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Nesting Ecology of Hawksbill Sea Turtles (*Eretmochelys imbricata*)
on Utila, Honduras

by

Lindsey Renee Eggers Damazo

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A Thesis submitted in partial satisfaction of
the requirements for the degree
Master of Science in Biology

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Each person whose signature appears below certifies that this thesis in his/her opinion is adequate, in scope and quality, as a thesis for the degree Master of Science.

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ABBREVIATIONS

BICA	Bay Islands Conservation Association
CCL_{max}	Curved Carapace Length maximum
CCL_{min}	Curved Carapace Length minimum
CCW	Curved Carapace Width
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for Conservation of Nature
LC	Location Class
PHB	Pumpkin Hill Beach
ProTECTOR	Protective Turtle Ecology Center for Training, Outreach, and Research, Inc.
PTT	Platform Transmitter Terminal
SCL	Straight Carapace Length
SCW	Straight Carapace Width
STAT	Satellite Tracking and Analysis Tool
TRT	Transitional Range of Temperatures
TSD	Temperature-dependent Sex Determination
TSP	Thermosensitive Period
TTR	Thermal Tolerance Range

ABSTRACT OF THE THESIS

Nesting Ecology of Hawksbill Sea Turtles (*Eretmochelys imbricata*)
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Lindsey Renee Eggers Damazo

Master of Science, Graduate Program in Biology
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Dr. Stephen G. Dunbar, Chairperson

The hawksbill sea turtle (*Eretmochelys imbricata*) has a circumtropical distribution and plays an important role in maintaining the health of coral reefs. Unfortunately, hawksbill populations have been decimated, and estimated numbers in the Caribbean are less than 10% of populations a century ago. The hawksbill is considered Critically Endangered, and researchers are coordinating worldwide efforts to protect this species. One country where we lack knowledge regarding hawksbills is Honduras. This study aimed to increase our understanding of hawksbill nesting ecology in Caribbean Honduras. Characteristics of hawksbill nesting activity and a nesting beach on the island of Utila were elucidated using satellite telemetry, beach profiling, vegetation surveys, beach monitoring, and nest temperature profiles.

We affixed satellite transmitters to two nesting hawksbills, and found the turtles migrated to different countries. One turtle traveled 403 km to a bay in Mexico, and the other traveled 181 km to a Marine Protected Area off Belize. This study presents the first description of hawksbill migration routes from Honduras, facilitating protection efforts for turtles that traverse international waters.

To investigate nesting beach and turtle characteristics, we conducted beach monitoring during the 2012 nesting season. Nesting turtle carapace sizes were similar to worldwide values, but hatchlings were heavier. To measure nest temperatures, we placed thermocouple data loggers in four nests and four pseudo-nests. Data suggested metabolic heating may be maintaining nest temperatures above the pivotal temperature. However, large temperature fluctuations corresponding to rainfall from Hurricane Ernesto (as determined using a time series cross-correlation analysis) make it difficult to predict sex ratios, and underscore the impact stochastic events can have on nest temperatures. We created topographic and substrate profiles of the beach, and found it was 475 m long, yet hawksbills preferentially nested along 80 m that differed from the remainder of the beach in having higher elevation and extensive forest cover. This is the first study from Honduras to report a regular nesting population of hawksbills as well as characterize a nesting beach for this species. It provides an important foundation for hawksbill research in Honduras, a region where we have insufficient knowledge to adequately protect this critically endangered species.

CHAPTER ONE

INTRODUCTION

Objectives and Hypotheses

The primary goal of this study was to collect data on nesting ecology and nesting beach characteristics of the hawksbill sea turtle in Honduras. Secondary goals included gathering data regarding: foraging sites of the females through satellite telemetry, nest temperature profiles, and the general topography of the nesting beach. I had three main objectives:

1). Affix satellite transmitters to two nesting hawksbills.

Hypothesis 1: Following nesting, hawksbills will migrate to distant foraging grounds.

2). Perform an elevation and habitat profile of the beach.

Hypothesis 2: Specific beach characteristics of locations where hawksbills nest will be dissimilar to characteristics on the remainder of the beach.

3). Place three thermocouple data loggers in each of four real nests and four control pseudo-nests.

Hypothesis 3: A significant difference will exist between temperatures of *in situ* hawksbill nests and ambient sand at equivalent depths.

Finally, to determine nesting turtle numbers and hatching success, I monitored the beach nightly throughout the nesting season.

Marine Turtles

Sea turtles represent some of the largest members of the class Reptilia. Currently, seven extant species of sea turtles exist, classified into two families. One species – the leatherback, *Dermochelys coriacea* – comprises the sole representative of the family Dermochelyidae. The remaining six species belong to the family Chelonidae, including: Green (*Chelonia mydas*), Loggerhead (*Caretta caretta*), Hawksbill (*Eretmochelys imbricata*), Olive ridley (*Lepidochelys olivacea*), Kemp's ridley (*Lepidochelys kempi*), and Flatback (*Natator depressus*). Members of the Chelonidae, known as the hard-shelled turtles, possess a streamlined shell (carapace) that is covered with keratinous plates called scutes. The forelimbs are large elongated flippers used for propulsion underwater, whereas the hind flippers are more compact and serve as rudders in locomotion. Sea turtles have an extensible neck, yet are unable to withdraw the head or limbs into the shell. Although predominantly oceanic, sea turtles have lungs and must breathe air. All sea turtles are long-lived, developing slowly from the juvenile to sexually mature stage. Depending on the species, the time between hatching and sexual maturity may be 10 to 35 years (Spotila 2004). Sea turtles are unique among reptiles, as they reside in the ocean, yet are dependent on land for egg laying and incubation. They are also the only group of reptiles to regularly undertake lengthy migrations, traveling hundreds to thousands of kilometers between their foraging grounds and nesting sites (Schofield et al. 2010).

Hawksbill Sea Turtles

The hawksbill sea turtle, *Eretmochelys imbricata,* was described by Linnaeus in 1766. It has been placed in its own genus due to certain physical characteristics that

separate it taxonomically from the other marine turtles. One obvious characteristic is the upper jaw, which has a sharp-crested ridge on the bony alveolar surface. It is this physical feature from which its common name "hawksbill" is derived (Spotila 2004). Other distinctive features include two pairs of prefrontal scales on the head, as well as the first costals on the carapace being unconnected with the nuchal scute (Pritchard 1997). On the carapace, the bottom edges of the laterals are often clearly imbricated (overlapping) (Wyneken 2003), indicative of the origin of the species name "imbricata." Sexually mature adult hawksbills have a mass of 27 – 90 kg (60 – 200 lb), but average approximately 70 kg (154 lb). Carapace lengths average 63 – 95 cm (25 – 37 in). Hawksbills become sexually mature at approximately 78 cm (31 in) in females and 69 cm (27 in) in males, with this growth period taking 20 to 30 years (Spotila 2004).

Female hawksbills mate and nest every 2 to 3 years (Witzell 1983). The remigration interval between nesting seasons varies, and appears to be associated with the ability of the turtle to accumulate sufficient fat reserves for successful vitellogenesis, migration, and nesting (Miller 1997). Hawksbills may travel long distances from their foraging grounds to a mating area in the region of a suitable nesting beach. Females mate at the beginning of the nesting season and store sperm to be used for subsequent oviposition events (Joseph and Shaw 2011). While female hawksbills do exhibit the polyandrous mating system found in all other sea turtle species, the majority of females mate with only one male each season, with two males being the reported maximum (Phillips et al. 2013).

Nesting occurs predominantly at night, although daytime nesting has been observed in hawksbills (Miller 1997; Hamann et al. 2003). The turtle emerges from the

sea and crawls up the beach seeking a place to dig the nest. When a suitable site has been located, the turtle begins by digging a body pit. Next, she proceeds to excavate a teardrop-shaped hole using her hind flippers (Fig. 1).
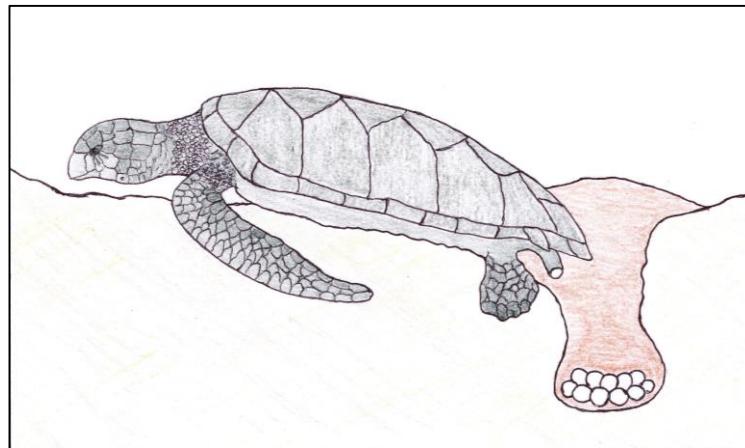
Figure 1. Illustration depicting the teardrop-shaped nest excavated using the hind flippers (Damazo 2014).

Once this hole has reached the appropriate depth and dimensions, she lays the eggs. Each spherical egg is approximately 32 – 40 mm (1.3 – 1.6 in) in size and has a soft, leathery shell. Hawksbills produce the highest average number of eggs per nest of all sea turtle species at approximately 130 (Spotila 2004), although the number of eggs deposited varies among individuals. Each egg has a mass of approximately 28 g (1 oz) when laid. Following the completion of oviposition, the female buries the nest with the rear flippers, then camouflages the entire nest site by flinging sand about with all four flippers. The entire nesting process takes approximately 45 to 90 minutes. The turtle then returns to the sea, leaving the eggs to incubate without further parental care.

A female hawksbill will lay 3 to 5 clutches in a nesting season, with an inter-nesting period of 13 to 16 days between clutches (Spotila 2004). The incubation period

for hawksbill eggs lasts from 51 to 74 days, depending on nest and ambient air temperatures, and varies by location. For example, in Guadeloupe, French West Indies, mean incubation duration was 61.8 days (Kamel 2013), and on Cousine Island in the Seychelles, Hitchins et al. (2004) found the average incubation duration was 58.1 days. Differences in incubation length among locations result from a variety of factors, although all are linked to temperature. For example, the color and composition of the sand, which can affect heat absorption, may vary between locations, or one beach may have higher quantities of shading vegetation that create a cooler nest environment. Nests laid in cool and/or rainy seasons incubate longer than nests laid in warmer, drier seasons (Spotila 2004). Nest depth and number of eggs in the clutch also influence nest temperature, which ultimately determines the incubation duration.

Newly hatched turtles must dig their way out of the nest to the surface. Upon breaking through the sand, hatchlings spill out of the nest *en masse* and rush towards the sea. To reduce the potential for predation, hatchlings typically emerge under cover of darkness. After reaching the ocean, hatchlings swim almost constantly for several days until they reach deep oceanic waters, where it is safer than the predator-filled waters directly offshore (Spotila 2004). During this time the hatchling may feed opportunistically on small organisms it encounters, such as planktonic larvae, but it is primarily nourished by the remainder of its yolk, which may sustain the hatchling for up to two weeks (Spotila 2004). Of all phases of sea turtle development, the least information is known about this pelagic stage. In fact, it has often been called the "lost years" because scientists know so little about what takes place during this period (Carr 1986; Musick and Limpus 1997). However, acquiring more knowledge regarding this life

stage is now possible due in part to recent work by Mansfield et al. (2012) that identified

successful methods for affixing satellite transmitters to small juvenile turtles. Working in

the Atlantic Ocean, Mansfield et al. (2014) used small solar-powered satellite transmitters

to track 17 juvenile loggerheads for up to 220 days, and found that turtles selected sea

surface habitats that provided thermal and foraging benefits. Further tracking of young

juvenile loggerheads and other species will provide more insights into the mystery of the

lost years.

Hawksbills exhibit a Type 2 life history pattern, undergoing development in the

oceanic zone, then moving to the neritic zone after reaching a carapace size of 20 – 35 cm

(8 – 14 in) (Bolten 2003). This growth process may take 1 to 3 years, at which point

juvenile hawksbills settle into near-shore habitats with hard substrate and coral reefs, and

begin shifting their diet from omnivory to almost exclusively spongivory (Spotila 2004).

