The Hatching and Emergence of Loggerhead Turtle (Caretta caretta) Hatchlings

Spring 1981

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THE HATCHING AND EMERGENCE OF LOGGERHEAD TURTLE (Caretta caretta) HATCHLINGS

BY

RICHARD J. DEMMER
B.S., Florida Technological University, 1976

THESIS

Submitted in partial fulfillment of the requirements for the degree of Master of Science: Biological Sciences in the Graduate Studies Program of the College of Arts and Sciences at the University of Central Florida; Orlando, Florida

Winter Term
1981
Loggerhead turtle (Caretta caretta) eggs were collected at the time of laying during the summer of 1977 on the beaches of Canaveral National Seashore and the Merritt Island National Wildlife Refuge in Brevard County, Florida. The eggs were placed in sand-lined buckets and maintained at ambient temperature in a house trailer hatchery. After 50 to 55 days of incubation whole or partial clutches were transferred to glass observation containers and covered to a depth of 20 cm.

Hatching and emergence behavior were visually observed and activity was timed on an event recorder that was activated by four motion switches placed within or above the clutch. Pipping of the eggs occurred at a mean of 60.5 days after egg deposition. Emergence occurred at a mean of 61.8 hours after pipping and 63.1 days after egg deposition. The hatching and emergence sequence was described. It was concluded that hatching and emergence were socially facilitated. A mechanism for socially facilitated hatching was proposed. Volumetric reduction of the nest before or during pipping was described. Emergence may be inhibited by rising temperatures in the morning and stimulated by falling temperatures within a certain range at night. Social facilitation, in addition to the obvious value of providing a means for reaching the surface, was apparently advantageous to hatchlings as they emerged and raced towards the surf en masse. Under these conditions predators are likely to be less efficient than they would be if hatchlings emerged singly.
ACKNOWLEDGEMENTS

I wish to thank Dr. Llewellyn M. Ehrhart, my graduate committee chairman for his encouragement and financial support through NASA contract No. NAS 10–8986. Thanks are also due to the other members of my graduate committee, Drs. David T. Kuhn, Peter C. H. Pritchard, I. Jack Stout and Henry O. Whittier for their advice, concern and review of my work. Very special thanks go to Gay Z. Shiver for her patience, encouragement and for typing my first draft.
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INTRODUCTION

With the possible exception of the geckos in the subfamilies gekkoninae and sphaerodactylinae (Bustard, 1968), reptiles have not evolved a cleidoic egg similar to that of birds. The eggshell of both calcareous-shelled eggs, as in the crocodilians (Bustard, 1971), and parchment-shelled eggs, as in most other reptiles (Packard et al., 1977), are permeable and allow the free exchange of moisture between the egg and the environment. This condition restricts reptiles to nesting in locations with the proper moisture balance. For this reason the eggs of many lizards and snakes are laid in such damp places as under rocks or in decaying vegetation. Some reptiles, especially lizards, dig burrows in which to lay their eggs. Aquatic reptiles must lay their eggs in a site which is dry enough to insure that the embryos do not suffocate but damp enough to keep them from dehydrating. For marine turtles the only place available is on a beach.

Parental care varies among reptiles. The Nile crocodile (Crocodylus niloticus), which guards its nest, responds to the croaks of the hatchlings by digging into the nest to help them escape (Bellairs, 1970). Skinks in the genus Eumeces (Noble and Mason, 1933) and the Indian brooding python (Python molurus bittatus) (Bellairs, 1970) brood their eggs. Most reptiles exhibit little parental care, however, other than to disguise the nest upon leaving it. All turtles are among this group (Pritchard, 1979). Yet
turtles and especially marine turtles are exposed to extraordinary hazards. Heavy predation of nests (Routa, 1967) and hatchlings (Carr, 1967), and inundation of the nest by rain (Ragotzkie, 1959), and high spring tides (Bustard and Greenham, 1968) are among the dangers marine turtle nests and hatchlings face. This may be one of the reasons that most marine turtles lay 100 eggs or more (Carr, 1967).

