

Chapter 8

Nest Site Selection, Oviposition, Eggs, Development, Hatching, and Emergence of Loggerhead Turtles

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As with all sea turtles, the production of the next generation of loggerhead turtles results from a synergism of the effects of the ecological conditions in the foraging area on the energetics of the female parent and of beach environmental conditions on development of the embryos. To be successful, reproduction must occur when environmental conditions support adult activity (e.g., sufficient quality and quantity of food in the foraging area, suitable beach structure for digging, nearby interesting habitat) (Georges et al. 1993). Further, the environmental conditions of the nesting beach must favor embryonic development and survival (i.e., modest temperature fluctuation, low salinity, high humidity, well drained, well aerated; Mortimer 1990, 1995). Additionally, the hatchlings must emerge to onshore and offshore conditions that enhance their chance of survival (e.g., less than 100% depredation, appropriate offshore currents for dispersal) (Georges et al. 1993).

General Reproductive Cycle and Nesting Distribution

All marine turtles prepare for reproduction in their foraging areas during the period (usually several years) before they migrate, at least short distances, to mating areas. The mating period precedes nesting and may last more than six weeks. After several weeks of mating, the males return to their foraging areas, and the females proceed to the nesting areas (Limpus 1985; Limpus and Miller 1993; Miller 1997). After producing several clutches of eggs during a reproductive period of several months, the females return to their feeding areas to recover from the effort of reproduction and migration. Following a quiescent period lasting a few to several years, females migrate to the mating areas, and the cycle continues (Limpus 1985; Limpus and Miller 1993; Miller 1997; Owens et al. 1989).

The cycle of energy accumulation, deposition, reorganization, and utilization in the foraging areas that support reproduction by loggerhead turtles has not been studied in detail; however, studies of other marine turtles provide the information for a general account. Following its reproductive effort, the female returns to the foraging area, where she is reproductively quiescent over a variable period of years (one to several years), and during this time she accumulates the energy to support her next reproductive effort (vitellogenesis, migration, egg production, oviposition, and return migration). Neophyte breeders are already in their foraging areas, having completed puberty (Limpus 1990). Only when the right mix of endogenous (e.g., hormone levels and/or fat reserves) and exogenous (e.g., photoperiod) factors interact (Licht 1980; Licht et al. 1982; Owens 1980; Wibbels et al. 1990, 1992) does vitellogenesis begin. Vitellogenesis requires 10–12 months for completion. The duration of each phase in the foraging area depends, in part, on the quality and quantity of food available (Bjorndal 1997). Loggerheads are carnivorous, feeding mainly on benthic invertebrates, especially mollusks (see Table 28 in Dodd 1988). Although the timing of reproduction in herbivorous green turtles has been linked to fluctuations in major weather patterns (Limpus and Nicholls 2000), reproduction in carnivores (e.g., loggerheads) does not appear to have a direct connection to climate fluctuations (Limpus and Miller 1993).

The loggerhead turtle is the exception to the tropical nesting pattern exhibited by the other sea turtles (Gasperetti et al. 1993; Hirth 1997; Limpus et al. 1988; Marquez 1994; Marquez et al. 1976; Sternberg 1981; Witzell 1983). The major portion of loggerhead nesting occurs in warm temperate and subtropical areas, with the exception of Masirah Island, Oman, (Gasperetti et al. 1993; Ross and Barwani 1995), several small nesting aggregations in the Caribbean (Dodd 1988) and minor, scattered nesting locations elsewhere in tropical areas (Dodd 1988). The nesting aggregation at Masirah Island is located inside the tropics, but its use is consistent with the general pattern of extratropical nesting by the species because the

upwelling from the cold Indian Ocean currents makes the area warm temperate to subtropical.

Loggerhead turtles spread their reproductive effort both temporally and spatially. Because they nest near or outside the tropics, loggerhead turtles must respond to a temporally limited nesting season. In the Northern Hemisphere the nesting season is between May and August, whereas in the Southern Hemisphere nesting occurs between October and March (Dodd 1988). The timing of nesting at specific sites may be more restricted, particularly toward the northern or southern extent of the nesting range. Spatial clumping occurs because loggerhead turtles concentrate their nesting at a few primary locations that are augmented by lower density, satellite nesting sites; in addition, a few isolated, low density nesting sites are known (Dodd 1988; Sternberg 1981).

Maturation, Courtship, and Mating

The straight carapace length of nesting loggerhead turtles ranges from approximately 70 to 109 cm (curved carapace lengths are slightly larger; see Table 7 in Dodd 1988). Minimum breeding size varies among populations of nesting loggerhead turtles and is not a good indicator of reproductive maturity because not all individuals begin to breed at the minimum size (Limpus 1985; Limpus et al. 1994). Individual turtles begin and finish puberty at different sizes (Limpus 1990); some individuals may be 10 cm or more longer than the minimum breeding size and still be immature or just starting puberty (Limpus et al. 1994). Based on gonad examination, the duration of puberty (morphological and functional maturation of the oviduct and ovaries or testis and epididymis) in loggerheads is on the order of 10 years for turtles in the western South Pacific (Limpus 1990).

After becoming reproductively ready, female and male loggerheads migrate from their foraging areas to copulate in the general vicinity of the nesting area (Limpus et al. 1992). Typically, female loggerhead turtles do not reproduce every year (Dodd 1988; Hirth 1980); however, male loggerheads may breed every year (Wibbels et al. 1990).

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Remigration intervals (period between reproductive seasons, *sensu* Limpus 1985) for loggerhead turtles vary from one to nine or more years (Dodd 1988; Limpus 1985), with the majority of females having two-, three-, or four-year cycles. The determination of the remigration interval for a population can be affected by the duration of the study, tag loss (Limpus 1992), partial coverage of a potential nesting area (Hughes 1982), long reproductively quiescent periods (Limpus 1985), or a change in annual survivorship that removes the turtles from the reproductive population.

Only a few studies provide the foundation for the current understanding of courtship and mating in loggerheads (Caldwell 1959; Caldwell et al. 1959; Ehrhart 1995; Limpus 1985; Wood 1953). Much more in-water observational research is needed to elucidate the details of the process. As with other species, the behaviors that comprise courtship are poorly described (Ehrhart 1995; Miller 1997). The few behaviors that have been recorded indicate that head movements, nuzzling/biting, or flipper movements, among others, may be used by the male to determine the receptiveness of the female. It is not known whether or not females exude a pheromone that signals her reproductive status, but field observations suggest this may be the case (Limpus, unpubl. observ.).

The male attempts to mount the female, while the female seemingly tries to avoid being mounted. Individuals may circle each other; the female may turn to face the male or attempt to leave the area while one or more males interact with her and each other. The female receives bites, mostly to her neck and shoulders, from the male before she is mounted. She also acquires damage to the shoulders of her carapace margin from the male's curved claws. The progressive healing of the mating damage during the nesting season indicates that mating occurs in the weeks just preceding the ovulatory cycle, and it follows that sperm are stored in the oviducts for use during the nesting season.

Insemination is achieved with the male's tail curled under the female's tail to bring the penis and cloaca into apposition. The penis is inserted into the female's cloaca, but details of this process are lacking. Mounting, and possibly

sperm transfer, may last for several hours, but the rate of transfer is not known. Data for green turtles suggest that the duration of penile insertion is related to the rate of fertilization, but this work was done in a captive situation and may not be completely applicable in the wild (Simon et al. 1975; Ulrich and Owens 1974; Witham 1970).

In the mating areas, mounted pairs are regularly seen at the surface of the water, but they may be seen anywhere in the water column. The male has little control of the position in the water because he uses his clawed front flippers to hang onto the carapace of the female; the female does the swimming and determines when the couple will surface for a breathe. The male may be able to influence the upward direction by raising his head and creating drag.

Philopatry and Nesting Site Fidelity

Philopatry (i.e., migration from nesting areas to foraging areas and return, *sensu* Carr 1975) among loggerhead turtles is relatively high. Based on returns of tagged turtles, for example, 1,404 of 1,433 loggerhead turtles (98%, data collected over nine seasons) were recaptured at the original tagging location in Australia (Limpus 1985). In Tongaland, South Africa, 93.1% (mode 800 m) and 91.1% (mode 400 m) returned to within 9.6 km of the original tagging site (Hughes 1974b). At Little Cumberland Island, Georgia, 51% (22 of 43) returned to within 16.6 km, 7% (3) returned to within 50 km, and 42% (18) returned at greater distances from the original tagging site (Bell and Richardson 1978). Besides being examples of philopatry, these data illustrate that thorough coverage of the local nesting site and adjacent areas is very important in obtaining appropriate data. Particularly in the Bell and Richardson study, coverage over distances greater than 50 km contributed valuable data on the distribution of nesting. More recently, genetic data have defined strong links between breeding turtles and the region of their birth (Bowen et al. 1993, 1994, 1995) rather than with the specific beach where hatching occurred.

Loggerhead turtles show a high degree of nesting site fidelity (*sensu* Carr 1975). Once it

has returned to the region of its birth and selected a nesting beach, a loggerhead turtle will tend to renest in relatively close proximity (0–5 km) during successive nesting attempts within the same and subsequent breeding season, although a small percentage of turtles will utilize more distant nesting sites in the general area (Bjorndal et al. 1983; Limpus 1985; Limpus et al. 1984a). Records of intra-seasonal nesting movements suggest that loggerhead turtles are capable of moving long distances but the proportion of individuals doing so is low (Limpus 1985). In general, loggerhead turtles return to the same beach to lay subsequent clutches following successful oviposition (Limpus 1985).