Although adult hawksbills have been known to feed in seagrass beds and

mangrove bays (Bjorndal and Bolten 2010; Bell 2013), most have a unique diet

consisting almost exclusively of sponges, with the sponge *Chondrilla nucula* being a

main prey item (Meylan 1988; Rincon-Diaz et al. 2011). This diet preference is important

for the health of coral reefs, since sponges and corals compete for space, and sponges are

often competitively superior. In particular, *C. nucula* is a very aggressive competitor with

corals for space (Hill 1998), and in many areas of the Caribbean is the dominant sponge

(Bjorndal and Jackson 2003). If sponge growth continues unchecked, the structure of the

reef may be compromised, detrimentally affecting many of the creatures that depend on

coral reef habitats. Studies indicate that predation on sponges by hawksbills is a vital

factor affecting the diversity and structure of coral reef habitats (Hill 1998; Leon and Bjorndal 2002; Bjorndal and Jackson 2003).

Studies of hawksbill foraging habits in Honduran waters are scant. However, recent work by Dunbar et al. (2008b) and Berube et al. (2012) in the waters off Roatán found that juvenile hawksbills consumed a variety of organisms. Sponges remained the primary prey item consumed, with *Melophlus ruber* and *Chondrilla caribensis* being the most common species present in diet samples. Many studies have shown that hawksbills frequently prey on *C. caribensis*, yet Berube et al. (2012) provided the first report of hawksbills preying on *M. ruber.*

Threats

Throughout human history the hawksbill has been exploited for consumptive, trade, and religious purposes (Frazier 2003). Archaeological evidence indicates that as early as the Bronze Age, approximately 6,000 to 4,000 years ago, sea turtles were an important food source for peoples living on the Arabian Gulf (Spotila 2004). The most prevalent use of hawksbills, however, was turning its exquisitely-colored carapace into a variety of "tortoiseshell" products. An extensive trade in tortoiseshell has been documented in ancient accounts by Greek, Arab, and Chinese cultures (Frazier 2003). Today, hawksbills are still hunted worldwide for their meat and eggs (Campbell 2003), yet the predominant use continues to be tortoiseshell products. The exploitation of hawksbills for this purpose is internationally widespread. In particular, Japan has a long history of fashioning hawksbill carapaces into tortoiseshell products known as "bekko," with evidence of such products having been discovered amongst the ruins of a city from

the seventh century (Campbell 2003). In the Seychelles off the east coast of Africa, commercial trade in tortoiseshell has been part of the culture for more than 200 years, and was only recently brought to an end in the 1990s by a government ban on tortoiseshell trade and export (Campbell 2003). The island of Palau, in the southeast Pacific, is another location where the hawksbill has figured prominently in native culture, with costal scutes being fashioned into bowls called "toluk" that were used as currency among women (Campbell 2003). Only in the last few decades have most countries banned the creation and sale of such products, brought about in part by the establishment of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 1973. This treaty instituted guidelines to assist governments in regulating international trade of threatened species, such as the hawksbill.

Despite the protective measures enacted, hawksbill populations have continued the precipitous decline that began during the last 3 to 4 centuries. An extensive review by McClenachan et al. (2006) examined historical nesting data in an effort to gain a more comprehensive picture of the changes affecting turtle populations in the Caribbean. Their results indicated that 20% of historic hawksbill nesting sites have been lost entirely, with another 50% diminished to perilously low numbers. On a global scale, estimated numbers of hawksbills are less than 10% of populations a century ago, and less than 5% of estimated numbers from several centuries before (Spotila 2004). The large-scale decimation of hawksbill populations for tortoiseshell is believed to be the primary cause of their low numbers today (Meylan and Donnelly 1999; Mortimer and Donnelly 2007). Although hawksbills and other sea turtles have been exploited for centuries, it is only

recently that we have begun to understand important aspects of their life history, such as their tendency to migrate between foraging and nesting grounds.

Sea Turtle Migration

The fact that sea turtles undertake large-scale migrations was first documented in the 1960s when Archie Carr published evidence that female green turtles nesting at Tortuguero, Costa Rica, were migrating from as far away as Mexico and Cuba (Carr and Ogren 1960). Data gathered over the last 50 years, first with the use of capture-mark-recapture and flipper tag returns, and then with more accurate satellite telemetry, have indicated that sea turtles may travel hundreds to thousands of kilometers between foraging sites and breeding grounds (Plotkin 2003).

The use of satellite telemetry for studying sea turtles began in earnest in the 1980s (Godley et al. 2008). This technique utilizes a small transmitter that is temporarily or permanently affixed to the carapace of the turtle. The transmitter signal is picked up and tracked by orbiting satellites, which convert the information to location data that indicate the approximate position of the turtle. The first transmitters were bulky and did not last long. However, in the last two decades transmitters have become progressively smaller and can often transmit signals for several years. Satellite transmitters have also been configured to record additional data, such as water temperature, dive depth and duration, and swimming speed (Hart and Hyrenbach 2009). This growth in satellite transmitter technology has greatly expanded our ability to determine turtle migration routes (Godley et al. 2008).

Distinctive migration patterns exist among sea turtle species, with three main patterns having been described by Plotkin (2003). The first pattern is exhibited by the primarily oceanic leatherbacks and east Pacific olive ridleys. These turtles migrate to oceanic waters in which they search for prey over vast areas that vary spatially and temporally. The second pattern is seen in flatbacks, loggerheads, and Kemp's ridleys. This group of turtles migrate to highly productive foraging areas over the continental shelves, often swimming along a coastline, with these areas varying on a small scale, yet being rather spatially and temporally predictable. The third pattern is displayed by green and hawksbill turtles, which migrate to and from small, well-established foraging areas near shore that do not vary greatly over time.

Hawksbill Migration

It was because of their fidelity to neritic foraging grounds that the question of whether or not hawksbills migrated remained debatable for many years (Witzell 1983). Only within the last three decades has the migratory status of hawksbills become well established (Plotkin 2003). Initial studies utilized flipper tag returns, and Meylan (1999a) used this method to demonstrate that Caribbean hawksbills were migrating from Tortuguero, Costa Rica, to a variety of countries, including Nicaragua, Honduras, and Panama. Troeng et al. (2005), adding satellite telemetry to a flipper tag return study, documented hawksbill migrations from Tortuguero, Costa Rica, to waters off Nicaragua and Honduras, including the Honduran island of Guanaja in the Bay Islands (Fig. 2). A study by van Dam et al. (2008) followed nesting hawksbills from Mona Island, Puerto Rico, and recorded migrations to countries as diverse as the French West Indies, the U.S.

Virgin Islands, the British Virgin Islands, Turks and Caicos, Nicaragua, and Honduras

(Fig. 3). In that study, the seven hawksbills that were tracked traveled between 84 and

2,051 km from the nesting beach to their foraging sites (van Dam et al. 2008).
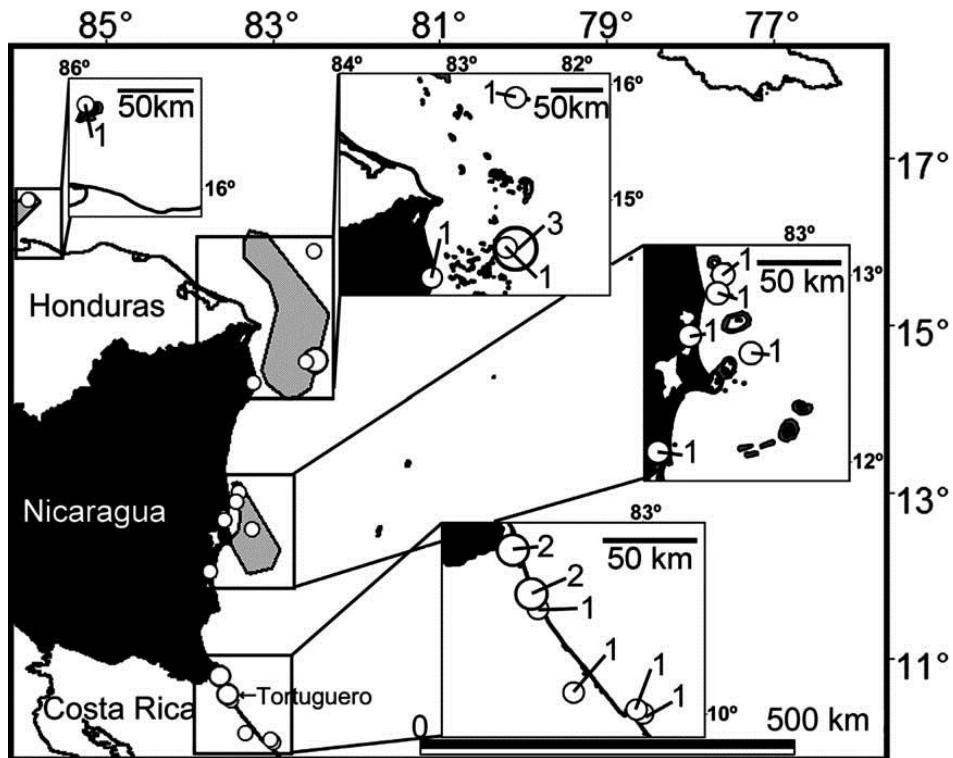
Figure 2. Recaptures of hawksbill turtles tagged at Tortuguero, Costa Rica. Open circles indicate recapture locations, coral reef concentrations indicated in grey (Bay Islands, Honduras; eastern Honduras/northern Nicaragua; central Nicaragua). Close-ups show recapture locations, number of hawksbills captured at each site, and coral reefs in grey (Troeng et al. 2005).
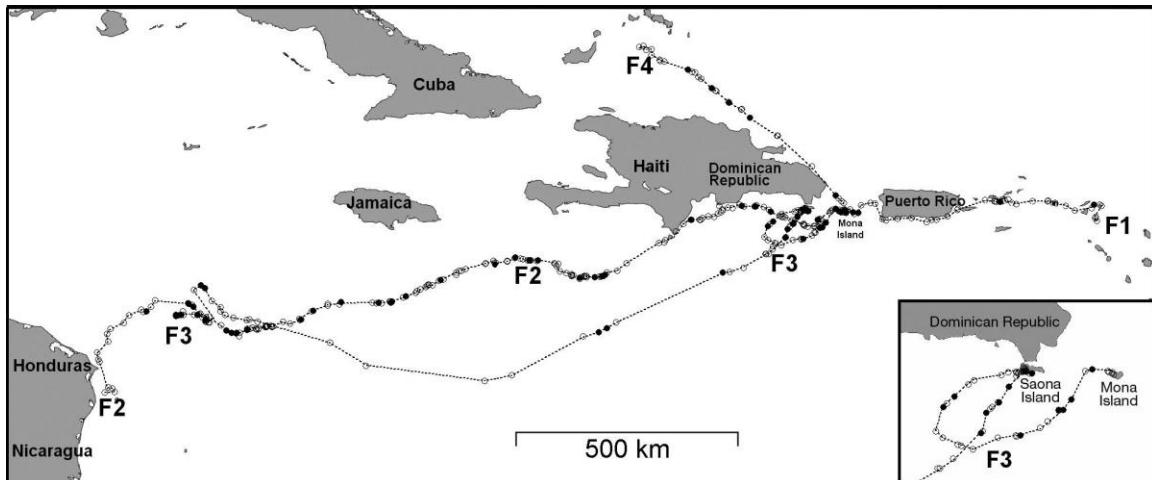
Figure 3. Migration tracks of female hawksbill turtles after nesting on Mona Island, Puerto Rico. Females F1 to F4. •: Argos location class 0-1-2-3; ○: location class A-B (van Dam et al. 2008).

Satellite telemetry is now a prominent component of hawksbill research, and facilitates the collection of information on a variety of geographic scales, as well as highlighting behavior during specific time periods. For example, Hawkes et al. (2012) tracked hawksbills between their nesting beach in the Dominican Republic and foraging sites in the Bahamas, Honduras, and Nicaragua, and determined that they demonstrated strong site fidelity. Hart et al. (2012) used satellite tracking to delineate hawksbill home ranges in the waters around the Dry Tortugas Islands off the southwest coast of Florida, while Walcott et al. (2012) employed satellite telemetry to document hawksbill behavior during the internesting period in the waters around Barbados. Unfortunately, despite great strides made with the assistance of new technologies, of the seven sea turtle species, the migration and movement patterns of hawksbills are still the least well known (Hawkes et al. 2012). While obtaining data on migrating turtles is often difficult, due to better access to turtles on the nesting beach we now possess more knowledge of hawksbill life history characteristics related to nesting behavior than at any time before.