The escape from the nest is probably more difficult for marine turtle hatchlings than it is for the hatchlings of any other reptile. The nest may be up to a meter deep for the leatherback turtle, Dermochelys coriacea (Hendrickson and Winterflood, 1961). The hatchlings of other turtles emerge individually but the nests are not as deep and they are equipped with claws that enable them to dig. Marine turtles, with their pliable flippers and deep nests, would have a difficult time emerging alone. It may well be that social facilitation, a mechanism whereby the risk of mortality is reduced through the combined efforts of the hatchlings as they hatch and escape the nest, developed in marine turtles as a response to the myriad of difficulties with which the hatchlings must deal.

The life cycle of marine turtles after embryological development may be divided into several developmental stages ranging from hatchling to adult. Each stage has a distinct set of behavioral patterns. The hatchling developmental stage can be subdivided into three substages: (1) the social facilitation substage (Carr and Hirth, 1961), (2) the frenzied substage (Carr, 1967; Frick, 1976; Mrosovsky, 1980), and (3) the passive drift substage (Fletemeyer, 1978; Witham, 1980). The present study deals with the social facilitation substage of
loggerhead turtle development. Early studies of loggerhead turtle hatchlings centered on the frenzied substage (Hooker, 1911; Parker, 1922) in which hatchlings, having emerged, raced in a frenzied manner across the beach and into the surf. Later studies dealt with the physical dimensions and condition of the hatchlings (Hughes et al., 1967). Caldwell (1959) recorded nest depths and days to emergence; and stressed the importance of nocturnal emergence. Caldwell also expressed an awareness of a socially facilitated emergence mechanism with the following sentence. "Those climbing up first loosen the sand and make the way easier for the last to hatch." Hendrickson (1958) shed light on the subject when he wrote of green turtles (Chelonia mydas) that, "...emergence was due to negative geotropism and sporadic movements of the hatchlings." Carr and Ogren (1959) made further observations of emerging hatchlings by placing a pane of glass in the side of a leatherback turtle nest. Carr and Ogren (1960) used the same technique to observe the nest of a green turtle. In the most thorough study of marine turtle hatchling emergence to date, Carr and Hirth (1961) demonstrated the advantage of social facilitation in the green turtle. They placed groups of one to ten eggs in simulated nests and then recorded the percent emergence of each. The concept of social facilitation was carried one step farther by Bustard (1972) when he concluded that synchronized hatching also demonstrated social facilitation.

Ehrenfeld (1979) provides a short review of the social facilitation of hatchling emergence. He concluded, "...it is likely that the main advantage to having more than one hatchling in close
contact is the mutual stimulation and reinforcement of the frenzied activity that is necessary to escape the nest."

Another aspect of hatching and emergence behavior is in relation to temperature. Bustard (1972) found that as a result of metabolic heat production, temperatures near the center of a nest were slightly higher than those on the periphery. Mrosovsky and Yntema (1979) found that a rise of one degree centigrade in mean incubation temperature caused a five day reduction in incubation time in loggerhead and green turtles, yet hatching has been found by Caldwell (1959) and Bustard (1972) to be simultaneous. Bustard (1972) believed that the movements of the more advanced embryos caused the less advanced ones to accelerate development.

Nocturnal emergence is also temperature related. Thermal inhibition of emergence was suggested for loggerhead turtles by Caldwell (1959), and for green turtles by Hendrickson (1958), Carr and Ogren (1960), Bustard (1967) and Mrosovsky (1968). Mrosovsky (1968) believed that photic inhibition above 28.5 degrees centigrade kept green and hawksbill turtle hatchlings from emerging during daylight hours. Mrosovsky (1980) makes no mention of this theory but suggests that a negative thermotaxis contributes to nocturnal emergence.

In this study, loggerhead hatching and emergence are described in detail. Several specific problems are also considered: (1) a mechanism for socially facilitated hatching; (2) volumetric reduction of the nest during hatching; (3) the role of hatchlings during emergence; (4) thermal inhibition of activity; and (5) the advantages
of socially facilitated emergence.
MATERIALS AND METHODS

Collection, Care, and Transfer of Egg Clutches

Loggerhead turtle eggs used in this study were collected between 2 and 25 June 1977 on the beaches of Canaveral National Seashore and the Merritt Island National Wildlife Refuge, both located in Brevard County, Florida (Figure 1).