Nesting Site Selection

Typical loggerhead nesting beaches tend to be sandy, wide, open beaches backed by low dunes and fronted by a flat sandy approach from the sea, although specific characteristics vary from rookery to rookery. For instance, in South Africa loggerheads are found on beaches with adjacent reefs or rocky outcrops (Hughes 1974a, 1974b), while in the Mediterranean loggerheads emerge primarily on beaches fronted by mostly sandy areas (Le Vin et al. 1998). In Japan, an analysis of 300 nesting beaches revealed that of the 23 factors studied, the most important was the softness of the sand, followed by distance from the nearest human settlement (Kikukawa et al. 1998, 1999).

Once a female has selected a beach on which to lay her eggs, she must choose where on the beach to dig the nest. There are serious outcomes from this choice. For instance, the eggs must be placed far enough from the tidal zone to avoid being eroded or excessively washed by high tides, which may be lethal to the developing embryos (Whitmore and Dutton 1985). At the same time, the eggs must not be placed so far from the ocean that the emerging hatchlings are at a greater risk to land predators (Blamires and Guinea 1998) or are unable to find the sea due to visual obstructions (Godfrey and Barreto 1995).

The place where the eggs are deposited will determine the developmental microenvironment of the nest and can affect many characteristics of

the hatchlings, including hatching and emergence success, sex ratio, fitness, vulnerability to nest predators, and so on. Because the character of the beach, including elevation, temperature, moisture, and humus content, changes with distance from the sea (Spotila et al. 1987), there is ample opportunity for females to select a particular type of environment into which to deposit their eggs. The research challenge is to identify the characteristics of the beach to which the turtle is responding, positively or negatively, and which she is ignoring.

More is known about cues that discourage nesting than about those that encourage nesting, principally as a result of the number of studies conducted on urban or developed beaches. For instance, artificial lighting on the beachfront reduces the number of nesting loggerheads, relative to those on beach areas free of lighting (Ehrhart et al. 1996; Witherington 1992). In the Florida Keys, nesting turtles seem to avoid areas backed by tall Australian pines (*Casuarina* sp.) (Schmelz and Mezich 1988), while loggerhead nests on an urban beach in Boca Raton, Florida, tended to be clustered in front of tall buildings, possibly because their silhouettes block the artificial light of the city (Salmon et al. 1995). Smaller structures on the beach, such as exposed pilings used to counter erosion, result in lower numbers of clutches being laid (Bouchard et al. 1998), and sand introduced as part of beach “renourishment” programs can lower the number of successful clutches laid, due to increased compaction or hardness (Crain et al. 1995).

In the absence of disturbance, loggerhead turtles tend to lay their eggs in nonrandom patterns (Martin et al. 1989; Hays and Speakman 1993; Mellanby et al. 1998). The challenge has been to discover the forces behind the pattern of nesting site selection. In general, the methodology of these studies has been to look for correlations between successful nesting attempts and environmental measures (e.g., sand temperature or moisture content, slope, distance from the high tide line or the vegetation line, etc.). Interestingly, many of the studies focused only on successful nests, ignoring unsuccessful nesting attempts in which a female emerged onto a nesting beach but did not lay any eggs.

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Table 8.1.
Factors That Have Been Related to Nest Site Selection in Loggerhead Turtles

Source	Site	Slope	Temp	Distance	Sand		Moisture	Compaction	Erosion	pH	Salinity
					Type						
3	Florida, USA							NS			
7	Florida, USA			NS							
6	Greece			NR							
4	Florida, USA	SC			SC		NS			NS	
5	Florida, USA							NS			
8	Florida, USA		SC								
9	Florida, USA	SC	NS				NS				NS
2	S. Carolina, USA	SC	SC		SC		SC				
1	N. Carolina, USA			NS							

Source Key: 1. Brooks 1989. 2. Cardinal et al. 1998. 3. Foote and Sprinkel 1995. 4. Garmestani et al. 1998. 5. Grant and Beasley 1998. 6. Hays and Speakman 1993. 7. Hays et al. 1995. 8. Stoneburner and Richardson 1981. 9. Wood and Bjorndal 2000.

Note: Temp. = temperature; NS = not significant; NR = nonrandom; SC = significant correlation.

From 10 to 75% of loggerhead nesting attempts are unsuccessful on many beaches (Dodd 1988); perhaps much could be learned from studying unsuccessful nesting behavior in conjunction with successful behavior.

Unfortunately, most results from studies of nesting site selection were inconclusive or contradicted the findings of other studies (Table 8.1). For instance, whereas Stoneburner and Richardson (1981) found that an abrupt rise in sand temperature was associated with the onset of nesting in turtles that crawled up the beach, Wood and Bjorndal (2000) found no relation between temperature changes and successful nesting events. Overall, although nest placement on the beach is largely nonrandom (but see Hays et al. 1995), it remains unclear what forces are behind the nesting site selection process in loggerhead turtles. If the multiple regression approach used by Kikukawa et al. (1998, 1999) were applied in other nesting areas to assess the relative importance of the factors influencing nesting site selection, perhaps an unambiguous picture would emerge.

Given that anthropogenic alteration of the beach environment can discourage nesting (e.g., through increased lighting, removal of vegetation, or placement of structures on the beach), it would be interesting to design an experiment that manipulated the beach environment to

stimulate nesting. For instance, Caillouet (1995) suggested the use of sea turtle decoys to stimulate turtles to nest on a particular beach. Perhaps this could be taken further by manipulating specific local environmental features of the beach while a sea turtle is choosing a nesting site in order to discover what factors drive the selection process. Although logistically challenging, the results of such a study might reveal far more about the selection process than traditional descriptive studies.

Nesting Beach Characteristics

Although it is not entirely clear why some beaches are used by sea turtles to deposit eggs and others are not, a potential nesting beach must meet several minimum requirements. It must be easily accessible from the ocean, be high enough to avoid being inundated frequently by high tides, and have enough sand cohesion to allow nest construction, and its sand must facilitate gas diffusion and have temperatures conducive to egg development (Mortimer 1990).

Because variability of physical and chemical characteristics was high in beach sand collected from 50 nesting areas from around the world, Mortimer (1990) suggested that "factors other than physiognomy of sand on nesting beaches

may be as important, or more important, in nest[ing] site selection" than the characteristics of the sand.

The result of beach and nesting site selection is that the eggs incubate in a low salinity, high humidity, well-ventilated substrate that is not inundated during development and provides insulation from the high beach surface temperatures while being in the temperature range that facilitates development (Ackerman 1980, 1997; Miller 1985; Maloney et al. 1990). Given the level of investigation concerning the nesting process, it seems odd that no one has been able to define the process by which the turtle (any species) selects its nesting beach or the site for the nest on the beach.

Nesting Process

All species of sea turtles share a core set of nesting behaviors (Bustard and Greenham 1969; Bustard et al. 1975; Ehrenfeld 1979; Schulz 1975). The process has been subdivided into 7–11 steps (Bustard and Greenham 1969; Bustard et al. 1975; Carr and Ogren 1960; Hendrickson 1982; Kaufmann 1968; Tufts 1972). Regardless of the number of steps, the general pattern includes emerging from the surf, ascending the beach, excavating the body pit, digging the egg chamber, oviposition, filling in the egg chamber, filling the body pit, and returning to the sea.

There are two types of gaits, alternating and simultaneous, used by sea turtles to move on the beach; they leave asymmetrical or symmetrical tracks, respectively, in the sand (Pritchard et al. 1983). The loggerhead uses an alternating gait and moves one front flipper and the hind flipper on the opposite side forward at the same time, moving only two flippers at a time. In many populations, the resulting track is approximately 90 cm wide and asymmetrical, with the marks made by the front flippers obviously offset and extending beyond the hind flipper marks.

Typically, loggerheads require between one and two hours to complete the nesting process (Hirth 1980). The description of the nesting process of the loggerhead by Pritchard and Trebbau (1984) is both descriptive and comparative (see also Bustard et al. 1975; Miller 1997).

Using the nesting process of loggerhead turtles as the model, Hailman and Elowson (1992) described 50 separate action patterns derived from the gait.

When the turtle first emerges from the waves, it may pause at the water's edge and be washed over by several waves before starting up the beach. For the most part, the turtle continues uphill while it is on the hard, sloping part of the beach. The turtle crawls a few meters, then pauses to rest, breathe, and possibly scrutinize its surroundings (Pritchard and Trebbau 1984). During this phase, loggerhead turtles, like all marine turtles, are easily disturbed by activity on the beach. Lighting, movement, and/or obstacles may cause a change in direction or may even cause the turtle to abandon the nesting effort. Several authors have been unable to identify the reason for the aborted nesting attempt; sometimes the female is deterred from nesting by "factors known only to the turtle" (Dodd 1988).

The occurrence rate of aborted nesting attempts varies among populations (e.g., it is high in the southeastern United States, low in Queensland, Australia; Dodd 1988; Limpus 1985). Whatever the cause(s), a loggerhead usually returns the same night or a following night for a further nesting attempt (e.g., 1.08 days; Limpus 1985), and the majority return to the same beach (87.5%; Limpus 1985).

Loggerhead turtles prepare the nesting site before digging the egg chamber by clearing away surface debris, using either simultaneous or alternating sweeps of the front flippers. The turtle "swims" forward as the area in front is cleared. Loose, dry substrate immediately under or behind the turtle may be cleared by its hind flippers (Hailman and Elowson 1992). Although the digging action obviously moves the turtle forward into the "body pit," the cue to stop excavating the body pit is unknown. In very dry or loose sand conditions a turtle will excavate a deeper body pit; digging a deeper body pit places the turtle at the level of firmer, possibly more cohesive, sand that will hold the shape of the egg chamber.

