak, showing human habitation and cultivation on the back-beach.

b.—Photograph of the beach at Tiga Ruang Menangis, Perhentian Besar Island, Trengganu, Malaya, showing undisturbed jungle behind the beach.

c.—Photograph of the encroaching jungle front on the beach at Tiga Ruang Menangis, Perhentian Besar Island, Trengganu, Malaya. The principal tree visible is a species of *Barringtonia*.

PLATE 2

a.—Photograph of a female *Chelonia mydas* in shallow water, prior to ascending the beach to nest. The turtle's carapace is about 75 cm. across.

b.—Photograph of the trails left in the sand of a nesting beach by a female *Chelonia mydas*. The observer is kneeling beside the trail left as the turtle returned to the sea after nesting; the ascending trail left by the same turtle is visible near the right hand margin of the photograph.

c.—Photograph of the trail left by a nesting female *Chelonia mydas* in damp sand. The impressions made by the animal's tail are visible in the centre of the trail.

PLATE 3

a.—Photograph of a nesting female *Chelonia mydas* using its foreflippers to excavate a body pit. The turtle's carapace was one metre long.

b.—Photograph of a nesting female *Chelonia mydas* excavating an egg hole. The left rear flipper is shown in the act of scooping out sand. In the sand at the sides of the carapace may be seen the impressions made as the turtle shifts from side during alternate use of the hind limbs for digging. The turtle's carapace was 73 cm. wide.

c.—Photograph showing interference between nesting female *Chelonia mydas* on a crowded beach. The wandering individual facing the camera had earlier disturbed the animal in the background, causing it to leave a partially completed nest. The individual facing the camera measured 78 cm. across its carapace.

PLATE 4

a.—Photograph of rear extremity of turtle and egg hole. A bit of plant root is silhouetted against one of the eggs. The eggs averaged 40 mm. in diameter.

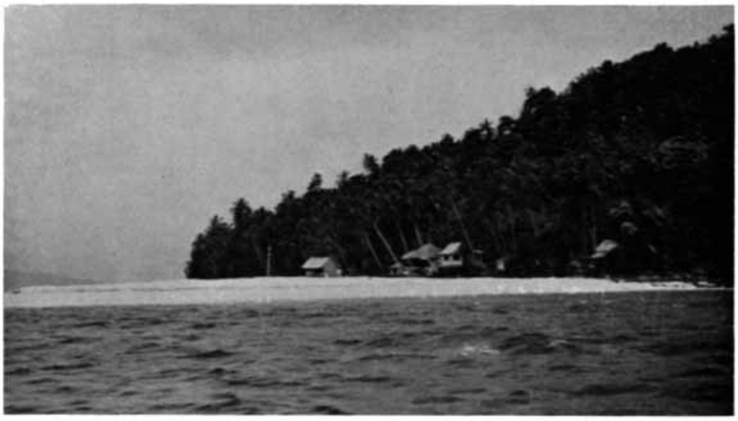
b.—Photograph of abonormal eggs and oviducal exuviae from *Chelonia mydas*.

c.—Photograph of female *Chelonia mydas* covering egg hole after laying has been completed. The right rear flipper is padding sand over the eggs; the left rear flipper is extended prior to gathering more sand. The carapace of this individual measured 104 cm. in length.

PLATE 5

a.—Photograph of a completed *Chelonia mydas* nest. The stick bearing a slip of white paper is situated directly over the buried egg mass; the observer is standing in the pit left by the turtle when she returned to the sea.

b, & c.—Photographs of an adult male *Chelonia mydas* showing (b) the heavy, prehensile tail, and (c) the recurved spurs on the front flippers. The turtle's carapace measured 94 cm. long.



a

b

c

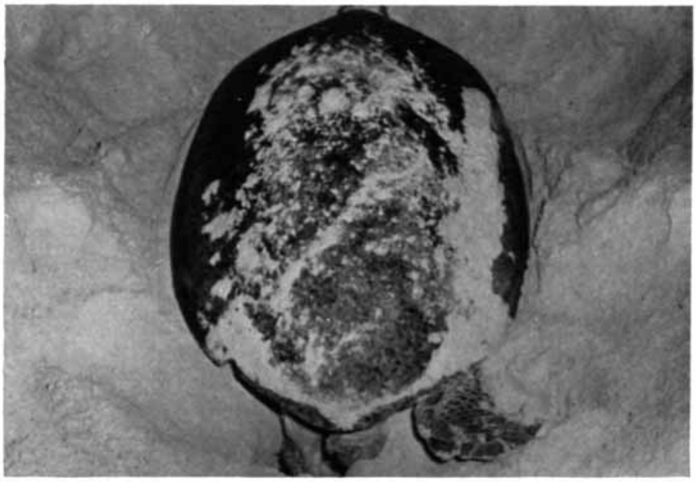
The Green Sea Turtle in Malaya and Sarawak.