Nest Site Selection in Sea Turtles

The selection of a nest site is of paramount importance in oviparous species. Sea turtle eggs incubate without parental care, and the successful development and hatching of the nest depends on a combination of biotic and abiotic factors. Despite understanding the significance of site selection in the nesting process, scientists have made little progress in elucidating the precise reasons a population or individual sea turtle selects a certain beach for nesting (Miller 1997). It does appear that all nesting beaches have similar characteristics, and Mortimer (1982) suggested that all have the following four:

> (1) the beach must be accessible from the sea

> (2) the beach should be high enough in elevation to keep nests from being flooded by either tides or the water table

> (3) the sand on the beach must allow adequate gas diffusion

> (4) the sand must be fine-grained and damp enough to prevent the nest cavity from collapsing during digging

Numerous studies have attempted to ascertain which factors are most important in sea turtle nest site selection. Results vary, and the importance of individual factors varies by species and occasionally by beach location. However, a few factors have consistently emerged. For example, loggerhead turtles appear to prefer sandy areas over vegetated areas (Serafini et al. 2009; Turkozan et al. 2011). Additionally, Mazaris et al. (2006) concluded beach width was the most important factor influencing nest site selection in loggerheads. In regard to microhabitat factors, a study on loggerheads by Karavas et al. (2005) investigating the structure and distribution of vegetation, as well as sand texture and pH, found nesting activity was positively correlated with well-sorted sand grain size,

and nesting activity decreased as fine sand along the length of the beach increased. Wood and Bjorndal (2000) measured beach slope, sand temperature, salinity, and water content along loggerhead tracks and at the nest site. Results in this study, in contrast to Mazaris et al. (2006), indicated that the most important factor in nest site selection was beach slope. Moisture, salinity, and temperature were not significant on their own, but it was proposed that turtles may use a combination of these signals to determine nest placement.

Leatherback turtles displayed individual preferences in nest site selection in a study by Kamel and Mrosovsky (2004). However, the turtles still displayed enough within-individual variation that it was not possible to predict nest placement. More recently, a study by Roe et al. (2013) examining broad and microhabitat characteristics of leatherback nesting beaches found that a number of factors positively correlated with leatherback nesting, including depth of the offshore approach, elevation and slope of the beach, intermediate sand grain size, and sand pH.

While these and other studies have brought to light information regarding nest site selection in different species, it appears the overall conclusion that can be reached at this stage is that sea turtles use multiple environmental cues during the process of selecting their nest sites, and these cues may vary by species and location (Mazaris et al. 2006).

Hawksbill Nest Site Selection

Hawksbills exhibit unique nesting attributes relative to other sea turtle species, as they often manifest a preference for nesting in vegetation, especially in Australia and the Caribbean (Spotila 2004). Horrocks and Scott (1991) were among the first to document this phenomenon, and found that hawksbills in Barbados preferred beaches with steeper

slopes and lower wave energy. Their results also indicated that on three beaches, hawksbills preferred to nest at 1.05, 1.18, and 1.10 m above mean sea level, and that hatching success was highest in nests that were located closest to the mean elevation. Working in Iran, Zare et al. (2012) found that 80% of hawksbill nests were laid at an elevation of 2 m or less above the high tide line, and that emergence success was highest in nests laid close to this elevation, dropping off at higher and lower elevations. Fish et al. (2005) found that hawksbills in Bonaire prefer beaches with steep slopes and to nest at a precise elevation, while work by Kamel and Delcroix (2009) on the island of Guadeloupe in the French West Indies supported the conclusion that hawksbills nest predominantly in areas of vegetation, including within the forest.

Hawksbills also show individual fidelity to specific beach habitat characteristics. Kamel and Mrosovsky (2005; 2006) conducted a series of studies on hawksbills in the French West Indies, and determined that individual populations of hawksbills may have genetically-based microhabitat preferences. Turtles nesting over several years chose sites that were very similar among seasons, even when environmental factors, such as beach width, forest width, forest composition, and weather conditions, changed. The two factors most consistent in nest site selection were the distance traveled into the forest and the amount of vegetation covering the nest. Of course, the selection of a nest site may have important implications for the internal temperature of the nest itself.

Nest Environment: Temperature and Metabolic Heating

For ectothermic organisms, temperature is one of the most important abiotic components of their environment. Sea turtles are no exception, and when it comes to the

nest environment, temperature has a powerful influence on incubation period, embryonic development, and sexual differentiation.

Within a certain temperature range, development occurs faster at warmer temperatures than it does at cooler ones. Thus, incubation duration typically decreases as nest temperature increases (Ackerman 1997). Developing sea turtle embryos have a thermal tolerance range (TTR), above and below which development ceases and the embryo will succumb if exposed to these temperatures for extended time periods.

All marine turtles exhibit temperature-dependent sex determination (TSD) (Wibbels 2003). Sea turtles lack heteromorphic sex chromosomes, and their gender is determined by the temperature at which the eggs incubate. Each species, and even different populations of the same species, have specific pivotal temperatures – the temperature at which an equal ratio of males to females will be produced. The transitional range of temperatures (TRT) is the range on either side of the pivotal temperature in which a varying ratio of males to females will occur. Beyond the TRT a nest will produce 100% males (at lower temperatures) or 100% females (at higher temperatures).

The time when sexual differentiation occurs is known as the thermosensitive period (TSP). Initial experiments suggested that the thermosensitive period corresponds with the middle third of incubation (Yntema and Mrosovsky 1982; Ackerman 1997), and this relationship is still supported by some sea turtle biologists (Spotila 2004). However, most experiments investigating TSD and TSP were conducted in laboratories under constant temperatures, which does not account for natural fluctuations, seasonal trends, or thermal gradients (Georges et al. 2005). Thus, models have been generated to account for temperature fluctuations during incubation (Georges et al. 1994; Georges et al. 2004). A

model proposed by Girondot et al. (2009) concluded that the TSP will not correspond with the middle third of incubation if a temperature trend is observed during development. However, these authors also stated that the model only applied to species that had undergone extensive study (Girondot et al. 2009). According to Glen and Mrosovsky (2004), no studies designed to determine the thermosensitive period have been conducted with hawksbills. Thus, further research should be conducted examining the relationship between temperature and hatchling development during incubation.

Embryonic growth is a metabolic process, and thus a nest will experience metabolic heating during incubation. This aspect of nest temperature has received less attention than TSD, and most studies regarding this factor began in response to the question of what effect metabolic heating may have on sex determination. Godfrey et al. (1997) investigated metabolic heating in leatherback nests, and discovered that metabolic warming was evident beginning at the earliest stages of development, but did not significantly affect temperatures during the thermosensitive period. These authors concluded that for leatherbacks, metabolic heating would only affect sexual differentiation when the sand temperature was very close to the pivotal temperature.

In response to a generally accepted belief that metabolic heating did not occur soon enough to affect sexual differentiation, Broderick et al. (2001) investigated metabolic heating in green turtle nests on Ascension Island, and discovered that taking the amount of metabolic heating into account consistently altered the hatchling sex ratio prediction, with increased female production of up to 30%. It was also shown that the amount of metabolic heating was related to the number of eggs laid and the number of hatchlings produced in a clutch. The authors therefore concluded that metabolic heating

must be taken into account when estimating sex ratios from sand temperatures on a

nesting beach.

Metabolic Heating and Hawksbills

To date, only a few studies have examined metabolic heating in hawksbill nests.

While the similarity of nesting habits enables the extension of many principles across

species, hawksbill nesting is unique in several respects that may be of consequence. For

example, hawksbills tend to nest under vegetation, digging relatively shallow nests that

are more likely to be affected by diel changes in air and sand temperature, and laying the

highest number of eggs of any sea turtle species, potentially affecting the amount of

metabolic heat produced within the nest.

The first study documenting metabolic heating in hawksbill nests was conducted

in Fiji by Raj (1976). In that study, three nests were relocated to a laboratory where the

eggs were incubated at uncontrolled room temperature. Measurements of the temperature

in the center of the nest were taken three times a day. The nest and room temperature

were equivalent for the first three weeks of incubation, then differed throughout the

remainder of the incubation period, with the nest temperature being higher.

Glen and Mrosovsky (2004) conducted a study on hawksbills in Antigua, placing

data loggers in the middle of the egg clutch, and found evidence of metabolic heating in

all nests (n = 15). During the middle third of incubation the nests experienced an average

rise in temperature of 1.1 °C, and, during the final third, an average temperature rise of

3.4 °C. In the French West Indies, utilizing data loggers in the center of the egg mass,

Kamel (2013) found metabolic heating in hawksbill nests was significantly lower when

nests were located under vegetation. Metabolic heating during the thermosensitive period of sexual differentiation averaged 0.92 °C in nests under vegetation, and 1.45 °C in nests laid in open sand. Results from these studies are intriguing, and highlight the need for additional studies to further investigate mechanisms by which metabolic heating and vegetation affect the thermal environment in hawksbill nests.

Basis for Study

Historical records indicate hawksbills were once abundant in the Caribbean Sea, with extensive nesting populations throughout this region (Dampier 1968; Meylan and Donnelly 1999). McClenachan et al. (2006) examined historical records to identify locations in the Caribbean that were important nesting areas for hawksbills. The region of the Bay Islands, located off the northern coast of Honduras, was described as one of seven major areas supporting significant numbers of nesting hawksbills during the first half of the 20th century (McClenachan et al. 2006). In their extensive report on the loss of sea turtle nesting beaches in the Caribbean, McClenachan et al. (2006) suggested that current conservation efforts aimed at protecting small numbers of nesting beaches that support large numbers of turtles may not be the most comprehensive strategy, and that conservation efforts should also focus on small nesting areas scattered throughout the Caribbean. A study on sea turtle nesting habitat in the wider Caribbean by Dow Piniak and Eckert (2011) came to a similar conclusion.

Currently, however, scientific knowledge is lacking in regard to the status of nesting hawksbills in Honduras (Meylan 1999b). Beach monitoring programs, estimates of hatching success, maps of nesting beaches, conservation programs, and other basic

information required for the protection and preservation of this species have been lacking. Recently, however, the Protective Turtle Ecology Center for Training, Outreach, and Research, Inc. (ProTECTOR) began implementing research and conservation efforts in Honduras (Dunbar 2007; Dunbar and Berube 2008; Dunbar et al. 2008a; Dunbar et al. 2008b; Dunbar et al. 2009; Dunbar 2010; Berube et al. 2012; Dunbar et al. 2013; Dunbar and Salinas 2013). Given its historical status as a key nesting ground, collecting information regarding nesting hawksbill populations in the Bay Islands is essential in enabling researchers to implement successful conservation strategies for this imperiled species.

Study Location

The Bay Islands are located in the Caribbean Sea approximately 50 km off the north coast of Honduras. The islands are extensions of the Bonacca Ridge, which forms the edge of the Honduran continental shelf. Thus, the south sides of the islands have fairly shallow waters, while on the north sides the shelf ends and slopes off into deep waters. The islands are also the southeastern termination of the Mesoamerican Barrier Reef System, which extends north along the coasts of Guatemala, Belize, and Mexico and terminates at the tip of the Yucatan Peninsula.

Utila is the smallest of the three Bay Islands at 11 km long and 5 km wide, and is located approximately 35 km from mainland Honduras (Fig. 4). It is a low-lying island with two-thirds of its surface covered by mangrove forests and swamps. The climate is tropical with an average year-round temperature of 29 °C (84 °F), and east-southeast trade winds blow steadily most of the year. Average annual rainfall is 254 cm (100 in).