The hind flippers are used to excavate the egg chamber (Schulz 1975). The shape of the egg chamber has been described as "flask

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shaped" (Schulz 1975) or as other similar shapes; however, Carthy et al. (in review) found that the nest shape had a thicker neck and a less round chamber than previously described. The nest measurements correlated well with several measurements of the size of the female (e.g., neck width \times straight carapace length, nest depth \times straight carapace width) and her reproductive output (e.g., number of eggs \times nest depth and minimum egg depth), but not with the length of bones in the hind flipper (hand) (Carthy et al., in review). The digging action creates a chamber with a narrower neck and a wider bottom (diameter of neck \cong 16–21 cm; chamber diameter \cong 23–26 cm; depth to top of eggs \cong 35 cm; depth to bottom of chamber \cong 60 cm; Carthy et al., in review) unless the dryness and particle size of the sand or buried debris causes the shape to alter (Bustard and Greenham 1968). Loggerhead turtles construct nests that are larger and deeper than those made by hawksbill turtles, which are smaller turtles (Carr et al. 1966), and smaller and shallower nests than those constructed by green turtles, which are larger turtles (Hirth 1997).

The alternating use of the hind flippers removes about a cup of sand at a time. The sand is placed by the digging flipper to the side of the chamber. As the turtle takes its weight on this flipper, some newly excavated sand falls on top of it. The alternate flipper throws the sand on top of it forward and extends into the nest chamber for another scoop. With occasional pauses to rest, the alternating process continues until the turtle's hind flippers cannot touch the walls or bottom of the chamber (Hailman and Elowson 1992). When a turtle missing one hind flipper attempts to dig, it uses the one good limb properly and moves the stump of the other in sequence as if it were actually removing sand. A turtle missing one hind flipper digs an improperly shaped nest that is not large enough to hold the entire clutch of eggs.

During oviposition both hind flippers of a loggerhead are extended outwards behind the turtle on the sand. When the cloaca contracts, the tip of the tail points downward and slightly forward; then as the eggs drop, the tail relaxes backward. With each contraction, the outer edges of the rear flippers curl. The eggs are laid

singly or in small groups (two or three, sometimes four).

Loggerhead turtles are relatively tolerant of external stimuli during egg laying. However, the level of indifference to disturbing stimuli varies among individuals; some may cease oviposition when tagged, while others may attempt to bite the tag area or the sand in front of them, and still others may show no response at all. Part of this variation is a function of the number of eggs already laid. As a general rule, turtles become more tolerant as they lay more eggs. Turtles are even more tolerant of disturbing stimuli while filling the egg chamber and covering the nesting site.

The nest chamber is filled by scraping sand into the hole with the hind flippers (Hailman and Elowson 1992); this sand was the last removed and is typically the moistest. When the neck of the chamber has been filled higher than the floor of the body pit, the sand is compacted by alternating use of the hind limbs. After compaction, the turtle resumes front flipper action like that used to excavate the body pit. Sand is thrown backwards along the carapace over the nesting site; as the turtle moves forward it continues throwing sand backwards. At the end of the process, the turtle has moved at least 1 m forward of the actual site of the egg chamber so that the remnant of the body pit is not above the eggs (Hailman and Elowson 1992). The primary outcome of this behavior is the reestablishment of insulating sand over the eggs to a depth approximating that of the beach surface, thus facilitating the rapid reestablishment of temperature and moisture in the sand above the eggs. Because most predators can locate a nest within a few days of oviposition or near emergence (Hopkins et al. 1979), camouflaging the nest is of secondary importance only, if it is important, at all.

Endocrine Regulation of Reproduction

There is continuing growth in the understanding of the role of the endocrine system in regulation of reproduction in the loggerhead turtle (Owens 1980, 1997). For adult female loggerheads in the foraging area, estradiol 17β (E_2) appears to be the stimulus for vitellogenesis in

the months leading up to migration (Wibbels et al. 1990). As E_2 increases during vitellogenesis, so too does testosterone. At the completion of the vitellogenic phase, the dramatic decrease in E_2 in synchrony with the rise in testosterone to its highest level appears to initiate migration to the breeding areas (Owens 1997). In addition, elevated testosterone levels may also influence courtship and mating behaviors (Wibbels et al. 1990).

Following successful courtship, ovulation may be stimulated by elevated levels of luteinizing hormone (LH) approximately two weeks prior to the first clutch being laid and within 48 hours after nesting for each successive clutch (Wibbels et al. 1992; Owens 1997). These elevated LH levels may also stimulate progesterone production by the ovary (Wibbels et al. 1992). Wibbels et al. (1992) hypothesized that elevated testosterone levels in the postmating female may sensitize follicles and corpora lutea to LH stimulation.

Females come ashore with undetectable levels of arginine vasotocin (AVT). When body pit construction begins, AVT levels increase, possibly via a neuroendocrine mechanism associated with the behavior. AVT levels reach their peak during early to midoviposition, and plasma concentrations of AVT decrease to baseline levels as the turtle returns to the water. AVT, which is produced in the neurohypophysis, is transported by the bloodstream to the oviducts, where it is believed to stimulate the synthesis of prostaglandin F (PGF) (Owens 1997). PGF and prostaglandin E_2 (PGE_2) are hypothesized to play active roles during oviposition; PGF stimulates oviducal contractions to move eggs through the oviducts in concert with PGE_2 , which promotes vaginal relaxation (Guillette et al. 1991). The level of PGE_2 increases during construction of the body pit and increases rapidly up to middle of oviposition. By late oviposition the levels have decreased sharply; they then decrease more slowly until the turtle is covering the nest, after which the levels approach the baseline before the turtle reenters the water (Guillette et al. 1991). The stimuli for PGE_2 synthesis and release are unknown and may involve AVT.

Whittier et al. (1997) hypothesize that testosterone and corticosterone interact over the period of successive nestings and may be involved in reproductive functions such as the mobilization of lipid reserves for egg production in loggerheads. The linkage between endocrine function and the stimulus to initiate postnesting migration to the home feeding area remains to be elucidated.

Reproductive Output

Loggerhead turtles follow the standard pattern of reproduction for sea turtles: "large clutches of relatively small eggs; multiple clutches produced during a well-defined nesting season; communal nesting in well-defined ancestral nesting areas; [and] careful construction of [a] covered nest" (Moll 1979). The potential negative impact of infrequent environmental perturbations (i.e., heavy rain, waves causing erosion) on the reproductive output for the season is reduced by laying sequential clutches of eggs at approximately two-week intervals in different places in the beach environment. This strategy enhances the probability of success of incubation by optimizing among the size and shape of the eggs, the number of eggs, the number of clutches laid in a nesting season, and when in the season the eggs are laid, in the context of the factors that influence the conditions of the beach.

Loggerhead turtles lay white, spherical, cleidonic eggs with flexible, aragonite shells (Miller 1985; Packard and DeMardo 1991) that are medium sized (4.0 cm, 36 g) compared with those of other species, which range from the small eggs of *Lepidochelys olivacea* (3.9 cm, 35 g) and *L. kempi* (3.8 cm, 30 g) to the large eggs of *Dermochelys coriacea* (5.3 cm, 90 g) and *Natator depressus* (5.1 cm, 80 g) (Ewert 1979; Van Buskirk and Crowder 1994). *Chelonia mydas* lays eggs that are slightly larger (4.5 cm, 48 g) and *Eretmochelys imbricata* lays eggs that are slightly smaller (3.8 cm, 28 g) than those of loggerhead turtles (Ewert 1979; Van Buskirk and Crowder 1994).

The number of eggs laid in each clutch varies between clutches as well as within and between populations (Dodd 1988; Hirth 1980;

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Limpus 1985). The overall range is 23–198, with a mean of 112.4 per clutch (mean of 19 populations; Van Buskirk and Crowder 1994). Some of the lower values are probably the result of counting eggs in clutches that were the remainder of disturbed nesting attempts (Limpus 1995); some may be real, albeit from females that were not functioning properly. Similarly, the very large clutch counts may result from counting eggs in two clutches laid in juxtaposed nests.

Like all other sea turtles, loggerhead turtles lay several clutches of eggs during a nesting season (Hirth 1980; Miller 1997; Van Buskirk and Crowder 1994:). The number of clutches produced results from several factors (Moll 1979), including (1) the energetics required to support reproduction, (2) the physiological control of ovulation that allows groups of eggs to be separated in space and time, and (3) the risks of mortality associated with the nesting beach and interesting habitat.

The extremes of the typical range vary from one to six clutches per season; the maximum number reported is seven (Lenarz et al. 1981). The mean number of clutches laid per season varies within populations (i.e., between seasons) and among populations (Hughes 1974a, 1974b; Limpus 1985); mean values are usually in the range of two to four. Unfortunately, determining the number of times a turtle nests during a reproductive season is difficult because of incomplete coverage of the nesting season or nesting area or loss of individuals from the nesting group (Hughes 1982). Further, remigrating turtles (i.e., those that have previously nested) may lay one or two more clutches per season than maiden nesting turtles (Lund 1986). Although nearly every nesting beach study reports the number of clutches laid per turtle, it is clear that the reproductive subtleties that impact on the number of clutches laid require better definition before the data are used to estimate the number of female turtles in the population (Marquez 1994) or other parameters of the population.

The internesting interval (*sensu* Limpus 1985) is the interval between when a turtle returns to the sea after laying a clutch of eggs and when she next emerges to lay, whether or not

that attempt is successful. Given this definition, the interesting period of loggerheads varies from about 12 to 16 days (Caldwell 1962; Dodd 1988; Hughes and Mentis 1967; Limpus 1985). Extremely short “interesting” intervals represent second attempts at laying a clutch following a disturbance, not new clutches (Miller 1985, 1997).

Fecundity is the product of the clutch count, the number of clutches per breeding season, and the number of breeding seasons in the life of the turtle (Limpus et al. 1984b). Unfortunately, the number of times a loggerhead turtle reproduces during its life is unknown.