Eggs were collected immediately after they were laid and placed into buckets of sand. Later that night the buckets were transported to a hatchery located in a house trailer (2.4 X 12.2 m) which was not air-conditioned. Two sizes of plastic buckets were used. One was 61.0 cm in diameter and 30.5 cm deep while the other was 25.4 to 30.5 cm in diameter and 30.5 cm deep. These buckets had several holes cut into the bottom to allow liquid to drain. The eggs were insulated from the side and bottom of the buckets by 3.0 to 6.0 cm of sand. Some clutches which were incubated in the smaller buckets were divided between two or three buckets as needed to hold the eggs conveniently. The buckets were occasionally sprinkled with water to keep the sand moist but not saturated.

The eggs were kept in the hatchery for 50 to 55 days, at which time they were transferred to observation containers. These containers were constructed from styrofoam coolers (Figure 2). One end was cut off and a plate of glass backed with red acetate was placed on top and taped into place. A series of holes was cut into the end of the
Figure 1. Clutches were collected in the area between the arrows.
Figure 2. Observation container assembly.
cooler which would serve as the bottom. The top of the cooler was made into a door which when taped shut, acted both to insulate the front and exclude light. Seven of these containers were constructed.

Care was taken during the transfer of eggs to the observation containers not to rotate or jolt them. Clutches or partial clutches ranging from 35 to 113 eggs were placed in the containers so that some of the eggs were next to the glass. The clutch was covered with 20 cm of sand.

Motion Switches: Construction and Installation

Motion switches were constructed (Figure 3) using the materials in Table 1 as follows: A 3.0 mm loop was made in the end of a 12.0 cm piece of 20 gauge zinc wire, and the wire was bent at a 90 degree angle 6.0 mm from the distant end of the loop. The other end of the wire was wrapped one time around a machine screw and secured with a nut. Ten centimeters of a 25 cm piece of insulated 24 gauge steel wire was stripped, and the stripped end was threaded through the loop in the first wire. A BB splitshot sinker was attached to the very tip of the stripped end. At a point 13 cm from the weighted tip of the steel wire, it was wrapped halfway around the machine screw and a washer was placed over it. A nut was screwed on but not so tightly that it could break the insulation on the steel wire. A number seven cork was drilled with a 0.318 cm drill bit, and the screw was placed through the hole with the head at the small end. A washer was placed on the end of the screw. About 1.3 cm of an 8.0 cm piece of insulated steel wire was stripped and the stripped end was wrapped one time around the end of the machine screw. Another washer was added, and then a nut
Figure 3. Motion switch assembly.
Table 1. The materials needed to construct a motion switch.

<table>
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<tr>
<td>15 milliliter test tube</td>
<td>1</td>
</tr>
<tr>
<td>Number 7 cork</td>
<td>1</td>
</tr>
<tr>
<td>0.397 x 3.387 centimeter machine screw</td>
<td>1</td>
</tr>
<tr>
<td>0.476 centimeter flat washer</td>
<td>3</td>
</tr>
<tr>
<td>0.476 centimeter hexagon nut</td>
<td>3</td>
</tr>
<tr>
<td>24 gauge insulated steel wire, 25 cm in length</td>
<td>1</td>
</tr>
<tr>
<td>24 gauge insulated steel wire, 8 cm in length</td>
<td>1</td>
</tr>
<tr>
<td>20 gauge uninsulated zinc wire, 12 cm in length</td>
<td>1</td>
</tr>
<tr>
<td>BB splitshot sinker</td>
<td>1</td>
</tr>
<tr>
<td>Electrical tape</td>
<td></td>
</tr>
<tr>
<td>Rust resistant paint</td>
<td></td>
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was used to secure the screw and wire to the cork. A slot was cut down one side of the cork and the first steel wire was pressed into it. The zinc and the weighted steel wire were adjusted so that they went straight away from the cork, so that when held horizontally, the steel wire did not touch the side of the loop while the apparatus remained motionless. The cork was then placed tightly in the end of a 15 ml test tube and was sealed with electrical tape. The cork, the end of the screw, and the tape were then sprayed with a rust resistant paint. Several coats were applied to assure that no moisture would enter and corrode the connections. The loose ends of the wires were then stripped and later connected to the Esterline-Angus event recorder. These connections were protected with electrical tape.