While rain occurs year-round, storms are more concentrated during the rainy season from October through January.
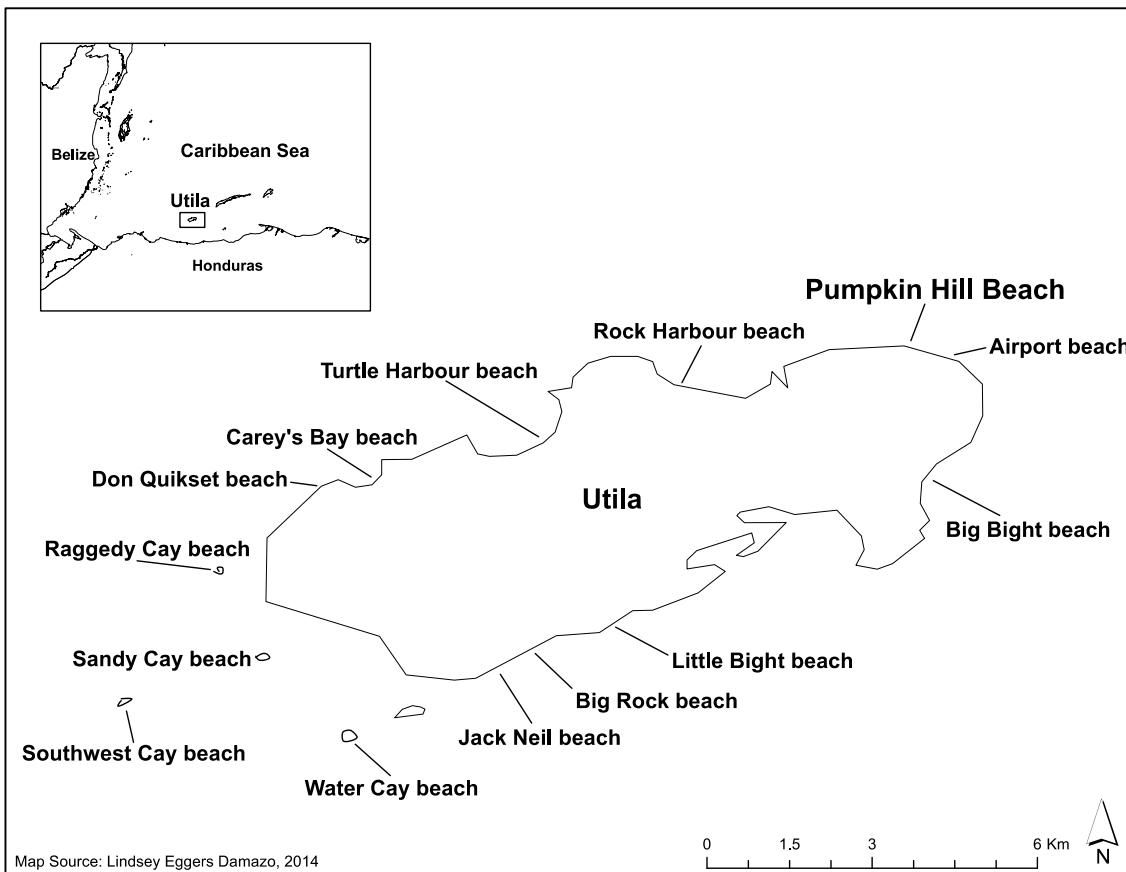
Figure 4. Map of Utila and nearby cays showing potential hawksbill nesting beaches. The study beach, Pumpkin Hill, is on the northeast corner of the island. Inset: Location of the Bay Islands in the Caribbean Sea (island of Utila in box).

Fourteen beaches on Utila and nearby cays have been assessed as potential nesting beaches for hawksbills (Fig. 4). However, nesting has been documented at only two of the beaches – Sandy Cay and Pumpkin Hill Beach (Dunbar et al. 2013). Nesting occurs primarily at Pumpkin Hill Beach, located on the northeast corner of the island just to the northwest of Pumpkin Hill (Fig. 4). Pumpkin Hill is an extinct volcano, and thus many beaches on the island consist of fossilized coral and igneous rock, interspersed with

stretches of sand. The accessible sandy area of Pumpkin Hill Beach stretches 475 m

interrupted by large spurs of sharp lava rocks, while directly offshore is a shallow

fringing reef that ends shoreward in a rocky outline at the edge of the sand. The beach is

bordered by low-lying vegetation along much of its shoreline, and the westernmost 80 m

is backed by extensive forest. Tidal changes for the region are microtidal, ranging from

30 – 35 cm (12 – 14 in).

Thesis Overview

In Chapter 2, I present the migration routes and foraging sites of two nesting

hawksbills revealed by satellite telemetry, and discuss the conservation implications of

their migration routes and destinations. In Chapter 3, nesting data from Pumpkin Hill

Beach are evaluated. Characteristics of the nesting beach are examined, and a detailed

topographic study of the beach is presented. I analyze the nest temperature findings from

the thermocouple data loggers and consider the consequences of temperature profiles

within the nest. Chapter 4 concludes the thesis with an overall summary of the research,

potential directions for future research, and an encapsulation of the conservation

implications put forward and addressed by this study.

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CHAPTER TWO

MIGRATION ROUTES OF POST-NESTING HAWKSBILL SEA TURTLES

(*ERETMOCHELYS IMBRICATA*) FROM THE BAY ISLANDS, HONDURAS

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Abstract

The use of satellite telemetry has extensively broadened our understanding of nesting sea turtle migration patterns. In this study, we affixed two platform transmitter terminals (PTTs) to nesting hawksbills on the island of Utila, Honduras. The first turtle, "Chel," spent 15 days in the waters off Utila, nested again, then set off in a northwest direction along the coast of the Yucatan Peninsula. This turtle reached her feeding grounds just south of Cozumel, Mexico after traveling for approximately 12 days. Over her migration, Chel traveled a straight-line distance of 403 km, with a total migration distance of 431 km, and a total recorded distance of 1,029 km. The second turtle, "Ginger," left Utila the day following tagging, navigating in a northwest direction through the islands off the coast of Belize for 7 days before halting her migration just south of Belize City. Ginger traversed a straight-line distance of 181 km and covered a total migration distance of 225 km, with a total recorded distance of 325 km. This study presents the first report on post-nesting hawksbill migration routes from the country of Honduras. Ascertaining the location of sea turtle migration routes is an integral step in protecting turtles that traverse international waters between their foraging and nesting sites, while migration data from these and other satellite-tagged turtles provide information that will strengthen conservation efforts for the species both locally and internationally.

Introduction

The hawksbill sea turtle, *Eretmochelys imbricata*, can be found in tropical waters around the globe (Witzell 1983). This species has been exploited by humans for centuries for its meat and eggs, but primarily because of its elaborately colored carapace which is rendered into tortoiseshell products and sold internationally (Pritchard 1997). Trade in tortoiseshell is the primary cause of the severe declines in hawksbill populations worldwide (Meylan and Donnelly 1999; Mortimer and Donnelly 2007). Due to these substantial decreases in numbers, the hawksbill turtle is currently listed as Critically Endangered on the International Union for Conservation of Nature (IUCN) *Red List of Threatened Species* (IUCN 2012).

One of the greatest threats to adult sea turtles is mortality inflicted by both commercial and subsistence fishing operations (Hays et al. 2003; Wallace et al. 2011). Many sea turtles, including hawksbills, migrate between foraging grounds and nesting sites. Studies indicate sea turtles sometimes travel along established migratory corridors between nesting and foraging sites. For example, Pendoley et al. (2014) found fidelity to migrating corridors in flatbacks (*Natator depressus*) off the northwest coast of Australia, and the same behavior was seen in migrating loggerheads (*Caretta caretta*) in waters off northeastern Brazil by Marcovaldi et al. (2010). If this type of fidelity to migratory corridors exists in a turtle population, and these corridor locations can be determined, then steps may be taken to protect turtles from fishing operations in these regions.

The advent of satellite telemetry has substantially expanded our ability to determine the migrating, foraging, and nesting patterns of sea turtles (Godley et al. 2008). The number of studies utilizing satellite telemetry to investigate marine turtle movements

has greatly increased over the last several decades, although in many cases, sample sizes remain small (Hart and Hyrenbach 2009). These studies demonstrate that both male and female sea turtles regularly undertake extensive migrations between nesting and foraging grounds. Initially, researchers suggested that hawksbills did not embark on these extensive migrations (Carr 1952; Witzell 1983; Plotkin 2003). However, studies conducted over the last three decades have demonstrated this is not the case. We now know, through both genetic analyses and satellite telemetry, that nesting hawksbills at a given site may aggregate from foraging grounds located in many different countries. For example, Meylan (1999a) collected tag return data on hawksbills in the Caribbean indicating that the turtles were migrating from Tortuguero, Costa Rica, to a variety of countries, including Nicaragua, Honduras, and Panama. Troeng et al. (2005) utilized flipper tag returns as well as satellite telemetry to document hawksbill migrations from Tortuguero, Costa Rica, to waters off Nicaragua and Honduras, including the Honduran island of Guanaja in the Bay Islands. A study by van Dam et al. (2008) followed hawksbills nesting on Mona Island, Puerto Rico, and documented their journeys to the French West Indies, Nicaragua, Honduras, Turks and Caicos, the U.S. Virgin Islands, and the British Virgin Islands. The seven nesting hawksbills in that study traveled between 84 and 2,051 km from the nesting beach to their foraging sites (van Dam et al. 2008).

Of the seven extant sea turtle species, the migration and movement patterns of hawksbills are the least well known (Hawkes et al. 2012). Historically, extensive nesting populations of hawksbills were present throughout the Caribbean (Dampier 1968). The Bay Islands, off the north coast of Honduras, have been listed as one of seven major nesting areas for hawksbills during the first half of the 20th century (McClenachan et al.

2006). Currently, little scientific information is available regarding the status of nesting hawksbills in Honduras (Meylan 1999b).

However, in the last several years, the Protective Turtle Ecology Center for Training, Outreach, and Research, Inc. (ProTECTOR) has been working to establish research and conservation protocols for hawksbills in Honduras. Initial efforts include nesting beach reconnaissance on the Bay Island of Roatán (Dunbar et al. 2008a) as well as workshops to facilitate positive change among indigenous fishermen (Dunbar 2007; Dunbar and Berube 2008). Additionally, Dunbar and Berube studied the foraging behavior and home range size of juvenile hawksbills around Roatán (Dunbar et al. 2008b; Berube et al. 2012).

This paper reports the results of the first satellite telemetry study of nesting hawksbills in the country of Honduras. The island of Utila was chosen for this study as it contains an established hawksbill nesting beach as determined by ProTECTOR and the Bay Islands Conservation Association (BICA) Utila. We describe the migration routes traveled by these turtles to reach their foraging grounds, and discuss the implications these conclusions have regarding hawksbill migration corridors in the Gulf of Honduras.

Methods

Study Area

Utila is the smallest of the three Bay Islands and is located approximately 35 km off the north coast of Honduras in the Caribbean Sea (Fig. 5). The Bay Islands lie at the southern end of the Mesoamerican Barrier Reef System, which extends north along the coasts of Guatemala, Belize, and Mexico, terminating at the tip of the Yucatan Peninsula.

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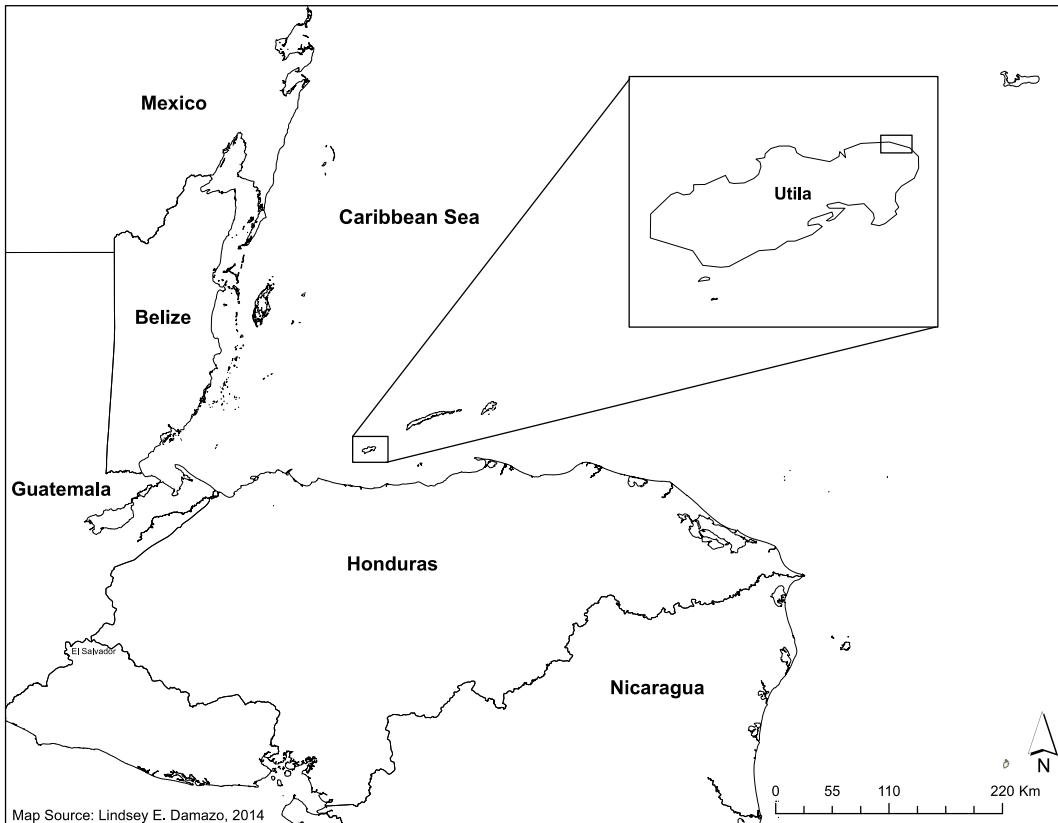
Figure 5. Map depicting the location of the island of Utila in relation to mainland Honduras and the Caribbean Sea. Inset: Island of Utila with the location of the study site, Pumpkin Hill Beach, indicated by the black box on the northeast corner of the island.