Egg Composition and Ovulation

A normal egg is composed of an aragonite shell attached to a shell membrane inside of which is albumen, which surrounds the vitelline membrane enclosing the yolk; the embryonic disk is contained on the vitelline membrane (Miller 1985; Packard and DeMarco 1991). The energy and chemical components of the eggs come from the food eaten and stored by the female while in her foraging area, not the nesting area. The follicles result from the metabolic processes of digestion of food, and the shell is constructed from calcium carbonate in the form of aragonite (orthorhombic CaCO_3). If the foraging area is known, studies of the energy and chemical transfer from the environment to the follicles and the impact on the turtle's reproductive success can be enhanced; without this linkage, biochemical analysis of eggs from the nesting beach is of limited value (e.g., Sakai et al. 1995).

When producing an average clutch of 110 eggs, loggerhead turtles infrequently fabricate eggs that are not normal, including yolkless eggs (*sensu* Hughes et al. 1967), multiyolked eggs, chain-form eggs, and shell-less eggs (*sensu* Limpus 1985). Yolkless eggs contain small granules of yolk material surrounded by albumen but have no vitelline membrane. In addition, they do not contain a zygote or embryo and have no propensity for development. Therefore, the yolkless egg is not strictly an “egg” and should not be included in clutch

counts. Yolkless eggs are seldom larger than 50% of the diameter of normal eggs and result from ovulatory debris or fragments of a ruptured yolk entering the oviduct and being layered with albumen and a shell (Miller 1985).

Multiyolked eggs occur in loggerhead turtle clutches on an irregular basis (Limpus 1985). Multiyolked eggs contain two or more yolks within a single shell with varying degrees of constriction between the yolks. As a general rule, the greater the constriction is between yolks, the greater the possibility that the embryo(s) will hatch. Chain-form eggs are an extreme form of the multiyolked egg; they are linked together by small connections of shell material in a chain so that each yolk and its surrounding albumen are separate. Shell-less eggs also occur infrequently; the yolk and albumen are usually encased in the shell membrane without the outer shell structure. The occurrence of multiyolked eggs, chain-form eggs, or shell-less eggs indicates a problem with the oviduct, the cause of which remains undefined (Miller 1985).

The ovary is comprised of a stroma (ovarian tissue) and previtellogenic follicles (diameter range 1–5 mm). The ovary may also contain evidence of ovulation; if ovulation has occurred recently, the corpora hemorrhagica are approximately 15–10 mm in diameter and are situated on postovulatory, fluid-filled vesicles in the stroma where the follicle was ovulated. If ovulation occurred some time in the past, corpora lutea or corpora albicantia will be present; the diameter will depend on the time since ovulation (range 2–8 mm). The oviduct is a long tube (> 4 m) containing a lining of specialized secretory cells that produce the albumen, shell membrane, and shell (Aitken and Solomon 1976; Solomon and Baird 1976). The female turtle arrives at her nesting area with more than enough mature follicles present in her ovaries to supply yolks for all the eggs to be laid during the season. The mature follicles will absorb water before ovulation and increase slightly in diameter from about 2.5 cm to about 3.0 cm. The unused follicles will be resorbed (become corpora atretica) in the months following the nesting season (Limpus and Miller, unpubl. data).

The hormonal control of ovulation has not been described in detail for loggerhead turtles;

it is assumed to be similar to the general cycle described for green turtles by Licht (1980) and Owens (1980). Ovulation coincides with a surge in the levels of luteinizing hormone and progesterone. The details that allow for the selective release of approximately 110 follicles from the two ovaries containing a total of several hundred other mature follicles await elucidation.

When ovulated, each follicle travels through the coelom from the ovary to the infundibulum of the oviduct, where it is fertilized by sperm presumably located in the folds of the infundibulum. Because the sperm from all inseminating males are mixed in the folds, the sperm from several different males are available to fertilize the ova that will form a clutch (Harry and Briscoe 1988).

Fertility and Development

Most eggs laid by loggerhead turtles are fertile. Combined counts of eggshell remnants and unhatched eggs opened to determine if any development had occurred indicate fertility is typically greater than 80% (Blanck and Sawyer 1981; Hughes 1970, 1974a, 1974b; Hughes and Mentis 1967; Hughes et al. 1967; Limpus 1985; Miller 1985, 1999). The level of fertility probably exceeds 95%; however, distinguishing between intraoviducal death and early embryonic death (before the formation of blood isles) within eggs that have been in the nest chamber for 60 or more days is difficult (Miller 1997). In eastern Australia, 100% of many hundreds of loggerhead eggs specifically examined for the presence of an embryo at oviposition contained an embryo, i.e., had been fertilized (Miller and Limpus, unpubl. observ.).

The fertilized ovum continues down the oviduct, where special cells in the lining of the anterior glandular region of the oviduct secrete albumen (Aitken and Solomon 1976). Once the yolk has been coated with albumen, the inner shell membrane is secreted from special cells in the shell-forming segment (Owens 1980; Solomon and Baird 1976, 1979). Following formation of the shell membrane, aragonite crystals begin to form the outer portion of the shell (Packard and Hirsch 1986; Packard et al. 1982; Schleich and Kastle 1988; Solomon and

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Baird 1976, 1979). The shell is not fully formed until at least the seventh day following ovulation (Miller 1985).

First cleavage begins within hours of fertilization, but development is suspended at middle gastrulation until oviposition (Bellairs 1991; Miller 1985). However once oviposited, development resumes within a few hours (four to eight hours, depending on temperature). Rough handling (movement involving rotation and/or jarring) of the eggs after development resumes causes rupturing of delicate membranes and results in the death of the embryo (Limpus et al. 1979; Miller 1985); the embryos remain susceptible to movement-induced mortality until the embryo and its membranes have developed through 20–25 days (about 50%) of incubation (Parmenter 1980).

The morphological changes that occur during development of marine turtles, including loggerheads, have been described for the Cheloniidae and Dermochelyidae (Miller 1985). In general terms, development involves three primary themes: (1) structural differentiation of body and organs (organogenesis), (2) functional development of organs and systems, and (3) embryonic growth.

Six stages of development, extending from first cleavage to middle gastrulation, are completed within the oviduct before the embryo enters a short diapause prior to oviposition (Miller 1985). At oviposition (stage 6; Miller 1985), the edges of the groove blastopore on the blastodisc curve slightly to the anterior. Shortly thereafter (stages 7–11), the neural groove forms, the head fold forms, the amnion arises and extends posteriorly to the vicinity of the first somite, and the number of somites increases to six. During stages 12–16, somites increase from 8 to 27, the first pharyngeal cleft opens, the mouth is shaped into a deep V, amnion covers the entire body, and the caudal amniotic tube has formed. By stage 14, blood islands appear around the periphery of the “yolk-sac” membrane, and the heart is S-shaped and beating. During stages 17–21, the pharyngeal clefts open, and the limb buds appear as small ridges on the lateral body and extend to become paddle shaped. The limb paddles twist to orient parallel with body. Late in this series

the carapace margin is indicated as a ridge on the lateral body wall, but the inframarginal scutes are not defined.

During stages 22–27 (middle third of development), species-specific characteristics become increasingly evident as the shape of the scales and the pigmentation of the carapace progress. Initially, the carapace is indicated as a lateral ridge before the anterior portion completes across the neck. The central, lateral, and marginal scales differentiate, and the claw is present on the first digit (stage 25). Pigmentation of the scales expands and darkens, while the scales of skin develop and become pigmented. The volume of extra-embryonic yolk is still greater than the volume of the embryo.

During the final third of development (stages 28–31), the scales of the carapace finish differentiation, and embryonic pigmentation is complete. The structure and pigmentation of the embryo look increasingly like those of a hatchling. The volume of the extra-embryonic yolk reduces to be approximately 50% the volume of the embryo.

Pipping (stage 31) occurs as the embryo ruptures the extra-embryonic membranes and the shell. At this time the embryo takes its first breath and membranous circulation shuts down. As the embryo struggles out of the shell (stage 32), the embryonic curvature of the body flattens, causing the internalization of the remnant yolk and a reduction in the transverse plastronal fold. During hatching, the extra-embryonic fluids of the amnion and allantois drain away; the activity in the nest chamber and in the climb to the beach surface abrades the extra-embryonic membranes.

Nest Environment

Embryos are vulnerable to extremes in environmental conditions in three areas: (1) moisture (including substrate humidity and salinity), (2) gas exchange, and (3) temperature (Ackerman 1980, 1991, 1997; Georges et al. 1993; Maloney et al. 1990; Miller 1985; Mortimer 1990; Packard and Packard 1988). Each of these variable conditions experienced by the developing embryo during incubation has an impact. However, they may not operate independently.

The potential for synergism among moisture, gas exchange, and temperature within the nest may change the impacts. For example, as temperature increases so does embryonic oxygen demand and the potential for environmental water vapor exchange.

Loggerhead turtle eggs become turgid soon after oviposition by absorbing water vapor from the surrounding sand; eggs usually increase in weight by 5–10%. Hatching success appears to be little affected by egg water exchange in the range of –10 to +30% of the initial egg mass (Ackerman 1997). However, excessive weight loss (water loss) is critical; eggs cannot lose more than 40% of their initial mass if they are to survive to hatching. The hydrologic conditions of the beach that influence change in the weight of the eggs include salt and organic material, and substrate (Ackerman 1997; Packard and Packard 1988).