Four motion switches were placed in the observation container as follows: One was placed in the center of the clutch, one at the top of the clutch, one 10.0 cm above the clutch, and one suspended at about 5.0 mm above the sand surface.

**Recording Apparatus**

The Esterline-Angus event recorder was connected as shown in Figure 4. Since the recorder used only a 12 volt current, an automotive battery was used to power it. This battery was kept continuously charged with a battery charger.

The observation containers were set on 5.0 X 10.0 cm pieces of lumber to allow free drainage and to discourage insects from entering the container through the drain holes.

**General Methods**

When observation commenced, the activity of the hatching and
Figure 4. Monitoring apparatus.
emerging hatchlings was recorded on the event recorder on chart tapes lined at five minute increments. Activity spikes were summed for each one hour time period. The number of days on which activity occurred within each hatchling group, during any given hourly period, was totaled for all hatchling groups (clutches). A three point moving average of the number of activity spikes per hourly period divided by the number of hours of activity per hourly period was calculated. The results were standardized by dividing all values by the highest value.

The clutches were also observed through the glass fronts of the containers for pipped eggs. After hatching the behavior of the hatchlings was observed in the same manner. Carr and Ogren (1960) observed green turtle hatchlings through a glass sided nest. They felt that light entering the nest during daylight hours inhibited hatchling activity. Hooker (1911) after several uncontrolled experiments concluded that loggerhead turtles were sensitive to blue light. Though no studies have been performed to determine the sensitivity of loggerhead turtles to various wave lengths of light, several reports indicate that green turtles are sensitive to light of the shorter wave lengths (Mrosovsky and Carr, 1968; Mrosovsky and Shettleworth, 1968; Ehrenfeld, 1968; Granda and Haden, 1970; Mrosovsky, 1972). In view of the similarity in marine turtle behavior it seems reasonable to assume that sensitivity of loggerhead turtles to light is similar to that of green turtles. Ehrenfeld and Carr (1967) found that peak sensitivity for green turtles was between 490 and 600 nm. Ehrenfeld (1968) found that the limits to light sensitivity in the green turtle to be 350 and 650 nm. Light transmitted by the red acetate used in the
observation containers was measured by a Tektronix rapid scan spectrometer. No light was transmitted between 420 and 580 nm (Figure 5). No behavioral change was noted when the door of the observation container was opened during the day or when an artificial light was used at night.

Sand temperatures were taken to establish the pattern of temperature fluctuations above the nest. Between 2 and 5 August 1977, temperatures were taken at a depth of 20 cm in two observation containers. These temperatures were to be taken hourly, but due to the tight schedule of observations and logistics there were two gaps (Figure 6). Supplementary temperatures were taken during the day on 6 July 1980 on the beach at Canaveral National Seashore. The average of temperatures collected at night between 12 July and 5 August 1976 on the beaches of the Merritt Island National Wildlife Refuge Canaveral National Seashore were also added to the graph (L. M. Ehrhart, personal communication). The temperatures taken on the beach fit well with those measured in the observation containers and together they gave a more complete picture of temperature fluctuations at the depth measured.

On the evenings after emergence between 18:00 and 20:00, hatchlings were taken to a site on the beach at the Merritt Island National Wildlife Refuge. They were released about ten meters from the surf. This allowed room for behavioral observations to be made as the hatchlings made their way to the surf.
Figure 5. Green turtles show no sensitivity to the wavelengths of light between the dotted lines. This is superimposed on the transmittance of the red acetate used in the observation containers.
Figure 6. The solid lines indicate temperatures taken at a depth of 20 cm within the observation containers between 2 and 5 August 1977. The dotted lines indicate temperatures taken during July and August at a depth of 20 cm on the beaches of Canaveral National Seashore and the Merritt Island National Wildlife Refuge.
RESULTS

General

The timing of the daily activity pattern of the hatchling mass at a depth of 10.0 cm or greater is shown in Figure 7. Shown in Figure 8 are the times of pipping, intense post hatching activities at a depth of less than 10.0 cm and the emergence times. It was apparent that although some activity occurred throughout the day, activity was most intense during the late afternoon and evening.