a

b

c

a



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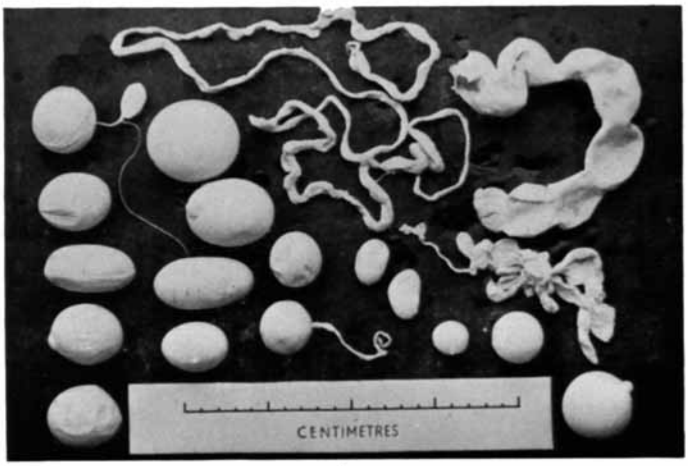

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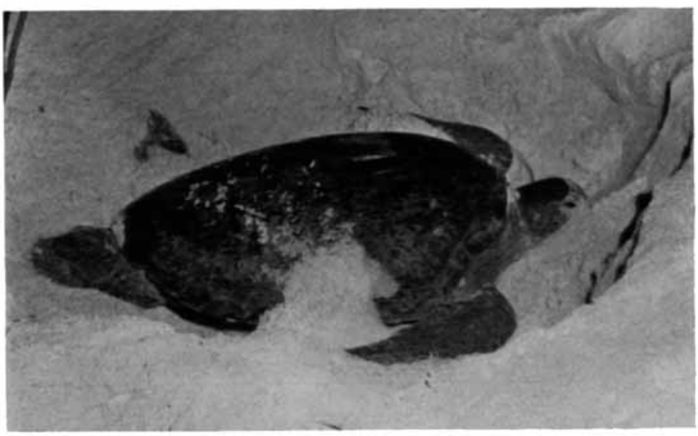

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The Green Sea Turtle in Malaya and Sarawak.

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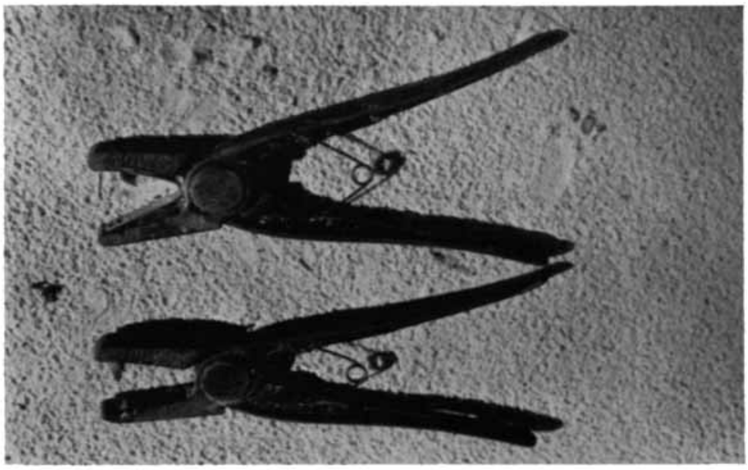