Because of the structure of the eggshell and of the beach, small differences in the partial pressure of gases occur between the eggs in the nest and the surrounding sand (Ackerman 1980, 1997), facilitating adequate gas exchange to support the demands of the developing embryos (Ackerman 1980, 1997; Prange and Ackerman 1974). Unfortunately, gas diffusion is affected by the water content (e.g., excessive rainfall) and particle size of the sand (Ackerman 1980, 1991; Kraemer and Bell 1980; Prange and Ackerman 1974; Ragotzkie 1959). Although the developing embryos usually receive adequate ventilation, inundation of the nest for several hours near the end of incubation may kill the entire clutch (Miller and Limpus, unpubl. observ.), presumably by reducing oxygen availability at the prepipping stages, when the oxygen demand is higher than during early developmental stages (Maloney et al. 1990). Beaches exposed to high tidal ranges have the potential for fluctuation of the water table below nests in response to tidal cycles to enhance flushing of CO₂ from and replenishment of O₂ to the nest environment from the atmosphere (Maloney et al. 1990).

Nesting beach temperatures are typically between 24 and 33°C, although short periods outside this range may occur occasionally (Bustard 1972; Caldwell 1959; Ewert 1979; Limpus

et al. 1985; Miller 1985, 1997). Eggs that incubate at temperatures lower than 22°C for the last third of incubation and those held at temperatures greater than 33°C for extended periods seldom hatch. Incubation period is an inverse function of temperature (Limpus et al. 1985; Miller 1985).

The sexual differentiation of loggerhead embryos is determined by temperature (Limpus et al. 1985; Mrosovsky 1980; Mrosovsky and Yntema 1980; Yntema and Mrosovsky 1979). The pivotal temperature varies between populations within a species (Limpus et al. 1985). Even though the generality that cooler temperatures produce males and warmer temperatures produce females holds, within fluctuating beach temperatures, the sex of the hatchlings is determined by the proportion of development at a temperature, not by the duration of exposure to the temperature (Georges et al. 1994).

Incubation Period, Hatching, and Emergence

Incubation period is defined as the time from oviposition to the hatchling leaving the eggshell. In constant temperature incubation studies with loggerheads, the minimum temperature for successful incubation is approximately 25°C; at this temperature development is normal but slow, taking approximately 13 weeks (Limpus et al. 1985; McGehee 1979; Miller 1985; Yntema and Mrosovsky 1980, 1982). The maximum temperature for successful incubation is 33°C in eastern Australia (Limpus et al. 1985) and 34°C in the eastern United States (McGehee 1979; Yntema and Mrosovsky 1980, 1982), with resulting incubation periods of approximately 6.5 weeks. At the upper extremes of temperature, development is rapid and the possibility of developmental abnormalities is higher. With constant temperature incubation in the 26–32°C range, a change of 1°C adds increases or decreases the incubation period by about five days (Mrosovsky 1980). In nesting beach studies, it has been more common to quantify the incubation-to-emergence period (IEP), which is the period from oviposition to hatchling emergence to the beach surface. The authors' observations indicate that in extremely

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loose dry sand, hatchling emergence to the beach surface can take up to two weeks longer than the incubation period (Limpus and Miller, unpubl. observ.).

In the nest chamber embryos use their caruncle to cut through the amnion, chorioallantoic membranes, and shell (Miller 1985). There is a reduction in natural nest volume as embryos hatch and extra-embryonic fluids (amnion and allantoic) drain away to leave space within the nest cavity (Kraemer and Richardson 1979). As a result of its struggles, the curled hatchling wiggles out of the eggshell and begins to flatten, with resulting internalization of the remaining yolk (Miller 1985). The residual eggshells are shuffled downward by the actions of the hatchlings (socially facilitated digging; *sensu* Carr and Hirth 1961). In cohesive sand, the hatchlings move the space in nest created by the fluid drainage upwards to the surface of the beach. Digging hatchlings pause when O₂ levels drop and CO₂ levels reach critical (albeit undefined) thresholds in the context of their ability to function anaerobically. As digging continues, the sand above the hatchlings is scratched away and settles down past them. Near the surface, the drier sand collapses into the chamber so that the hatchlings emerge out of a depression in the sand.

Loggerhead turtle eggs typically have 80% (or higher) hatching success (i.e., number of hatchlings leaving their eggs), unless external factors (e.g., depredation, environmental conditions, microbial infection, etc.) interfere (National Research Council 1990).

Hatchlings typically emerge onto the beach surface more than two days after hatching from their eggs. The time between hatching and emergence is a function of the depth of the nest and the compaction of the sand. Emergence usually occurs during the early part of the night (Limpus 1985) and is controlled, at least in part, by the difference in the sand temperature experienced by the hatchlings as they approach the surface (Bustard 1967; Mrosovsky 1968). Recently, Moran et al. (1999) examined the theories advanced to explain the behavior. Their results indicate that the cue for emergence onto the beach surface by hatchlings paused several centimeters below is controlled by a critical

threshold temperature above which hatchlings do not emerge. As hatchlings dig toward the surface they reach the lower limit of the heat absorbed by the sand. At sunset, the gradient of latent heat contained in the sand reverses. An hour or more after the temperature at the level of the hatchlings has dropped below the threshold level, the hatchlings begin to dig toward the surface, arriving on the beach in the early evening. The drop in temperature below the threshold also causes clutches of hatchlings to emerge on cool, cloudy, and/or rainy days.

As a general rule, emergence success (number of hatchlings reaching the beach surface) is slightly lower than hatching success because not all hatchlings that struggle out of their eggshells actually make the climb to the beach surface. Some are malformed and cannot climb, and others die within the nest chamber (Miller 1985).

Hatchling loggerhead turtles are about 45 mm (range, 35–49 mm) in straight carapace length and weigh about 21 g (range, 17–27 g) (see Tables 22–25 in Dodd 1988). The size of the hatchlings is reasonably consistent around the world; the hatchlings weigh slightly less than 50% of their ovipositional egg weight (Hirth 1980).

If they emerge during the day, hatchlings face two significant problems: (1) potentially lethal temperatures and (2) predators. At some nesting beaches the surface temperature of the sand during midday may exceed 45°C; under direct sun, hatchlings die or receive severe burns from the sand, causing them to die later or be unable to swim (Miller and Limpus, unpubl. observ.). Day or night, before reaching the relative safety of deep offshore water, hatchlings potentially face a wide range of terrestrial and aquatic predators including both invertebrates (i.e., ants, crabs, etc.) and vertebrates (i.e., fish: sharks and teleosts; reptiles: *Varanus* sp. and others; birds: gulls, crows, egrets, raptors, and many others; and mammals: raccoons, rats, cats, dogs, foxes, bears, and others; see Table 21 in Dodd 1988). Depredation may or may not be less while crossing the beach at night when surface sand temperatures are sublethal. Darkness may afford hatchlings the best chance of successful dispersal from the nesting site to the open ocean.

Conclusions

Reproduction in loggerhead turtles follows the same general pattern that is found in other sea turtles. Loggerhead turtles gather the energy necessary for reproduction over several years, while in their foraging areas, before they migrate to mate and then move to subtropical nesting areas. Loggerhead turtles return to beaches in the region in which they were hatched (philopatry), typically after intervals of two to four years (although much longer intervals have been recorded). They return to nesting sites with a high degree of accuracy (high nesting site fidelity) within the reproductive season. The nesting beaches they use facilitate embryonic development by having low salinity, high humidity, and a well ventilated substrate that is not inundated during development. Loggerhead turtles lay clutches containing about 110 eggs that are round and medium sized compared with those of other sea turtles. The duration of incubation varies inversely with temperature. Sex is determined by nest temperature. Hatching and emergence success of loggerhead turtles are typically high (greater than 80%). Emergence is typically nocturnal and is controlled by a threshold temperature above which the hatchling do not emerge.

Although some aspects of the reproductive biology are well known (e.g., sequential nesting behavior, number of eggs in a clutch), others are not. The control of ovulation, energy conversion metabolism, and nesting site selection cues, all require detailed investigation.

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LITERATURE CITED

- Ackerman, R. A. 1980. Physiological and ecological aspects of gas exchange by sea turtle eggs. *American Zoologist* 20:575-583.
- . 1991. Physical factors affecting the water exchange of buried reptile eggs. *In* D. C. Demming

and M. W. J. Ferguson (eds.). *Egg incubation; its effects on embryonic development in birds and reptiles*, 193-211. Cambridge, U.K.: Cambridge University Press.