The island of Utila is 11 km long and 5 km wide, and two-thirds of the island is covered by swamp and mangrove forests. Fourteen beaches (including nearby cays) have been assessed as potential nesting beaches for hawksbills (Dunbar et al. 2013), yet only two of these beaches have documented nesting. One is Pumpkin Hill Beach, where this study took place during the 2012 nesting season, in conjunction with beach monitoring conducted jointly by ProTECTOR and BICA Utila. From June 23 to August 15, surveillance procedures involved walking the beach nightly from 18:00 to 04:30 hours. We walked the length of the beach once per hour, as Stapleton and Eckert (2008)

determined that hourly patrols will encounter almost all nesting turtles. Two nesting

hawksbills found during beach monitoring were selected for PTT application.

Data Collection

Morphometric data in the form of minimum and maximum curved carapace

length (CCL$_{min}$ and CCL$_{max}$) and curved carapace width (CCW) measurements were

obtained prior to transmitter attachment, along with photographs of the face scale

patterns, dorsal head scale patterns, and the carapace for individual identification. We

tagged turtles with metal Inconel 651-style tags (Archie Carr Center for Sea Turtle

Research, Gainesville, FL) on the right front and right rear flippers, with tags placed on

the proximal scale on the trailing edge of the flippers (as per Dunbar and Berube 2008) .

Platform Transmitter Terminal (PTT) Attachment

The PTTs were SPOT 5 (Wildlife Computers, Redmond, Washington) model

SPOT-293A Backmounts with dimensions of 72 x 56 x 24 mm and a dry mass of 110 g.

Following the acquisition of morphometric data, we prepared the carapace for PTT

application. The second vertebral scute was selected for PTT placement. We ensured that

no epibionts existed on the scute, then rinsed it with water to clean off any dirt or sand.

Next, we rubbed the area with steel wool, smoothed it with sandpaper, and then lightly

scored it in a cross-hatch pattern with scissors. Following this, we wiped isopropyl

alcohol on the scute to remove particles from the sanding process and to dry the scute.

The PTT was then activated with a magnet. We applied Sika Anchorfix two-part epoxy to

the bottom of the PTT, then set it onto the second vertebral scute with the antenna

pointing posteriorly. Additional epoxy was piped around the edges and top of the PTT and allowed to dry for 30 to 60 minutes.

Tracking

PTTs were set to transmit locations every other hour. Location data from the PTTs were obtained using the Argos system, then downloaded and analyzed using the Satellite Tracking and Analysis Tool (STAT) (Coyne and Godley 2005) and mapped with Maptool (SEATURTLE.ORG 2002). We used Argos location classes (LC) 1, 2, 3, A, and B. Argos provides accuracy estimations for location classes 1, 2, and 3, yet no such estimations are given for LC A and B. Class A locations have been shown by Hays et al. (2001) to have accuracy levels similar to LC 1. Class B location accuracy is more questionable and thus often removed from analysis (Troeng et al. 2005; Cuevas et al. 2008; Marcovaldi et al. 2010). However, in the current study some areas only provided Class B locations. For that reason, we included these data points, which has been done by Blumenthal et al. (2006) and van Dam et al. (2008). Data points were removed from analysis if they required a straight-line travel speed > 5 km/hr or were conspicuously erroneous, such as being unrealistically far inland, as described by Hays et al. (2001).

Results

The first PTT was fixed on turtle U-007-12, named "Chel," who was discovered nesting at 02:55 on July 11, 2012. After collection of morphometric data (Table 1), the PTT was applied and the epoxy allowed to set for approximately 30 minutes. During the

final 10 minutes of set time the turtle had finished covering the nest, attempted to return

to the water, and was restrained by hand.

Table 1. Morphometric data from the hawksbills with PTTs from Pumpkin Hill Beach.

Turtle	Turtle ID	Tag Number	CCL_{min}[1] (cm)	CCL_{max}[2] (cm)	CCW[3] (cm)
Chel	U-007-12	FR: YYJ294 RR: YYJ391	77.0	84.5	66.7
Ginger	U-011-12	FR: YYJ202 RR: YYJ262	79.5	81.8	66.0

[1]CCL_{min} is curved carapace length measured from the nuchal notch to the notch of the supracaudal scutes. [2]CCL_{max} is curved carapace length as measured from the nuchal notch to the tip of the supracaudal scutes. [3]CCW is curved carapace width measured at the widest point of the carapace.

The turtle returned to the water at 03:50 at N16.12337° and W086.88595°, and

the PTT began returning location data immediately. During this first encounter with Chel,

efforts to flipper-tag the turtle were not successful. However, she returned to the beach 15

days later to lay another nest and was successfully tagged at that time.

The PTT on Chel produced a total of 173 transmissions, of which 118 were used

(Table 2) in determining her travel pattern and location during 90 days of tracking.

Table 2. Number and type of Argos location classes (LC) used in mapping travels of the two hawksbills with PTTs from Pumpkin Hill Beach.

Turtle	LC 3	LC 2	LC 1	LC A	LC B
Chel	1	5	1	15	96
Ginger	3	2	3	8	42

After PTT attachment, Chel spent 15 days on the southeast side of Utila, returning to Pumpkin Hill Beach to lay a second recorded nest. Later that day, following nesting, she began traveling northwest across open water toward Belize, staying east of the Belizean islands for 5 days. Turning west, the turtle then moved along the southern-most peninsula of Quintana Roo, Mexico, and continued a northward migration near the coast for the 7-day journey up the Yucatan Peninsula. Chel ended her travels in the Bahía de la Ascensión, just south of Cozumel, Mexico, after a travel time of approximately 12 days (Fig. 6). The PTT attached to Chel continued transmitting for an additional 63 days, which she spent within the Bahía de la Ascensión.

During migration, Chel traveled a straight-line distance of 403 km, with a total migration distance of 431 km. Total movement distance recorded was 1,029 km. The final signal from the PTT affixed to Chel was received on October 9, 2012, for a total of 90 transmission days (Table 3).

Table 3. Travel and distance data for the hawksbills with PTTs from Pumpkin Hill Beach.

| Turtle	Straight-line distance traveled	Total migration distance	Total distance recorded	Number of transmission days
Chel	403 km	431 km	1,029 km	90
Ginger	181 km	225 km	325 km	19
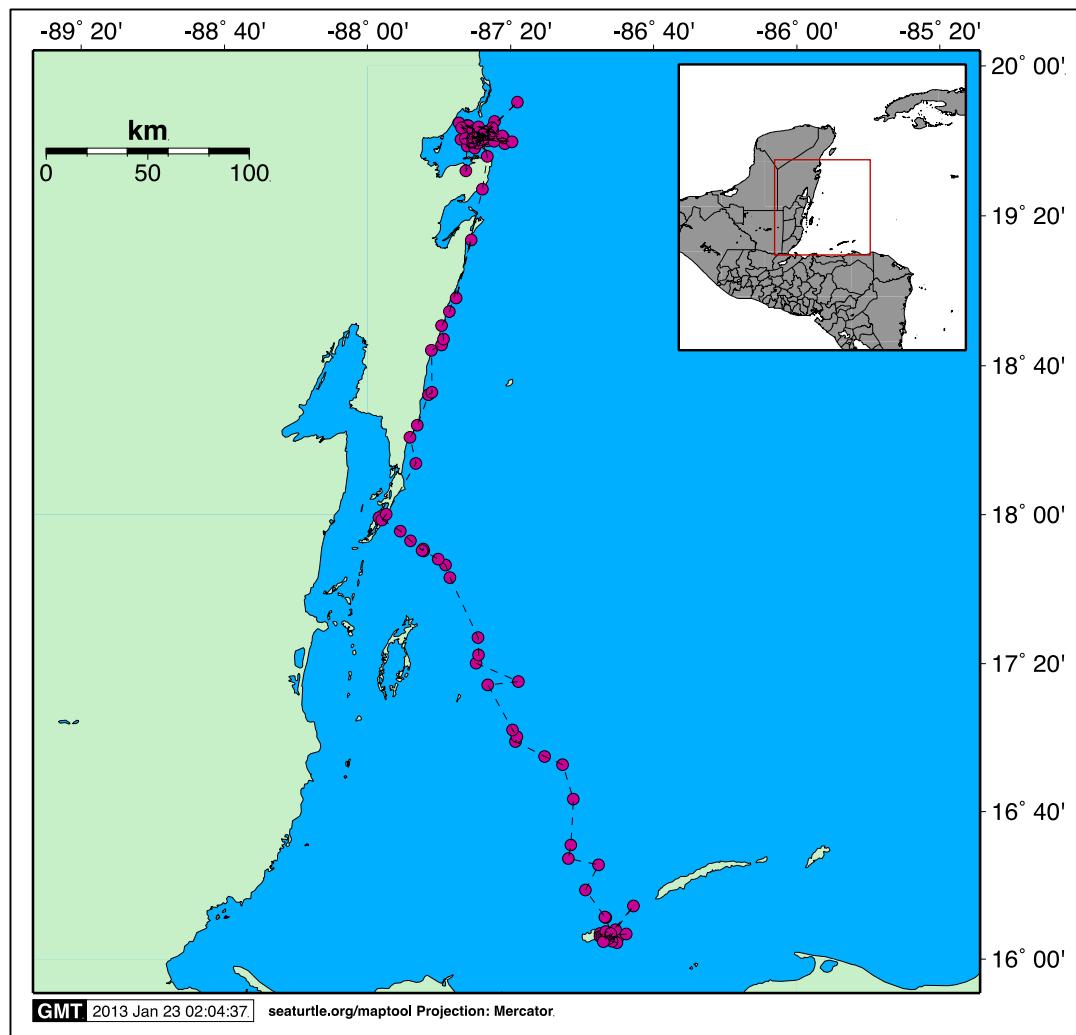
Figure 6. Map of the migratory pathway taken by Chel from Utila to the coast of Mexico.

We launched the second PTT on August 12, 2012 at 23:50 affixed to turtle U-011-12, named "Ginger," while she completed nesting on Pumpkin Hill Beach. Following morphometric data collection (Table 1) and PTT application, the epoxy dried for 60 minutes while the turtle finished covering the "nest" (she was moved to the side after completion of oviposition to enable us to apply the PTT without endangering the nest). The turtle returned to the water at 00:30 at N16.12344° and W086.88614°.

The PTT on Ginger provided a total of 76 transmissions, 58 of which were

deemed useable (Table 2) to determine her location during the 19 days she was tracked.

Ginger left Utila the day following nesting and PTT attachment, and set off in a

northwest direction. After 4 days of travel she entered the waters of Belize, passed the

cays at the south end of Glover's Reef Atoll, and changed to a due north course just south

of Ragged Cay. Three days later she halted her northward migration about 10 km off the

coast, just south of Belize City and approximately 15 km south of the Drowned Cayes

(Fig. 7), for a total travel time of 7 days. Signals were received from this area for the next

12 days, indicating Ginger remained in this region for that duration. Transmissions from

the PTT on Ginger ceased on September 3, 2012, after a total of 19 days (Table 3).