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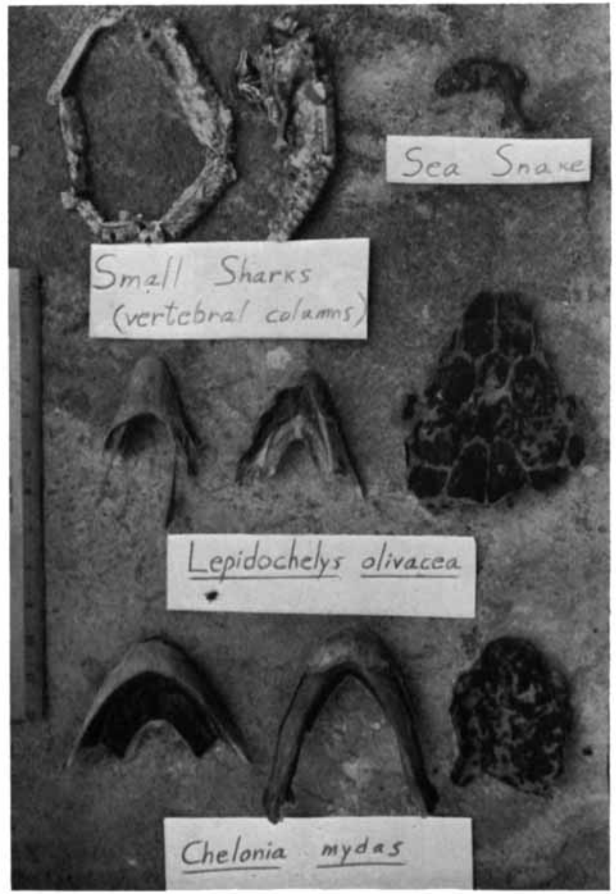

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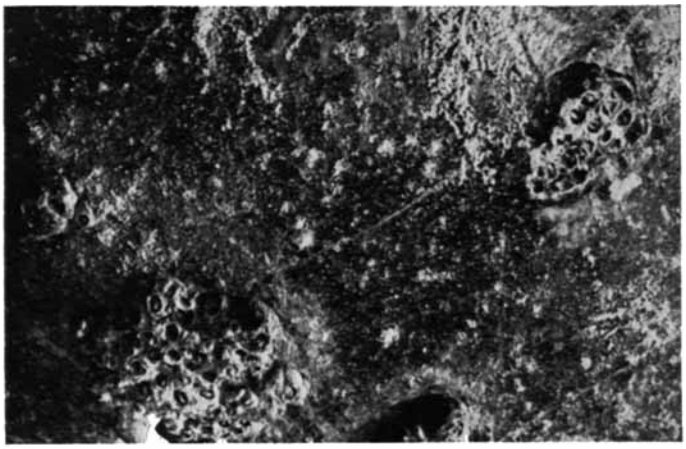

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The Green Sea Turtle in Malaya and Sarawak.

PLATE 6

a. & b.—Photographs of a pair of *Chelonia mydas* left stranded *in copula* on a breeding beach. The male's foreflippers are hooked by their recurved spurs onto the carapace of the female (a); the long, heavy tail of the male is curled forward and under the female's tail in copulatory position (b). The carapace of the male turtle measured 94 cm. long.

c.—Photograph of the pygal region of a female *Chelonia mydas* showing copper tag attached to the carapace during the 1952 marking programme. Tag measures about 4 cm. across.

PLATE 7

a.—Photograph of special tools used in the 1953 marking programme. Upper instrument is a special applicator plier, with monel metal tag inserted ready for use; lower instrument is one of the same special pliers fitted with a steel chisel point, for piercing the hard flipper scales preliminary to tagging.

b.—Photograph of one of the monel metal tags used for tagging turtles during 1953.

c.—Photograph of a female *Chelonia mydas* bearing a monel metal tag on the base of the trailing edge of the right fore flipper.

PLATE 8

a.—Photograph of a portion of the turtle hatchery on Talang Talang Besar Island, Sarawak. Four of the wire enclosures contain hatchling turtles which emerged during the preceeding night.

b.—Photograph of a ghost crab, *Ocypoda ceratopthalma*, at the entrance to its burrow, feeding on a hatchling *Chelonia mydas*. Carapace of the crab measured 45 mm. across.

c.—Photograph of an adult female *Chelonia mydas* with amputated left hind limb and pygal carapace damage, presumed to be results of shark attacks. Turtle's carapace measured 91 cm. across.

PLATE 9

a, & b.—Photographs of the stomach contents of a large tiger shark (*Galeocerdo* sp.) caught off Talang Talang Besar Island, Sarawak. Plate a shows remnants of fore and hind flippers; Plate b shows fragments of heads of sea turtles as well as other food items.

c.—Photograph of encrusting barnacles, *Chelonibia testudinaria* (Linn.) from carapace of *Chelonia mydas*.

PLATE 10

a, b, & c.—Photographs of burrowing barnacles (*Stephanolepas muricata* Fisher) from *Chelonia mydas*. Plate a shows a portion of a turtle's carapace with groups of embedded barnacles. Plate b shows a dorsal view of a stalked tumour mass containing barnacles. Plate c shows barnacles dissected out. Openings of barnacle tubes measured from 8 to 10 mm. in diameter.