- . 1997. The nest environment and the embryonic development of sea turtles. *In* P. L. Lutz and J. Musick (eds.). *The biology of sea turtles*, 83-106. Boca Raton, Fla.: CRC Press.
- Aitken, R. N., and S. E. Solomon. 1976. Observations on the ultrastructure of the oviduct of the Costa Rican green turtle (*Chelonia mydas* L.). *Journal Experimental Marine Biology Ecology* 21:75-90.
- Bell, R., and J. I. Richardson. 1978. Analysis of tag recoveries from loggerhead sea turtles (*Caretta caretta*) nesting on Little Cumberland Island, Georgia. *Florida Marine Research Bulletin* 33:20-24.
- Bellairs, R. 1991. Overview of early stages of avian and reptilian development. *In* D. C. Demming and M. W. J. Ferguson (eds.). *Egg incubation: Its effects on embryonic development in birds and reptiles*, 371-383. Cambridge, U.K.: Cambridge University Press.
- Bjorndal, K. A. 1997. Foraging ecology and nutrition of sea turtles. *In* P. L. Lutz and J. Musick (eds.). *The biology of sea turtles*, 199-231. Boca Raton, Fla.: CRC Press, Boca Raton.
- Bjorndal, K. A., A. B. Meylan, and B. J. Turner. 1983. Sea turtles nesting at Melbourne Beach, Florida. I. Size, growth and reproductive biology. *Biological Conservation* 26:65-77.
- Blamires, S. J., and M. L. Guinea. 1998. Implications of nest site selection on egg predation at the sea turtle rookery at Fog Bay. *In* R. Kennett, A. Webb, G. Duff, M. Guinea, and G. Hill (eds.). *Marine turtle conservation and management in Northern Australia*, 20-24. Proceedings of a workshop held at the Centre for Indigenous Natural and Cultural Resource Management and Centre for Tropical Wetlands Management, Northern Territory University, Darwin, Australia.
- Blanck, C. E., and R. H. Sawyer. 1981. Hatchery practices in relation to early embryology of the loggerhead sea turtle, *Caretta caretta* (Linné). *Journal of Experimental Marine Biology and Ecology* 49:163-177.
- Bouchard, S., K. Moran, M. Tiwari, D. Wood, A. Bolten, P. Eliazar, and K. Bjorndal. 1998. Effects of exposed pilings on sea turtle nesting activity at Melbourne Beach, Florida. *Journal of Coastal Research* 14:1343-1347.
- Bowen, B. W., J. C. Avise, J. I. Richardson, A. B. Meylan, D. Margaritoulis, and S. R. Hopkins-Murphy. 1993. Population structure of loggerhead turtles, *Caretta caretta*, in northwestern

139 Nest Site Selection through Hatchling Emergence

- Atlantic Ocean and Mediterranean Sea. *Conservation Biology* 7:834–844.
- Bowen, B. W., N. Kamezaki, C. J. Limpus, G. R. Hughes, A. B. Meylan, and J. C. Avise. 1994. Global phylogeography of the loggerhead turtle (*Caretta caretta*) as indicated by mitochondrial DNA haplotypes. *Evolution* 48:1820–1828.
- Bowen, B. W., F. A. Abreu-Grobois, G. H. Balazs, N. Kamezaki, C. J. Limpus, and R. J. Ferl. 1995. Trans-Pacific migrations of the loggerhead turtle (*Caretta caretta*) demonstrated with mitochondrial DNA markers. *Proceedings of the National Academy Sciences* 92:3731–3734.
- Brooks, W. B. 1989. Nesting activity of the loggerhead sea turtle (*Caretta caretta*) on Bald Head Island, North Carolina. In S. A. Eckert, K. L. Eckert, and T. H. Richardson (compilers). *Proceedings of the ninth annual workshop on sea turtle biology and conservation*, 211–213. NOAA Technical Memorandum NMFS-SEFSC-232.
- Bustard, H. R. 1967. Mechanism of nocturnal emergence from the nest in green turtle hatchlings. *Nature* 214:317.
- . 1972. *Sea turtles: Their natural history and conservation*. London: Collins.
- Bustard, H. R., and P. Greenham. 1968. Physical and chemical factors affecting hatching in the green sea turtle, *Chelonia mydas* (L.). *Ecology* 49:269–276.
- . 1969. Nesting behaviour of the green sea turtle on a Great Barrier Reef island. *Herpetologica* 25:93–102.
- Bustard, H. R., P. Greenham, and C. J. Limpus. 1975. Nesting behaviour of loggerhead and flat-back turtles in Queensland, Australia. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C* 78:111–122.
- Caillouet, C. W., Jr. 1995. Sea turtle decoys—could they be used to establish nesting colonies? *Marine Turtle Newsletter* 68:22–23.
- Cardinal, J. L., B. Willis, B. Weaver, and E. T. Koepfler. 1998. Influence of meteorological and beach sand physical characteristics upon nest location of the loggerhead sea turtle (*Caretta caretta*). In R. Byles and Y. Fernandez (compilers). *Proceedings of the 16th annual symposium on sea turtle biology and conservation*, 30. NOAA Technical Memorandum NMFS-SEFSC-412.
- Caldwell, D. K. 1959. The loggerhead turtles of Cape Romain, South Carolina (abridged and annotated manuscript of W. P. Baldwin, Jr., and J. P. Loftin, Jr.). *Bulletin of the Florida State Museum, Biological Series* 4:319–349.
- . 1962. Comments on the nesting behavior of Atlantic loggerhead sea turtles, based primarily on tagging returns. *Quarterly Journal Florida Academy of Sciences* 25:287–302.
- Caldwell, D. K., A. F. Carr, and L. Ogren. 1959. The Atlantic loggerhead sea turtle. 1. Nesting and migration. *Bulletin of the Florida State Museum, Biological Series* 4:295–308.
- Carr, A. F. 1975. The Ascension Island green turtle colony. *Copeia* 1975:547–555.
- Carr, A. F., and H. Hirth 1961. Social facilitation in green turtle siblings. *Animal Behavior* 9:68–70.
- Carr, A. F., and L. Ogren. 1960. The ecology and migrations of sea turtles. 4. The green turtle in the Caribbean Sea. *Bulletin of the American Museum of Natural History* 121:1–48.
- Carr, A., H. Hirth, and L. Ogren. 1966. Ecology and migrations of sea turtles. 6. The hawksbill turtle in the Caribbean Sea. *American Museum Novitates* 2248:1–29.
- Carthy, R. R., K. A. Bjorndal, and A. B. Bolten. In review. Nest morphology of the loggerhead sea turtle (*Caretta caretta*).
- Crain, D. A., A. B. Bolten, and K. A. Bjorndal. 1995. Effects of beach renourishment on sea turtles: Review and research initiatives. *Restoration Ecology* 3:95–104.
- Dodd, C. K., Jr. 1988. Synopsis of the biological data on the loggerhead sea turtle *Caretta caretta* (Linnaeus 1758). USFWS Biological Report 88:1–110.
- Ehrhart, L. M. 1995. A review of sea turtle reproduction. In K. A. Bjorndal (ed.). *Biology and conservation of sea turtles*, rev. ed., 29–39. Washington, D.C.: Smithsonian Institution Press.
- Ehrhart, L. M., D. A. Bagley, L. T. Uong, and R. D. Owen. 1996. Marine turtle nesting at Archie Carr National Wildlife Refuge in 1994: Another record-breaking year for loggerhead and green turtle nest production. In J. A. Keinath, D. E. Barnard, J. A. Musick, and B. A. Bell (compilers). *Proceedings of the 15th annual symposium on sea turtle biology and conservation*, 79–83. NOAA Technical Memorandum NMFS-SEFSC-387.
- Ehrenfeld, D. 1979. Behavior associated with nesting. In M. Harless and H. Morlock (eds.). *Turtles: Perspectives and research*, 417–434. New York: J. Wiley and Sons.
- Ewert, M. 1979. The embryo and its egg: Development and natural history. In M. Harless and H. Morlock (eds.). *Turtles: Perspectives and research*, 333–413. New York: J. Wiley and Sons.
- Foote, J., and J. Sprinkel. 1995. Beach compactness as a factor affecting turtle nesting on the west coast of Florida. In K. A. Bjorndal, A. B. Bolten, D. A. Johnson, and P. J. Eliazar (compilers). *Proceedings of the 14th annual symposium on sea*