Ginger traveled a straight-line distance of 181 km and a migration distance of 225 km,

with a total displacement of 325 km.
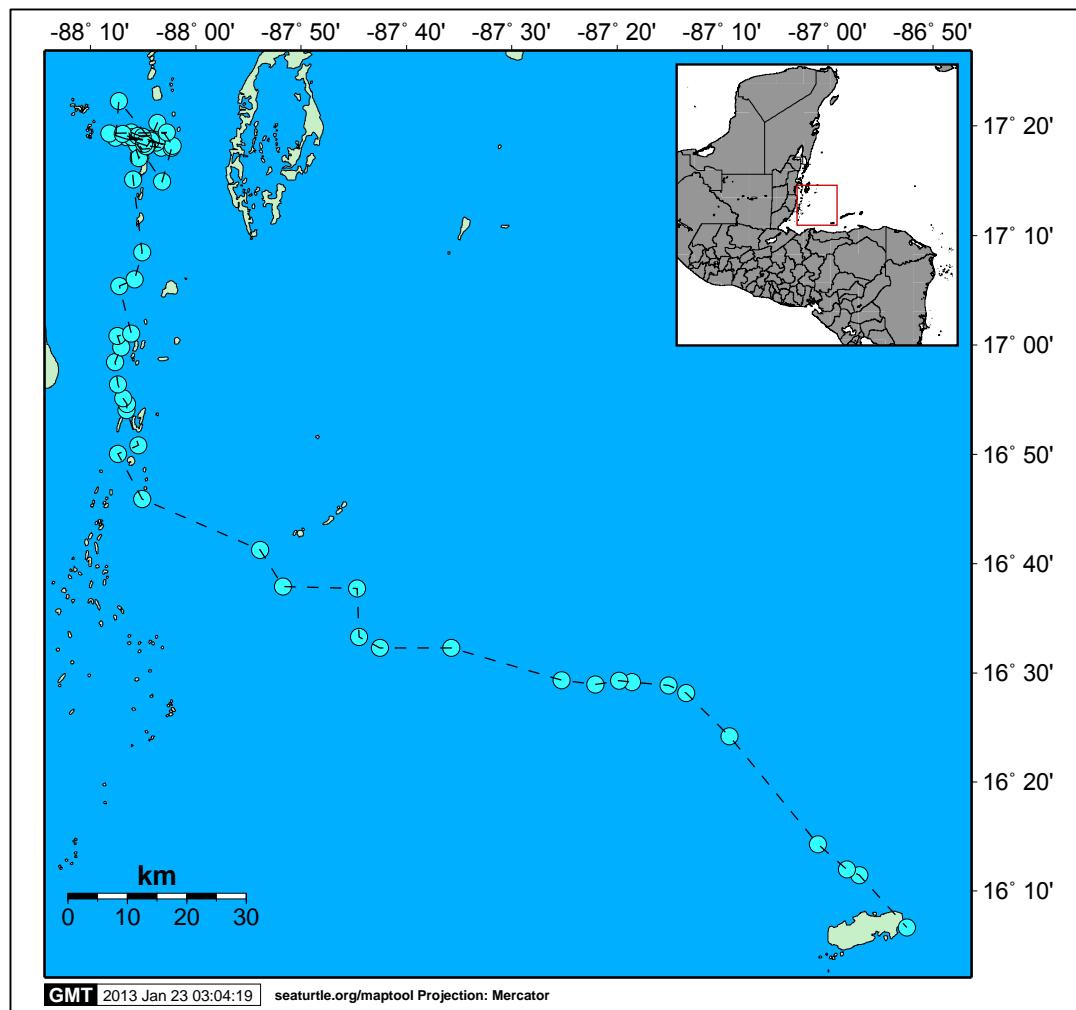
Figure 7. Map of the migratory pathway taken by Ginger from Utila to waters off Belize.

Discussion

Two nesting hawksbills from Pumpkin Hill Beach were fitted with PTTs, and their post-nesting migrations tracked for 90 and 19 days, respectively. Travel patterns indicated both turtles left Utila immediately following nesting and held to a steady travel pace for 7 to 12 days until reaching foraging grounds in Mexico and Belize, respectively.

Chel and Ginger are the first nesting hawksbills from the country of Honduras to be tracked using satellite telemetry. Both were considered to have reached their post-

nesting foraging grounds because they ceased to exhibit directional movement after 3 consecutive days, as per the criteria used by Zbinden et al. (2008) to determine when a foraging area had been reached by post-nesting loggerheads in the Mediterranean Sea.

Because hawksbills have only recently been shown to undergo migrations between their foraging and nesting grounds, there is a paucity of data regarding the length of these migrations, and the available data vary. Migrations may cover short distances of 25 to 200 km, as seen in hawksbills tracked by Balazs et al. (2000) and Parker et al. (2009) in the Hawaiian Islands, and by Mortimer and Balazs (2000) in the Granitic Seychelles. Other studies indicate hawksbills may travel from 200 km to over 2,000 km in their journey between nesting and foraging areas. Miller et al. (1998) were among the first to document this long-distance behavior in hawksbills in northeastern Australia. Subsequent studies (Cuevas et al. 2008; van Dam et al. 2008) have also established this behavior in Caribbean hawksbills. Still, no consensus has been reached explaining why some hawksbills travel short distances between their foraging sites and nesting beaches, whereas others travel great distances through seemingly suitable foraging habitat (Plotkin 2003). van Dam et al. (2008), after tracking 7 post-nesting hawksbills from Mona Island, Puerto Rico, suggested post-nesting hawksbills return to areas of known resource availability to ensure adequate nourishment after the severe energy depletion of nesting.

Categories of migration lengths have been described by Plotkin (2003) as short-range (25 – 200 km) or long-range (over 200 km). In the current study, the turtles shared a nesting beach (nesting within 75 m of each other). However, Ginger undertook a short-range migration of 181 km, whereas Chel traveled over 400 km to reach her foraging grounds. Our results indicate that the nesting beach at Pumpkin Hill supports females that

travel varying distances and migrate from different countries, a finding consistent with other hawksbill migration studies (Miller et al. 1998; Mortimer and Balazs 2000; Troeng et al. 2005; van Dam et al. 2008). Recent analysis of mitochondrial DNA from foraging hawksbills off the island of Roatán further suggests they originate from a wide variety of source populations in various countries (Wingers and Dunbar, unpubl. data).

Migration Corridor and Nesting Site Fidelity

Chel and Ginger both traveled in a northwest direction after leaving the island of Utila, initially heading towards Belize. Rimkus, working on the coast of Belize, recently documented a satellite-tagged hawksbill from Belize traveling southeast to the north coast of Honduras (T. A. Rimkus, pers. comm.). Additionally, research in the cays just south of Belize City, where Ginger's final PTT transmission was located, supports the hypothesis that the cays may act as an important corridor for migrating hawksbills (L. Searle, pers. comm.). Hawkes et al. (2012) found strong nesting and foraging site fidelity in Caribbean hawksbills tracked from the Dominican Republic, including migration to foraging areas in Honduran waters, and migration corridor fidelity has been demonstrated in hawksbills in northern Brazil by Marcovaldi et al. (2012). If the waters around Belize and Honduras are hawksbill migration corridors, then commercial and artisanal fisheries may pose threats to migrating sea turtles in this area, especially where fishing coincides with the beginning and end of nesting season. Understanding the significance of this region for migrating turtles will aid researchers in developing appropriate protective measures for areas of high-use by both fishermen and sea turtles in the Gulf of Honduras.

Limitations of Satellite Telemetry

A small number of high-quality location classes and a greater number of low-quality location classes were received in the current study, and similarly low numbers of high-quality location classes have been reported in other studies (Cuevas et al. 2008; Doyle et al. 2008; Seminoff et al. 2008). Several explanations for this occurrence have been suggested. The PTT antenna orientation on the turtle affects the amount of time the antenna is above water and able to send and receive signals. Antennas oriented anteriorly will emerge from the water longer than those oriented posteriorly. However, because hawksbills forage and rest in hard-substrate habitat, attached PTTs are generally oriented posteriorly to maximize transmitter life. This antenna orientation makes it less likely the antenna will be above water long enough for satellites to establish a high-quality location (Troeng et al. 2005), resulting in a lower number of accurate location classes. Additionally, after recapturing green turtles (*Chelonia mydas*) tracked using satellite telemetry in the Hawaiian Islands, Schroeder and Balazs (2000) found evidence that subsidence of transmissions within a few weeks of reaching a foraging area is often the result of antenna wear. Green and hawksbill turtles both exhibit a migratory pattern of traveling to fixed foraging locations close to shore (Plotkin 2003). This similarity, combined with the hard substrate of hawksbill foraging habitat, suggests hawksbill transmitters could be experiencing antenna wear at foraging sites. Since our data suggest both Chel and Ginger reached their foraging grounds, the antenna orientation and foraging style may provide a reasonable explanation for the lower number of high-quality location classes received, and explain the timing of transmission signal cessation.

Conclusions

The data obtained from tracking Chel and Ginger represent the first efforts to fill the gaps in our knowledge regarding nesting hawksbills in Caribbean Honduras. This study found that hawksbills nesting in close proximity migrated both long and short distances to foraging sites in different countries. Additionally, it appears the Gulf of Honduras may be an important migratory corridor for hawksbills. These results underscore the need to obtain a more complete understanding of the migration patterns of sea turtles in this region in order to mitigate deleterious interactions with fisheries. Furthermore, it is clear that international cooperation will be required for the development and implementation of conservation management strategies that will adequately protect this critically endangered species.

Acknowledgements

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CHAPTER THREE

BEACH AND NEST CHARACTERISTICS OF A HAWKSBILL (*ERETMOCHELYS*

IMBRICATA) NESTING SITE IN CARIBBEAN HONDURAS

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Abstract

Information on hawksbill turtle (*Eretmochelys imbricata*) nesting ecology is lacking for the country of Honduras. This study aimed to increase our understanding of hawksbill nesting in Caribbean Honduras. We conducted nightly beach monitoring on the island of Utila between June 23 and August 15, 2012. Five hawksbills laid seven nests, from which we recorded nest characteristics and hatching statistics. Nesting turtle carapace sizes were comparable to other regions, yet hatchlings were heavier. Additionally, we instrumented four nests with multiple thermocouple data loggers to record nest temperature profiles relative to control pseudo-nests. All four nests had a mean temperature above the pivotal temperature of 29.2 °C during the thermosensitive (middle) portion of incubation, whereas three of the pseudo-nests had temperatures less than 29.2 °C, suggesting metabolic heating may be maintaining nest temperatures above the pivotal temperature. However, large temperature fluctuations corresponding to rainfall from Hurricane Ernesto (as determined using a time series cross-correlation analysis) complicate efforts to estimate sex ratios. Findings from this study underscore our need to better understand the effects stochastic rainfall events have on the nest environment if we are to adequately address effects of global climate change. The nesting beach was 475 m long, yet hawksbills preferred to nest on the westernmost 80 m that was at a higher elevation and backed by extensive forest. This is the first study from Honduras to establish the presence of a regular nesting population of hawksbills as well as characterize a nesting beach.

Introduction

The hawksbill sea turtle, *Eretmochelys imbricata*, is a critically endangered species found primarily in the tropics (Spotila 2004). Extensive research on hawksbill nesting has been conducted in many regions of the Caribbean, including Antigua (Mrosovsky et al. 1992; Richardson et al. 1999; Glen and Mrosovsky 2004; Richardson et al. 2006), Barbados (Horrocks and Scott 1991; Beggs et al. 2007), Cuba (Moncada et al. 1999; Santos et al. 2006), Guadeloupe (Kamel and Mrosovsky 2005; Kamel and Delcroix 2009), Puerto Rico (Diez et al. 1998), Costa Rica (Bjorndal et al. 1985), Mexico (Cuevas et al. 2010), and the Wider Caribbean Region (Dow Piniak and Eckert 2011).