Hatching

The first indication that hatching had begun was a single spike on the event recorder chart registered by the motion switch placed within the clutch. On the five occasions when immediate examination of the clutch was possible, one or more pipped eggs were visible through the glass front of the observation container. The mean number of days elapsed between egg deposition and hatching was 60.5 (Figure 9).

The times when eggs first began to pip for 15 clutches are plotted in Figure 8. There was no apparent pattern for hatching related to temperature. After pipping a hatchling would lie in the eggshell with one or both front flippers protruding. It remained in this position for up to 26.6 hours (Figure 10). During this quiescent period the hatchling's shell began to straighten and harden. Most pipping was concentrated within a few hours. In clutch A3142 this period lasted for three hours and in A3158 it lasted for one half hour.
Figure 7. An index of daily activity patterns is shown here. Only hatching and posthatching activity that occurred at a depth of ten centimeters or greater was used to formulate the graph. Note that activity peaks at about 20:00 hours.
Figure 8. The average daily temperature fluctuations at a depth of 20 cm for July and August are shown. Below that curve are plotted the emergence times for 19 clutches, the first observation of intense posthatching activity for 15 clutches and the hatching times for 15 clutches.
Figure 9. The number of days from egg deposition to pipping. The mean is indicated by the horizontal line, the range by the vertical line and the standard deviation by the box. The number above the vertical line is n.
Figure 10. The number of hours which hatchlings of five clutches remained quiescent.
As the eggs collapsed, the cavity ceiling lost its support and eventually a cone shaped segment fell, creating a new cavity above the nest (Figure 11). This was observed to occur in all clutches. It always occurred before the hatchlings crawled from their eggshells to begin moving upward in their first display of negative geotaxis.

Emergence

The first upward movement was necessarily individual since the hatchlings were separated from one another by their eggshells and fallen sand, but it was not difficult for them because the sand was loosely scattered over the eggs. It took several hours for the hatchlings to gather in the cavity above the nest. The length of time required for this was not determined since hatchlings often approached the cavity from points not visible through the glass front. Also, by that time motion switches in and just above the clutch were tightly packed in sand and eggshells. Single stragglers could not stimulate the switches to cause a spike on the event recorder chart.

Once the hatchlings had gathered above the nest, activity seemed to be more responsive to temperature. Intense activity was restricted to the evening hours between 18:00 and 24:00 (Figure 8). Only one observation contradicted this pattern. A3177 became very active at about 09:00 on 3 August. Although it was a cloudy day, there were other cloudy days, but no other group of hatchlings showed intense activity except in the evening.

As the hatchlings continued to move upward, they scraped the ceiling with their front flippers, sand fell and was pushed downward by other hatchlings attempting to move upward through the mass. As
Figure 11. Pictured is the period after volumetric reduction has occurred and when the hatchlings have begun to climb individually to the new cavity created when a cone-shaped segment of the ceiling fell.
sand from the ceiling was added to the floor, the cavity moved upward.

When the hatchlings had arrived at a point just below the surface, the sand seemed to boil with spasms of activity that came at intervals of about one minute and lasted about five seconds. Such spasms were carefully observed in clutches U1, A3149, A3154, and A3144. They were noted to occur in six others. In clutch A3149 this behavior was occurring when observation commenced at 18:45 on 9 August. It continued until 20:44, at which time the hatchlings emerged. During this behavioral phase some of the topmost hatchlings were seen to raise their heads above the sand. These hatchlings then ceased activity. Though they remained motionless they were often lifted completely out of the sand by the hatchlings beneath them. Emergence came when one of those hatchlings, with its head or complete body out of the sand, simply crawled away. When it did all those in the group beneath it followed. The emergence times for 19 clutches are plotted in Figure 8. The mean number of days elapsed between egg deposition and emergence was 63.1 (Figure 12). The mean number of hours elapsed between pipping and emergence was 61.8 (Figure 13).

When released on the beach the hatchlings had no further use for geotaxis or social facilitation. As they moved down the beach toward the surf, they followed slightly different paths that caused them to spread out across the beach. Their orientation appeared to be visual as they moved around objects without hitting them and often turned a little north where the last rays of the sun were sometimes visible.
Figure 12. The number of days from egg deposition to emergence.
Figure 13. The number of hours from pipping to emergence.
DISCUSSION

General

Studies of green turtles (Hendrickson, 1958; Carr and Ogren, 1960; Carr and Hirth, 1961; Bustard, 1967; 1972; Mrosovsky, 1968), leatherback turtles (Carr and Ogren, 1959; Hendrickson and Winterflood, 1961), hawksbill turtles (Mrosovsky, 1968) and loggerhead turtles (Caldwell, 1959) indicate that hatchling behavior while escaping the nest is similar for most species of marine turtles.