- turtle biology and conservation, 217–220. NOAA Technical Memorandum NMFS-SEFSC-351.
- Garmestani, A. S., H. F. Percival, K. M. Portier, and K. G. Rice. 1998. Evaluation of physical parameters as indicators of nesting beach selection for the loggerhead sea turtle in the Ten Thousand Islands of Florida. *In* S. P. Epperly and J. Braun (compilers). Proceedings of the 17th annual symposium on sea turtle biology and conservation, 53–54. NOAA Technical Memorandum NMFS-SEFSC-415.
- Gasperetti, J., A. F. Stimson, J. D. Miller, J. P. Ross, and P. Gasperetti. 1993. Turtles of Arabia. *In* W. Buttiker and F. Krump (eds.). Fauna of Saudi Arabia, vol. 13, 170–367. Jeddah, Saudi Arabia: National Commission for Wildlife Conservation and Development and Meteorology and Environmental Protection Administration.
- Georges, A., C. J. Limpus, and C. J. Parmenter. 1993. Natural history of the *Chelonia*. *In* C. J. Glasby, G. J. B. Ross, and P. L. Beesley (eds.). Fauna of Australia. Vol. 2A, Amphibia and reptilia, 120–128. Canberra: Australian Government Publishing Service.
- Georges, A., C. J. Limpus, and R. Stoutjesijk. 1994. Hatchling sex in the marine turtle *Caretta caretta* is determined by proportion of development at a temperature, not daily duration of exposure. *Journal of Experimental Zoology* 270:432–444.
- Godfrey, M. H., and R. Barreto. 1995. Beach vegetation and sea-finding orientation of turtle hatchlings. *Biological Conservation* 74:29–32.
- Grant, G. S., and J. Beasley. 1998. Correlations of loggerhead turtle nesting activities with beach erosion rates on Topsail Island, North Carolina. *In* S. P. Epperly and J. Braun (compilers). Proceedings of the 17th annual symposium on sea turtle biology and conservation, 182–183. NOAA Technical Memorandum NMFS-SEFSC-415.
- Guillette, L. J., Jr., K. A. Bjorndal, A. B. Bolten, T. S. Gross, B. D. Palmer, B. Witherington, and J. M. Matter. 1991. Plasma estradiol-17 β , progesterone, prostaglandin F, and prostaglandin E₂ concentrations during natural oviposition in the loggerhead turtle (*Caretta caretta*). *General and Comparative Endocrinology* 82:121–130.
- Harry, J. L., and D. A. Briscoe. 1988. Multiple paternity in the loggerhead turtle (*Caretta caretta*). *Journal of Heredity* 79:96–99.
- Hailman, J. P., and A. M. Elowson. 1992. Ethogram of the nesting female loggerhead (*Caretta caretta*). *Herpetologica* 48:1–30.
- Hays, G. C., and J. R. Speakman. 1993. Nest placement by loggerhead turtles, *Caretta caretta*. *Animal Behaviour* 45:47–53.
- Hays, G. C., A. Mackay, C. R. Adams, J. A. Mortimer, J. R. Speakman, and M. Boerema. 1995. Nest site selection by sea turtles. *Journal of Marine Biological Association of the United Kingdom* 75:667–674.
- Hendrickson, J. R. 1982. Nesting behavior of sea turtles with emphasis on physical and behavioral determinants of nesting success or failure. *In* K. A. Bjorndal (ed.). Biology and conservation of sea turtles, 53–57. Washington, D.C.: Smithsonian Institution Press.
- Hirth, H. F. 1980. Some aspects of the nesting behavior and reproductive biology of sea turtles. *American Zoologist* 20:507–523.
- . 1997. Synopsis of biological data on the green turtle, *Chelonia mydas* (Linnaeus 1758). USFWS Biological Report 97(1):1–120.
- Hopkins, S. R., T. M. Murphy, Jr., K. B. Stansell, and P. M. Wilkinson. 1979. Biotic and abiotic factors affecting nest mortality in the Atlantic loggerhead turtle. Proceedings of the annual conference of the Southeastern Association of Fish and Wildlife Agencies 32:213–223.
- Hughes, G. R. 1970. Further studies on marine turtles in Tongaland, 3. *Lammergeyer* 12:7–25.
- . 1974a. The sea turtles of South-east Africa. I. Status, morphology, and distribution. Investigational Report no. 35 of the Oceanographic Research Institute, Durban, South Africa.
- . 1974b. The sea turtles of South-east Africa. II. Investigational Report no. 36 of the Oceanographic Research Institute, Durban, South Africa.
- . 1982. Nesting cycles in sea turtles—typical or atypical? *In* K. A. Bjorndal (ed.). Biology and conservation of sea turtles. Washington, D.C.: Smithsonian Institution Press.
- Hughes, G. R., and A. Mentis. 1967. Further studies on marine turtles in Tongaland, 2. *Lammergeyer* 3:55–72.
- Hughes, G. R., A. Bass, and M. Mentis. 1967. Further studies on marine turtles in Tongaland. *Lammergeyer* 7:4–54.
- Kaufmann, R. 1968. Zur Brutbiologie der Meeresschildkröte, *Caretta caretta caretta* L. *Mitt. Instituto Colombo-Aleman de Investigaciones Cientificas* 2:47–56.
- Kikukawa, A., N. Namezaki, K. Hirate, and H. Ota. 1998. Factors affecting nesting beach selection by sea turtles: A multivariate approach. *In* S. P. Epperly and J. Braun (compilers). Proceedings of the 17th annual symposium on sea turtle biology and conservation, 65–66. NOAA Technical Memorandum NMFS-SEFSC-415.
- . 1999. Factors affecting nesting beach selection

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- by loggerhead turtles (*Caretta caretta*): A multivariate approach. *Journal of Zoology* 249:447–454.
- Kraemer, J. E., and R. Bell. 1980. Rain-induced mortality of eggs and hatchlings of loggerhead sea turtles (*Caretta caretta*) on the Georgia coast. *Herpetologica* 36:72–77.
- Kraemer, J. E., and J. I. Richardson. 1979. Volumetric reduction in nest contents of loggerhead sea turtles (*Caretta caretta*) (Reptilia, Testudines, Cheloniidae) on the Georgia coast. *Journal of Herpetology* 13:255–260.
- Lenarz, M. S., N. B. Frazer, M. S. Rolston, and R. B. Mast. 1981. Seven nests recorded for loggerhead turtle (*Caretta caretta*) in one season. *Herpetological Review* 12:9.
- Le Vin, D. A., A. C. Broderick, and B. J. Godley. 1998. Effects of offshore features on the emergence point of marine turtles in Northern Cyprus. In R. Byles and Y. Fernandez (compilers). Proceedings of the 16th annual symposium on sea turtle biology and conservation, 91–92. NOAA Technical Memorandum NMFS-SEFSC-412.
- Licht, P. 1980. Evolutionary and functional aspects of pituitary gonadotropins in the green turtles, *Chelonia mydas*. *American Zoologist* 20:565–574.
- Licht, P., D. Owens, K. Clifton, and C. Penaflores. 1982. Changes in LH and progesterone associated with nesting cycle and ovulation in the olive ridley sea turtle, *Lepidochelys olivacea*. *General and Comparative Endocrinology* 48:247–253.
- Limpus, C. J. 1985. A study of the loggerhead sea turtle, *Caretta caretta*, in eastern Australia. Ph.D. Dissertation, University of Queensland, St Lucia, Australia.
- . 1990. Puberty and first breeding in *Caretta caretta*. In T. H. Richardson, J. I. Richardson, and M. Donnelly (eds.). Proceedings of the 10th annual workshop on sea turtle biology and conservation, 81–84. NOAA Technical Memorandum NMFS-SEFSC-278.
- . 1992. Estimation of tag loss in marine turtle research. *Wildlife Research* 19:457–469.
- Limpus, C. J., and J. D. Miller. 1993. Family Cheloniidae. In C. J. Glasby, G. J. B. Ross, and P. L. Beesley (eds.). *Fauna of Australia*. Vol. 2A. Amphibia and Reptilia, 113–138. Canberra: Australian Government Publishing Service.
- Limpus, C., and N. Nicholls. 2000. ENSO regulation of Indo-Pacific green turtle populations. In G. Hammer, N. Nicholls, and C. Mitchell (eds.). *Applications of seasonal climate forecasting in agricultural and natural ecosystems*, 339–408. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Limpus, C. J., V. Baker, and J. D. Miller. 1979. Movement induced mortality of loggerhead eggs. *Herpetologica* 35:335–338.
- Limpus, C. J., P. J. Couper, and M. A. Read. 1994. The loggerhead turtle, *Caretta caretta*, in Queensland: Population structure in a warm temperate feeding area. *Memoirs of the Queensland Museum* 37:195–204.
- Limpus, C. J., A. Fleay, and M. Guinea. 1984a. Sea turtles of the Capricorn Section, Great Barrier Reef. In W. T. Ward and P. Saenger (eds.). *The Capricorn Section of the Great Barrier Reef: Past, present and future*, 61–78. Brisbane: Royal Society of Queensland and Australian Coral Reef Society.
- Limpus, C. J., A. Fleay, and V. Baker. 1984b. The flatback turtle, *Chelonia depressa*, in Queensland: Reproductive periodicity, philopatry, and recruitment. *Australian Wildlife Research* 11:579–587.
- Limpus, C. J., P. Reed, and J. D. Miller. 1985. Temperature dependent sex determination in Queensland sea turtles: intraspecific variation in *Caretta caretta*. In G. Grigg, R. Shine, and H. Ehmann (eds.). *Biology of Australian Frogs and Reptiles*, 343–351. Sydney, Australia: Surrey Beatty and Sons.
- Limpus, C. J., E. Gyuris, and J. D. Miller. 1988. Reassessment of the taxonomic status of the sea turtle genus *Natator* McCulloch 1908, with a re-description of the genus and species. *Transactions of the Royal Society of South Australia* 112:1–9.
- Limpus, C. J., J. D. Miller, C. J. Parmenter, D. Reimer, N. McLachlan, and R. Webb. 1992. Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. *Wildlife Research* 19:347–358.
- Lund, F. 1986. Nest production and nesting-site tenacity of the loggerhead turtle, *Caretta caretta*, on Jupiter Island, Florida. Master's Thesis, University of Florida, Gainesville.
- Maloney, J. E., C. Darian-Smith, Y. Takahashi, and C. J. Limpus. 1990. The environment for development of the embryonic loggerhead turtle (*Caretta caretta*) in Queensland. *Copeia* 1990:378–387.
- Martin, R. E., R. G. Ernest, N. Williams-Walls, and J. R. Wilcox. 1989. Long-term trends in sea turtle nesting on Hutchinson Island, Florida. In S. A. Eckert, K. L. Eckert, and T. H. Richardson (compilers). Proceedings of the ninth annual workshop on sea turtle biology and conservation, 111–113. NOAA Technical Memorandum NMFS-SEFSC-232.
- Marquez M., R. 1994. Synopsis of biological data on the Kemp's ridley turtle, *Lepidochelys kempi* (Garman 1880). NOAA Technical Memorandum NMFS-SEFSC-343.