Hawksbills manifest distinctive nesting characteristics relative to other sea turtle species. Most notably they prefer to nest in vegetation, especially in Australia and the Caribbean (Spotila 2004; Kamel and Delcroix 2009). This preference for nesting under vegetation can have important effects on the nest environment. Hawksbills also tend to select beaches with a steep slope and to nest at certain elevations. For example, Horrocks and Scott (1991) found hawksbills nested at 1.05, 1.18, and 1.10 m above mean sea level on three beaches on the island of Barbados. Fish et al. (2005) determined that hawksbill nesting in Bonaire was significantly correlated with beach slope, while Zare et al. (2012) found that 80% of hawksbill nests (n = 28) were laid at an elevation of 2 m or less above the high tide line on the island of Shidvar in Iran.

Nest Temperature

As with other marine turtles, hawksbills exhibit temperature-dependent sex determination (Wibbels 2003). If incubated at a certain pivotal temperature, nests will

produce a 1:1 ratio of males to females. This pivotal temperature varies by species, and even within species by region (Wibbels 2003). Within a transitional range of temperatures (TRT), nests incubated above the pivotal temperature tend to produce a greater proportion of females, and below the pivotal temperature tend to produce a greater proportion of males. At temperatures beyond the range of the TRT, 100% males or 100% females result.

An important thermal element within the nest is metabolic heating, defined as the increase in temperature due to heat created by metabolism of embryos within the eggs (Raj 1976). Measurement of metabolic heating is achieved by comparing nest temperatures to temperatures in the sand at equivalent depths. Metabolic heating is often reported to be strongest, or only present, during the final third of incubation (Godley et al. 2001; Hewavisenthi and Parmenter 2002; Zbinden et al. 2006; Kamel 2013). However, other studies have found metabolic heating during the middle third of incubation (Broderick et al. 2001; Glen and Mrosovsky 2004; Mickelson and Downie 2010; DeGregorio and Williard 2011). Because the middle third of incubation is believed to correspond to the thermosensitive period of sexual differentiation (Yntema and Mrosovsky 1982), the potential effects of metabolic heating are important to elucidate.

Only a few studies have investigated metabolic heating in hawksbill nests. In Antigua, Glen and Mrosovsky (2004) found metabolic heating in all nests (n = 15). During the middle third of incubation, the nests experienced an average temperature that was 1.1 °C above control nests, and during the final third an average temperature 3.4 °C above the control (Glen and Mrosovsky 2004). Kamel (2013) found metabolic heating to be significantly lower when nests were located under vegetation. During the

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thermosensitive period, increased temperatures from metabolic heating averaged 0.92 °C in nests under vegetation, but 1.45 °C in nests laid in open sand (Kamel 2013).

Egg placement within the nest is another important factor related to nest temperatures. Eggs nearer the center of the clutch will experience higher temperatures than those located at the edges. Also, because temperatures at the top of the nest will be more affected by diel temperature changes than at the bottom of the nest, eggs at the top of the clutch may experience higher temperatures and/or greater temperature fluctuations than those located in the middle or at the bottom. Due to the relatively shallow nature of hawksbill nests, ascertaining whether or not a spatial difference in temperature exists within the nest is of interest.

Basis for Study

Until now, the only information available regarding hawksbill nesting in the country of Honduras was limited reports confirming individual hawksbill nesting on the islands of Roatán (Dunbar and Berube 2008; Dunbar et al. 2013) and Cayos Cochinos (Hasbun 2002). A review of the status of hawksbills in the Caribbean by Meylan (1999) reported that numbers in the Bay Islands were "badly depleted," and that the hawksbill population had "declined around Utila" in the previous 10 to 15 years. A comprehensive report by McClenachan et al. (2006) listed the Gulf Islands of Honduras (which include the islands of Roatán and Utila) as a major historical nesting site for hawksbills. The authors discussed the current conservation practice of protecting a few beaches that host large numbers of nesting turtles, and suggested an additional strategy of acquiring data from the 90% of smaller nesting beaches scattered throughout the Caribbean, to help

preserve genetic diversity and protect against stochastic events (McClenachan et al. 2006). As a small chain of islands, the Gulf Islands of Honduras (also known as the Bay Islands) are both historically important and simultaneously overlooked as hawksbill nesting habitat.

This study aimed to confirm the presence of a population of regular nesting hawksbills on Pumpkin Hill Beach on the island of Utila. Secondary goals included characterizing the nesting beach through topographic and vegetation surveys, and investigating aspects of the thermal profiles within the nests.

Methods

Study Location

The Bay Islands are located approximately 50 km off the north coast of Honduras. Utila is the smallest of the three Bay Islands and is situated roughly 35 km north of the Honduran mainland (Fig. 8). The island is 11 km long and 5 km wide, and over two-thirds of its surface is covered by mangrove swamps. The tropical climate averages temperatures of 29 °C year-round, with an average annual rainfall of 254 cm.
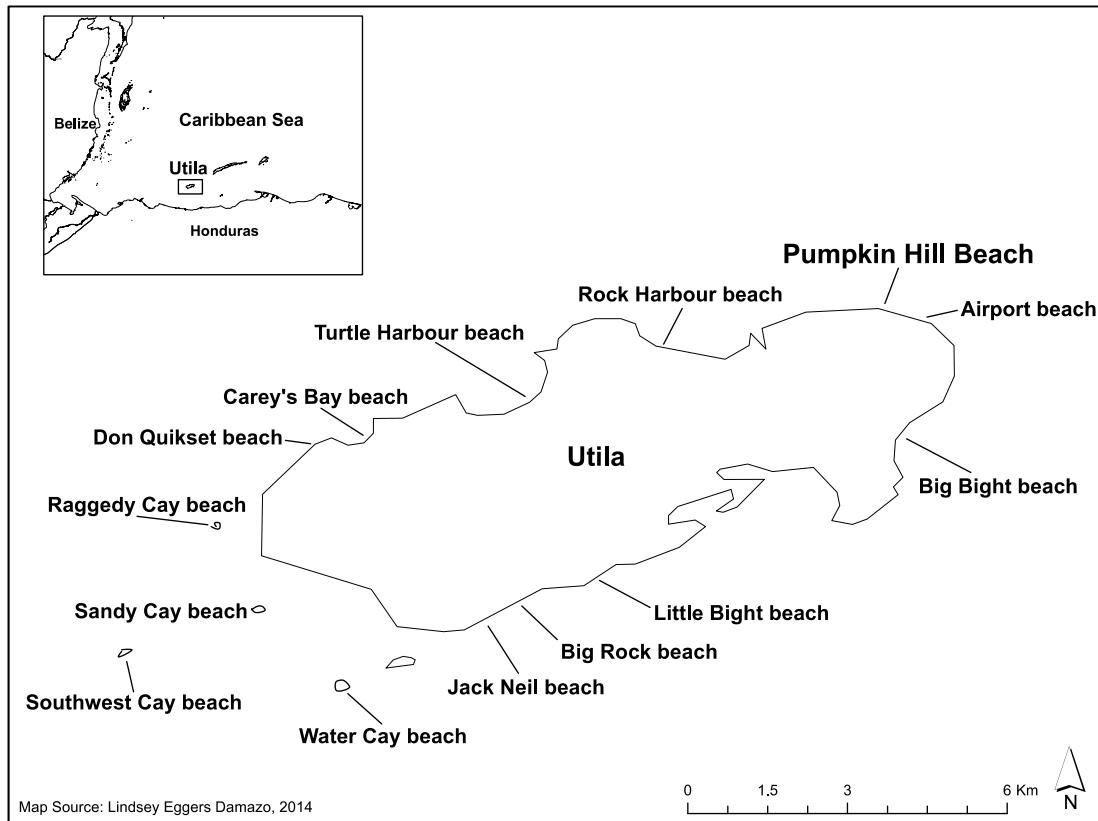
Figure 8. Map showing the island of Utila and potential hawksbill nesting beaches. Inset: Map of Utila (inset) in relation to Honduras and the Caribbean Sea.

Fourteen beaches on Utila (including nearby cays) have been assessed by the Bay Islands Conservation Association (BICA) and the Protective Turtle Ecology Center for Training, Outreach, and Research, Inc. (ProTECTOR) as possible nesting beaches for hawksbills (Fig. 8). Still, nesting has been documented at only two of these beaches – Sandy Cay and Pumpkin Hill Beach (Dunbar et al. 2013). The majority of nesting occurs at Pumpkin Hill Beach along the northeast side of the island (Fig. 8), which lies to the northwest of the extinct volcano Pumpkin Hill. Pumpkin Hill Beach is 475 m long and consists of sand interrupted by spurs of lava rock. The beach is bordered by low-lying

vegetation along most of its shoreline, with an area at the westernmost end backed by extensive forest.

Beach Profiling

Topographic data were gathered using a contractor level (Model L6-20, David White, Watseka, IL) mounted on a tripod. We took sightings on a 2-m long, 1-inch diameter PVC pipe with a measuring tape affixed along its length. Data points were collected in a grid pattern of 5-m increments in the X-direction (beach length – parallel to the waterline) and 2-m increments in the Y-direction (beach width – perpendicular to the waterline). The X-direction extended the length of the beach, and the Y-direction extended 20 m up the beach from the high tide line. We followed compass headings to ensure measurement lines remained at right angles. Measurements were taken to the nearest 0.1 cm, as this was the scale of the measuring tape, but accuracy would not be this precise due to natural variation of the substrate. We recorded substrate type (trees, vegetation, sand, or rocks) at each point, and took photographs of each vegetation type encountered for later identification.

Beach Monitoring

This study was conducted during the 2012 nesting season in conjunction with the beach monitoring program instituted by ProTECTOR and BICA Utila. We monitored Pumpkin Hill Beach nightly between 18:00 and 04:30 from June 23 to August 15. Beach crews walked the length of the beach once every hour, as per Stapleton and Eckert (2008). When nesting turtles were encountered we collected morphometric data,

including minimum and maximum curved carapace length (CCL$_{min}$ and CCL$_{max}$) and curved carapace width (CCW). Identification photographs were taken of the dorsal surface of the head, along with both lateral face scale patterns. We tagged each turtle with metal Inconel 651-style tags (Archie Carr Center for Sea Turtle Research, Gainesville, FL) in the right front and right rear flippers, with tags placed on the proximal scale on the trailing edge of the flippers as per Dunbar and Berube (2008).

Following oviposition, we carefully moved the turtle to the side of the nest to allow access to the egg chamber, then removed eggs by hand and placed them in a container lined with sand from the nest. Nest chamber width and depth were recorded, and we counted the eggs as they were returned to the nest. Ten eggs were randomly selected, gently cleaned of excess sand, weighed to ± 0.1 g, and the diameter of each measured to ± 0.05 mm with Vernier calipers. After all eggs had been returned, we covered and camouflaged the nest by hand.

Hatchling Measurements

After 52 days of incubation, beach crews monitored nests for signs of hatching. A wire-mesh cage approximately 45 cm high was placed around the nest to capture escaping hatchlings, but was not left unattended due to concerns of potential poaching. Upon emergence, hatchlings were placed in an insulated container lined with damp sand. Due to the presence of predatory ants, nests were excavated immediately. According to standard procedure, we recorded the number of live and dead hatchlings in the nest, then opened unhatched eggs and categorized them as fully, partially, or undeveloped embryos.

We transported hatchlings to a makeshift laboratory for processing, during which we placed each one in a weighing boat on a portable digital balance (DCT Dune model, Adam Equipment), weighing it to the nearest 0.1 g. Straight carapace length (SCL) and straight carapace width (SCW) were measured to ± 0.05 mm using Vernier calipers. After completing measurements, we released the hatchlings on the beach at dusk near their original nest site.

Nest Temperature

To measure temperature in the nest, we placed three DS1922L iButtons (Maxim Dallas Semiconductor, San Jose, CA) in each of four *in situ* hawksbill nests and four control pseudo-nests. The first four nests encountered received iButton data loggers. Following oviposition, nest and egg measurements proceeded as described above, except data loggers were inserted before the eggs were returned to the nest. Each iButton was enfolded in plastic wrap, secured with a twist-tie, and attached with zip ties to a 1-inch diameter, 36-cm long PVC pipe. We spaced iButtons evenly 4 to 8 cm apart (depending on nest depth) at the top, middle, and bottom of the nest. The PVC pipe allowed for precise knowledge of the location of each iButton within the nest. Each nest had a corresponding control pseudo-nest located 1 m away (parallel to the waterline), constructed of similar dimensions and containing a pipe with an identical iButton arrangement. iButtons recorded temperature every hour for the duration of incubation.

The amount of shade cover provided by vegetation at a nest site was classified as absent, partial, or complete, and based on this each nest was labeled as unshaded, partially shaded, or shaded.