The incubation and emergence times for loggerhead turtles in this study and the study by Caldwell (1959) are similar to the incubation and emergence times of other species of marine turtles (Hendrickson, 1958; Carr and Ogren, 1959; 1960; Hendrickson and Winterflood, 1961; Bustard, 1972). It has been shown that incubation time for green and loggerhead turtles is dependent on incubation temperature (Mrosovsky and Yntema, 1979). In a review of marine turtle reproductive biology, Hirth (1980) pointed out that incubation time for marine turtles is generally shorter than for other turtle species. A comparison of all known incubation times of all genera of marine turtles listed by Hirth indicated a median of about 60 days.

A Mechanism for Socially Facilitated Hatching

Mrosovsky and Yntema (1979) showed that the length of incubation decreased five days for every one degree centigrade rise in mean incubation temperature. Results by McGehee (1979) support this
finding. Since eggs on the periphery of the clutch are incubated at a slightly lower temperature than those near the center, due to metabolic heating, it seems likely that they would hatch several days later than those at the center (Bustard, 1972). My observations, those of Caldwell (1959) and Bustard (1972), indicate that hatching is simultaneous. A mechanism may exist which allows eggs incubated at slightly different temperatures to hatch simultaneously.

Bustard (1972) hypothesized that waves of movement, produced by the more advanced embryos, stimulate the less advanced embryos to increase their rate of development. To test this he divided a clutch of green turtle eggs into three equal groups. One was incubated at the temperature found at the center of a nest. The other two were incubated at the temperature found at the nest periphery. One of the latter was subjected to periodic pressure from a mechanical prodder, beginning ten days prior to the predicted hatch date. The unprodded portion which was incubated at the temperature found at the nest periphery hatched four or five days after the portion incubated at the higher temperature. The prodded portion hatched only one day after the portion incubated at the higher temperature. With this experiment, Bustard clearly showed that movement of the embryos can cause earlier hatching, but he did not prove that the rate of development of the less advanced embryos is increased.

The following observations support an alternate hypothesis. Kraemer and Richardson (1979) believed that embryonic development ends five to ten days before hatching. If that assumption is true then some turtles might spend more time within the egg after embryological
development than others, thereby accounting for the fact that some hatchlings had already internalized the yolk sac while others had not. Those that had not, may have been the less advanced embryos referred to by Bustard (1972). Just before hatching the embryos increase activity (Bustard, 1972). Decker (1967) showed that this also occurred in the snapping turtle (Chelydra serpentina). I also observed movement in the eggs in the days just before hatching.

An alternate hypothesis is that when marine turtles reach the end of embryological development, they can be stimulated to the intense activity necessary for pipping, but they are not inclined to be active without stimulation. Individual turtles become increasingly active for several days after the end of embryonic development. As more embryos reach full term and are stimulated by the more advanced turtles, activity becomes more widespread and more intense. When pipping occurs the hatchlings that are less advanced have not internalized their yolk sac, but do so in the quiescent period immediately following pipping.

Volumetric Reduction of the Nest

At about the time of hatching, marine turtle nests undergo a volumetric reduction. Hendrickson (1958) and Carr and Hirth (1961) found that this reduction occurs when the nest contents change from spherical eggs with interstices, to a more compact configuration of flattened eggshells and elongate hatchlings. When this change occurs the ceiling loses its support and eventually caves in. Kraemer and Richardson (1979), found that most volumetric reduction occurs before hatching when the eggs undergo a rapid
evaporative water loss. McGehee (1979) found that when eggs were incubated in sand 50% saturated with distilled water, there was no weight loss before hatching, but at 25% saturation, a weight loss occurred. Packard et al. (1977) noted that most studies of parchment type eggs in which water gain or loss is reported do not indicate the water potential of the incubating substrate. With further investigation it may be found that the time of volumetric reduction is variable and dependent on the nest environment. The actual time of volumetric reduction is probably not important as long as it does not occur early enough to allow additional packing of sand in the nest before hatching. This would hamper the emergence because hatchlings are dependent upon the space provided by volumetric reduction to maneuver, especially just after hatching, as they struggle individually through the eggshells and sand to congregate above the nest. I made no attempt to determine when volumetric reduction occurred, but it is my belief that very little occurred as a result of evaporative water loss before hatching. In one case I examined eggs on the day before hatching and found them turgid.