- Marquez M., R., O. A. Villanueva, S. C. Penaflores. 1976. Sinopsis de datos biológicos sobre la tortuga golfina *Lepidochelys olivacea* (Eschscholtz 1829). Sinopsis sobre la Pesca (INP/S2, SAT), INP 2.
- McGehee, M. A. 1979. Factors affecting the hatching success of loggerhead sea turtle eggs (*Caretta caretta caretta*). Master's Thesis, University of Central Florida, Orlando.
- Mellanby, R. J., A. C. Broderick, and B. J. Godley. 1998. Nest site selection in Mediterranean marine turtles at Chelones Bay, Northern Cyprus. In R. Byles and Y. Fernandez (compilers). Proceedings of the 16th annual symposium on sea turtle biology and conservation, 103–104. NOAA Technical Memorandum NMFS-SEFSC-412.
- Miller, J. D. 1985. Embryology of marine turtles. In C. Gans, F. Billett, and P. F. A. Maderson (eds.). Biology of the Reptilia, vol. 14A, 269–328. New York: Wiley-Interscience.
- . 1997. Reproduction in sea turtles. In P. L. Lutz and J. A. Musick (eds.). The biology of sea turtles, 51–80. Boca Raton, Fla.: CRC Press.
- . 1999. Determining clutch size and hatching success. In K. L. Eckert, K. A. Bjorndal, F. A. Abreu-Grobois, and M. Donnelly (eds.). Research and management techniques for the conservation of sea turtles, 124–129. IUCN/SSC Marine Turtle Specialist Group Publication 4, Gland, Switzerland.
- Moll, E. O. 1979. Reproductive cycles and adaptations. In M. Harless and H. Morlock (eds.). Turtles: Perspectives and research, 305–331. New York: J. Wiley and Sons.
- Moran, K. L., K. A. Bjorndal, and A. B. Bolten. 1999. Effects of the thermal environment on the temporal pattern of emergence of hatchling loggerhead turtles *Caretta caretta*. Marine Ecology Progress Series 189:251–261.
- Mortimer, J. A. 1990. The influence of beach sand characteristics on the nesting behavior and clutch survival of green turtles (*Chelonia mydas*). Copeia 1990:802–817.
- . 1995. Factors influencing beach selection by nesting sea turtles. In K. A. Bjorndal (ed.). Biology and conservation of sea turtles, 45–51. Washington, D.C.: Smithsonian Institution Press.
- Mrosovsky, N. 1968. Nocturnal emergence of hatchling sea turtles: Control by thermal inhibition of activity. Nature 220:1338–1339.
- . 1980. Thermal biology of sea turtles. American Zoologist 20:531–547.
- Mrosovsky, N., and C. L. Yntema. 1980. Temperature dependence of sexual differentiation in sea turtles: Implications for conservation practices. Biological Conservation 18:271–280.
- National Research Council. 1990. The decline of the sea turtles: Causes and prevention. Washington, D.C.: National Academy Press.
- Owens, D. W. 1980. The comparative reproductive physiology of sea turtles. American Zoologist 20:549–563.
- . 1997. Hormones in the life history of sea turtles. In P. L. Lutz and J. A. Musick (eds.). The biology of sea turtles, 315–341. Boca Raton, Fla.: CRC Press.
- Owens, D. W., T. Wibbels, D. Comuzzie, D. Rostal, and C. Limpus. 1989. Sea turtle reproductive chronology: The model and the questions. In S. A. Eckert, K. L. Eckert, and T. H. Richardson (compilers). Proceedings of the ninth annual workshop on sea turtle biology and conservation, 135–137. NOAA Technical Memorandum NMFS-SEFSC-232.
- Packard, G. C., and M. J. Packard. 1988. The physiological ecology of reptilian eggs and embryos. In C. Gans and R. Huey (eds.). Biology of the Reptilia. Vol. 16, Ecology B, 525–607. New York: Alan R. Liss Press.
- Packard, M. J., and K. F. Hirsch. 1986. Scanning electron microscopy of eggshells of contemporary reptiles. Scanning Electron Microscopy 1986:1581–1590.
- Packard, M. J., and V. G. DeMarco. 1991. Eggshell structure and formation in eggs of oviparous reptiles. In D. C. Deeming and M. W. J. Ferguson (eds.). Egg incubation: Its effects on embryonic development in birds and reptiles, 53–69. Cambridge, U.K.: Cambridge University Press.
- Packard, M. J., G. C. Packard, and T. J. Boardman. 1982. Structure of eggshells and water relations of reptilian eggs. Herpetologica 38:136–155.
- Parmenter, C. J. 1980. Incubation of the eggs of the green sea turtle, *Chelonia mydas*, in Torres Strait, Australia: The effect of movement on hatchability. Australian Wildlife Research 7:487–491.
- Prange, H. D., and R. A. Ackerman. 1974. Oxygen consumption and mechanism of gas exchange of green turtle (*Chelonia mydas*) eggs and hatchlings. Copeia 1974:758–763.
- Pritchard, P. C. H., and P. Trebbau. 1984. The turtles of Venezuela. Society Study Amphibian Reptiles Contributions to Herpetology 2.
- Pritchard, P. C. H., P. Bacon, A. Berry, A. Carr, J. Fletemeyer, R. Gallagher, S. Hopkins, R. Lankford, M. Marquez, L. Ogren, W. Pringle, H. Reichart, and R. Witham. 1983. In K. A. Bjorndal and G. H. Balazs (eds.). Manual of sea turtle research and conservation techniques, 2nd ed. Washington, D.C.: Center for Environmental Education.

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- Ragotzkie, R. 1959. Mortality of loggerhead turtle eggs from excessive rainfall. *Ecology* 40:303–305.
- Ross, J. P., and M. A. Barwani. 1995. Review of sea turtles in the Arabian area. In K. A. Bjorndal (ed.). *Biology and conservation of sea turtles*, rev. ed., 373–383. Washington, D.C.: Smithsonian Institution Press.
- Sakai, H., H. Ichihashi, H. Suganuma, and R. Tatsukawa. 1995. Heavy metal monitoring in sea turtles using eggs. *Marine Pollution Bulletin* 30:347–353.
- Salmon, M., R. Reiners, C. Lavin, and J. Wyneken. 1995. Behavior of loggerhead sea turtles on an urban nesting beach. I. Correlates of nest placement. *Journal of Herpetology* 29:560–567.
- Schleich, H. H., and W. Kastle. 1988. Reptile eggshells SEM atlas. Stuttgart: Gustav Fischer.
- Schmelz, G. W., and R. R. Mezich. 1988. A preliminary investigation of the potential impact of Australian pines on the nesting activities of the loggerhead turtle. In B. A. Schroeder (compiler). *Proceedings of the eighth annual workshop on sea turtle biology and conservation*, 63–66. NOAA Technical Memorandum NMFS-SEFSC-214.
- Schulz, J. P. 1975. Sea turtles nesting in Surinam. *Zoologische Verhandelingen Vitgegeven Door Bet Rijksmuseum van Natuurlijke Historie te Leiden* 143:1–144.
- Simon, M. H., G. F. Ulrich, and A. S. Parkes. 1975. The green sea turtle (*Chelonia mydas*): Mating, nesting, and hatching on a farm. *Journal of Zoology* 177:411–423.
- Solomon, S. E., and T. Baird. 1976. Studies on the eggshell (oviductal and oviposited) of *Chelonia mydas* L. *Journal of Experimental Marine Biology and Ecology* 22:145–160.
- . 1979. Aspects of the biology of *Chelonia mydas* L. *Oceanography Marine Biology Annual Reviews* 17:347–361.
- Spotila, J. R., E. A. Standora, S. J. Morreale, and G. J. Ruiz. 1987. Temperature dependent sex determination in the green turtle (*Chelonia mydas*): Effects on the sex ratio on a natural nesting beach. *Herpetologica* 43:74–81.
- Sternberg, J. 1981. *The worldwide distribution of sea turtle nesting beaches*. Washington, D.C.: Center for Environmental Education.
- Stoneburner, D. L., and J. I. Richardson. 1981. Observations on the role of temperature in loggerhead turtle nest site selection. *Copeia* 1981:238–231.
- Tufts, C. E. 1972. Report on the Buritaca Marine Turtle Nesting Reserve with emphasis on biological data from “Operacion Tortuga 1972” and recommendations for the future. Mimeographed report, Inderena, Bogota.
- Ulrich, G. F., and D. W. Owens. 1974. Preliminary note on reproduction of *Chelonia mydas* under farm conditions. *Proceedings of the World Mariculture Society* 5:205–214.
- Van Buskirk, J., and L. B. Crowder. 1994. Life-history variation in marine turtles. *Copeia* 1994:66–81.
- Whittier, J. M., F. Corrie, and C. Limpus. 1997. Plasma steroid profiles in nesting loggerhead turtles (*Caretta caretta*) in Queensland, Australia: relationship to nesting episode and season. *General and Comparative Endocrinology* 106:39–47.
- Whitmore, C. P., and P. H. Dutton. 1985. Infertility, embryonic mortality, and nest-site selection in leatherback and green sea turtles in Suriname. *Biological Conservation* 34:251–272.
- Wibbels, T., D. W. Owens, C. J. Limpus, P. C. Reed, and M. S. Amoss, Jr. 1990. Seasonal changes in serum gonadal steroids associated with migration, mating and nesting in the loggerhead sea turtle (*Caretta caretta*). *General and Comparative Endocrinology* 79:154–164.
- Wibbels, T., D. W. Owens, P. Licht, C. J. Limpus, P. C. Reed, and M. S. Amoss, Jr. 1992. Serum gonadotropins and gonadal steroids associated with ovulation and egg production in sea turtles. *General and Comparative Endocrinology* 87:71–78.
- Witham, R. 1970. Breeding of a pair of pen-reared green turtles. *Quarterly Journal of the Florida Academy of Sciences* 33:288–290.
- Witherington, B. E. 1992. Behavioral response of nesting turtles to artificial lighting. *Herpetologica* 48:31–39.
- Witzell, W. N. 1983. Synopsis of biological data on the hawksbill turtle, *Eretmochelys imbricata* (Linnaeus 1766). *FAO Fisheries Synopsis* 137.
- Wood, F. G. 1953. Mating behavior of captive loggerhead turtles. *Copeia* 1953:184–186.
- Wood, D. W., and K. A. Bjorndal. 2000. Relation of temperature, moisture, salinity, and slope to nest site selection in loggerhead sea turtles. *Copeia* 2000:119–128.
- Yntema, C. L., and N. Mrosovsky. 1979. Incubation temperature and sex ratio in hatchling loggerhead turtles: A preliminary report. *Marine Turtle Newsletter* 11:9–10.
- . 1980. Sexual differentiation in hatchling loggerheads (*Caretta caretta*) incubated at different controlled temperatures. *Herpetologica* 36:33–36.
- . 1982. Critical periods and pivotal temperatures for sexual differentiation in loggerhead sea turtles. *Canadian Journal of Zoology* 60:1012–1016.