The Role of Emerging Hatchlings

Hendrickson (1958) described the upward movement during emergence as being the result of negative geotropism and the sporadic movements of the hatchlings. In 1960, Carr and Ogren played down the role of negative geotropism, saying that the hatchlings' emergence could not be attributed to that alone. Carr and Hirth (1961) describe the ascent as "...a witless collaboration and a loose sort of division of labor in which the turtles on top scratch down the ceiling,
those on the sides undercut the walls, and those on the bottom pack down the filtering sand and initiate spasms of activity as they become restless. These observations of green turtle hatchlings resemble closely the observations made on loggerhead turtle hatchlings in this study. It was apparent that the same mechanism described by Carr and Hirth (1961) also occurs in loggerhead turtles, but it was also apparent that negative geotaxis is the underlying behavior that unites the hatchlings and that the so called, "loose division of labor", is just the result of hatchlings doing the same thing in a different place: that is, those on top in their upward quest cause the ceiling to fall while those on the sides undercut the walls and those on the bottom may initiate spasms of activity as they try to climb upward through the mass of hatchlings.

**Thermal Inhibition of Activity**

Temperature fluctuations at a depth of one meter are minimal but they increase steadily as the surface is approached (Hendrickson, 1958; Carr and Hirth, 1962). For this reason hatchlings are exposed to greater temperature extremes and longer periods of high temperature as they near the surface. Bustard (1967) found that green turtle hatchlings cease activity at around 33 degrees centigrade. If loggerhead turtle hatchlings have a similar thermal limit to activity, it is not surprising that emergence is nocturnal since surface temperatures rise rapidly and remain above 33 degrees centigrade for most of the daylight hours (McGehee, 1979). In this study hatchlings began their upward movement at about 20 cm below the surface. At this depth it is not unusual for temperatures to fluctuate five or six
degrees centigrade (Figure 6). In view of this it is not surprising that loggerhead turtle hatchlings were found to have a marked daily activity pattern (Figure 7). Had nests been buried at a greater depth, the activity during early posthatching might have been more constant. Figure 7 indicates that some activity took place throughout the day but was greatest during the evening hours before midnight. The switches which recorded the data used to generate Figure 7 were all located at a depth of ten cm or greater and the most intensive posthatching activity occurred within ten cm of the surface. It can be seen in Figure 8 that intense posthatching activity and emergence occurred between 18:00 and 01:30. This supports observations by Hendrickson (1958), Caldwell (1959), Bustard (1967; 1972) and Mrosovsky (1968; 1980) that emergence is generally nocturnal. It is of interest to note that emergence (Figure 8) of loggerhead turtle hatchlings in this study did not occur after 01:30. At this time temperatures were still falling. It seems likely that a lower thermal limit inhibits emergence during the predawn hours but there is no other report of this. Such a limit might keep hatchlings from emerging just after dawn when temperatures are low but when daylight would expose the hatchlings to avian predators. Later in the morning, temperatures reach the same range at which hatchlings emerge during the evening but there were no daytime emergences in this study and they are reported in the literature as being rare (Bustard, 1967; Mrosovsky, 1968). Mrosovsky (1980), referring to his work with green and hawksbill turtles, suggests that a negative thermostaxis keeps hatchlings from emerging during the morning. This is unlikely as hatchlings make no
effort to move away from the warm sand above, instead they become inactive. It is possible that Mrosovsky was referring to inhibition by rising temperatures. The results presented in Figures 7 and 8 support this possibility but also support the possibility that hatchlings are stimulated by falling temperatures. If this is true it is apparent in Figure 8 that both upper and lower thermal limits would curtail activity, insuring against emergence just before dusk and just after dawn. All of the mechanisms just discussed may have some part in the assurance of nocturnal emergence.

The Advantages of Social Facilitation

The most obvious advantage of social facilitation is that hatchlings need each other's help to reach the surface. Carr and Hirth (1961) reburied from one to ten eggs in simulated nests. Of 22 eggs buried singly only six hatchlings emerged. In the 23 simulated nests with eight to ten eggs per nest, emergence was 100%. Ehrenfeld (1979) stated, "...it is likely that the main advantage of having more than one hatchling in close contact is the mutual stimulation and reinforcement of the frenzied activity necessary to escape the nest." While escaping the nest may be the most important function of social facilitation, there is another benefit not realized until after emergence. The hatchlings which have little chance of escaping the nest alone also have little chance of escaping predation on the beach or in the surf. Carr (1967) refers to the rapidity with which hatchlings erupt from the nest and cross the beach to the surf. Bustard (1972) observed that on Heron Island, Australia, the rookery produced more hatchlings per night than the carnivorous fish could eat. Holling (1959) found
that a predator searching randomly for prey is more efficient if the prey population is dense. Although this sounds somewhat contradictory it is not. When hatchlings emerge they spread out as though each one was oriented in a slightly different direction. A compromise is made. A predator on the beach, happening onto a group of hatchlings must take a few steps between each capture. At the same time the hatchlings are rapidly moving toward the surf. As the predator handles individuals, the remaining hatchlings are moving into the surf and safely away from terrestrial predators. The hatchlings swim straight into the surf (Frick, 1976). Their frantic swimming and spreading probably minimizes the losses again as the aquatic predators in the surf dart back and forth capturing as many as possible before the hatchlings have passed through the surf zone and dispersed.
Hatching was found to occur at any time, regardless of time or temperature. Hatching was found to occur almost simultaneously and was believed to be socially facilitated. It was hypothesized that embryos which reach the end of development first become increasingly active over a period of several days before hatching. As these unhatched turtles become more active those just reaching the end of embryological development are stimulated to become active. When all embryos have reached the end of embryological development, activity is most intense and pipping occurs. The mean number of days elapsed between egg deposition and pipping was found to be 60.5. After pipping the hatchlings lie quiescent for up to 26.6 hours while their shell straightens and begins to harden. At about the time of hatching volumetric reduction of the nest occurred. Afterwards a cone-shaped segment of the nest cavity ceiling fell over the eggs and hatchlings. The hatchlings exhibited negative geotaxis as they climbed individually through the eggshells and fallen sand to the cavity above the nest which was created when volumetric reduction occurred and as they continued to the surface. Social facilitation proceeded in a manner similar to that described for green turtles by Carr and Hirth (1961). The top hatchlings scraped the ceiling with their front flippers causing sand to fall. The sand filtered down, facilitated by hatchling activity. As sand was removed from the ceiling and added to the floor
the cavity moved upward. The activity of the hatchlings was found to be most intense between 18:00 and 24:00. Activity at a low level occurred throughout the day. Emergence occurred as the temperature was falling. It was suggested that there is both an upper and lower thermal limit to post hatching activity. It was hypothesized that hatchling emergence was inhibited by rising temperatures in the morning and stimulated by falling temperatures within the range where emergence has been observed. When loggerhead turtle hatchlings reached a point just below the surface the sand seemed to boil with their activity. Some of those on top raised their heads above the sand. When they did this they immediately ceased activity. As those hatchlings below continued to be active, the group rose higher. Those quiescent hatchlings on the surface were sometimes raised completely out of the sand. Emergence came when one of those top hatchlings simply crawled away. When that happened all those below followed. The mean number of days between egg deposition and emergence was 63.05 with a range of 61.2 to 67.8 days. The mean number of hours between pipping and emergence was 61.8 with a range of 29.3 to 133.8 hours. It was concluded that the main advantage of socially facilitated emergence is that it is necessary because hatchlings are not able to emerge alone. It was believed that another advantage is that hatchlings emerging simultaneously have a better chance because under those conditions predator efficiency is reduced. If hatchlings emerged singly, the predators could capture each one as it did, but when hatchlings emerge simultaneously, each predator can only capture a few before they have passed through the surf zone and dispersed.
LITERATURE CITED