A pivotal temperature has not yet been calculated for the region of Honduras, so for this paper we used the commonly reported pivotal temperature of 29.2 °C described for Caribbean hawksbills (Mrosovsky et al. 1992).

For purposes of discussion, nests were given alphabetical designations corresponding to the order in which they were laid during the nesting season.

Data Analysis

Topographic and substrate data were analyzed and plotted using MATLAB (The MathWorks, Natick, MA). Beach slope was calculated by dividing the change in height by the distance from the high tide line.

Morphometric data from nesting and hatchling turtles were analyzed using the StatPlus:mac LE (AnalystSoft, Inc.) attachment to Microsoft Excel (Microsoft Corporation, Redmond, WA). A linear mixed effects regression model was run on hatchling mass and nest temperature data using RStudio (RStudio, Boston, MA).

Nest temperature data were downloaded using OneWireViewer software (Maxim Dallas Semiconductor, San Jose, CA) and plotted using Microsoft Excel. A total of 24 data loggers were deployed, of which 18 provided useable data. We ran paired t-tests in MATLAB to compare temperatures in the nest to the corresponding pseudo-nest. We compared overall mean nest temperature to mean pseudo-nest temperature, and mean nest temperature to mean pseudo-nest temperature for each third of incubation.

Utila did not possess a weather station, so rainfall and air temperature data were obtained from La Ceiba (located roughly 38 km to the south). The amount of rainfall received by each nest was calculated using the total amount of rainfall that occurred on

the dates corresponding to the incubation period. For the purposes of the cross-correlation analysis, due to the substantial amount of rain occurring during Hurricane Ernesto, potential discrepancies between amounts received in La Ceiba and on Pumpkin Hill Beach were considered negligible.

A time series cross-correlation analysis on the nest temperature, control nest temperature, air temperature, and amount of rainfall was run in MATLAB. This analysis tested the probability that the factors were correlated while taking into account the continuity of the data. The time series measured a 0-day to 1-day delay. A 1-day delay signified that if the ambient temperature and/or amount of rainfall changed today, the nest temperature would change tomorrow, while a 0-day delay signified that if the ambient temperature and/or amount of rainfall changed today, the nest temperature would also change today.

The alpha value for all tests was 0.05, and values are reported with ± mean standard error.

Results

Beach Profiling

A diagram depicting the overall change in elevation on Pumpkin Hill Beach is provided in Figure 9. The elevation of the highest point, at 4 m, was located at the western end, with elevation gradually sloping down to the lowest point at the eastern end of the beach. Hawksbills nested predominantly on the westernmost 80 m. Nests were located at a mean elevation of 3.4 ± 0.1 m above the high tide line, beach slope at nest sites ranged from 14.7° to 24.7°, and mean beach slope across all nests was $18.2° \pm 1.2°$. The locations of nests A – G are shown in the inset in Figure 9.

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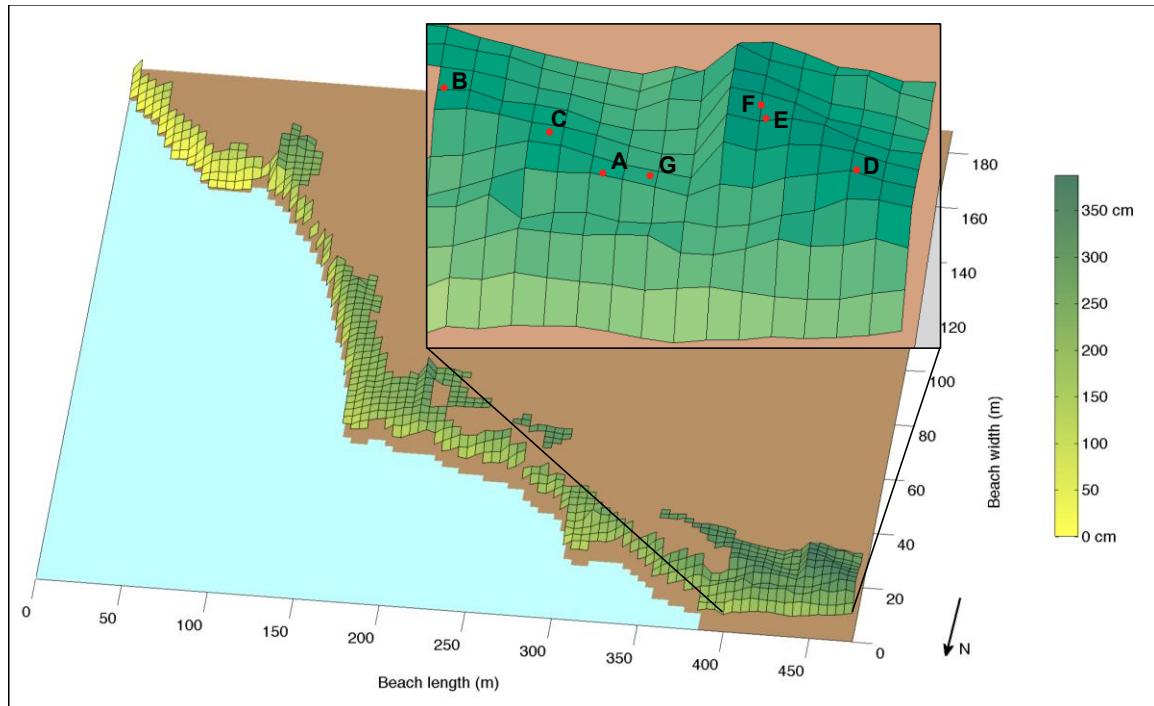
Figure 9. Diagram depicting elevation change along Pumpkin Hill Beach. Yellow indicates the lowest measured point on the beach, scaling up to dark green indicating the highest elevation on the beach. Inset: Nest locations (red dots labeled A – G) at the westernmost end of the beach.

We also plotted substrate type (trees, vegetation, sand, or rocks), and found the heaviest tree cover was located on the western end of the beach where hawksbills preferentially nested (Fig. 10). Of the seven nests successfully laid, four (57.2%) were within the forest or forest border, and three (42.8%) were laid among low-lying vegetation. Thus, we found that 100% of nests were laid in association with vegetation.

64
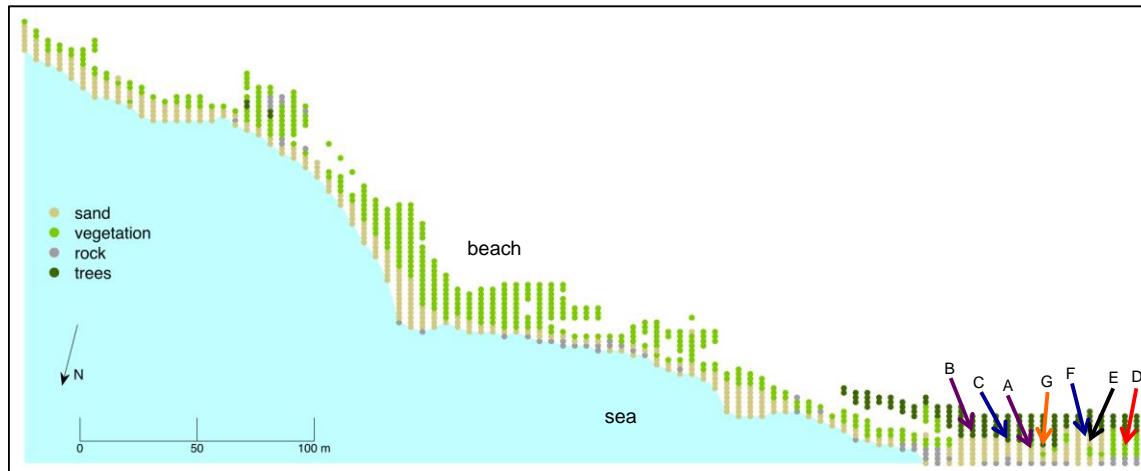
Figure 10. Diagram showing the distribution of substrate types along Pumpkin Hill Beach. Arrows indicate approximate positions of nests A − G. Nests with arrows of the same color were laid by the same turtle.

We documented 14 species of vegetation on Pumpkin Hill Beach, detailed in

Table 4. Vegetation data indicated the westernmost 80 m of beach had 51.4% tree

coverage, in contrast to only 3.8% tree coverage on the remainder of the beach.

Table 4. Vegetation species documented on Pumpkin Hill Beach.

Scientific name	Common name	Vegetation description
Acoelorrhaphe wrightii	Everglades Palm	Palm tree
Caesalpinia bonduc	Gray Nickerbean	Trailing vine
Cakile lanceolata	Coastal Searocket	Succulent herb
Canavalia rosea	Baybean	Trailing vine
Coccoloba uvifera	Seagrape	Shrub
Hymenocallis latifolia	Spider Lily	Herb
Ipomoea pes-caprae	Beach Morning Glory	Trailing vine
Scaevola taccada	Beach Naupaka	Shrub
Sesuvium portulacastrum	Sea Purslane	Prostrate herb
Sphagneticola trilobata	Singapore Daisy	Trailing vine
Suriana maritima	Bay Cedar	Shrub
Terminalia catappa	Indian-almond	Evergreen tree
Thespesia populnea	Portia Tree	Small tree
Tournefortia gnaphalodes	Sea Lavender	Shrub

Nesting Turtles and Hatchlings

Between June 23 and August 15 we recorded five turtles that laid seven nests, with internesting intervals of 15 days for both re-nesting turtles. Table 5 displays nesting turtle morphometric data and nest statistics.

Table 5. Nesting hawksbill morphometric and nest data.

Turtle ID	CCL_{min}[1] (cm)	CCL_{max}[2] (cm)	CCW[3] (cm)	Eggs laid	Mean egg mass (g)	Mean egg diameter (mm)	Date laid	Nest depth (cm)	Nest diameter (cm)
U-007-12	77.0	84.5	66.7	139	28.1	37.16	7-11-12	25	25
U-007-12	77.0	84.5	66.7	164	27.4	34.63	7-26-12	19	31
U-008-12	80.0	84.2	68.0	133	29.3	34.36	7-30-12	21	21
U-008-12	80.0	84.2	68.0	143	27.6	37.72	8-14-12	21.5	29.5
U-009-12	78.0	79.3	68.6	138	n/a	n/a	8-15-12	n/a	n/a
U-010-12	76.4	78.5	68.3	126	28.3	37.89	8-12-12	22.5	23.8
U-011-12	79.5	81.8	66.0	145	23.9	36.47	8-12-12	21.5	25

[1]CCL_{min} is curved carapace length measured from the nuchal notch to the notch of the supracaudal scutes. [2]CCL_{max} is curved carapace length as measured from the nuchal notch to the tip of the supracaudal scutes. [3]CCW is curved carapace width measured at the widest point of the carapace.

Table 6. Hatchling morphometric and nest success data from the four nests that contained iButtons.

Nest ID	Eggs laid	Mean nest temp (°C)	Incubation (days)	Mean hatchling mass (g)	Mean hatchling SCL[1] (mm)	Mean hatchling SCW[2] (mm)	Hatching success (%)	Nest success (%)
A	139	30.6	55	15.6	40.66	28.40	69.8	61.9
B	164	29.8	59	15.0	41.55	29.33	65.2	64.6
C	133	30.1	54	15.7	41.80	29.57	77.4	77.4
D	126	32.1	51	16.7	41.33	28.59	79.4	75.4

[1]SCL is straight carapace length measured from the nuchal notch to the tip of the supracaudal scutes. [2]SCW is straight carapace width measured at the widest point of the carapace.

Table 7. Hatching and egg data from the four nests that contained iButtons.

Nest ID	Eggs laid	Emerged	Live in nest	Dead in nest	Unhatched	Live pipped	Dead pipped	Fully developed embryos	Partially developed embryos	Undeveloped embryos
A	139	64	22	11	42	0	1	0	6	35
B	164	86	20	1	57	1	0	10	5	42
C	133	0	17	0	28	88	0	1	9	18
D	126	73	22	5	26	0	2	2	9	15

Nesting turtle CCL_{min} ranged from 76.4 to 80.0 cm with a mean of 78.2 ± 0.69 cm,

CCL_{max} varied from 78.5 to 84.5 cm with a mean of 81.7 ± 1.23 cm, and CCW spanned

66.0 to 68.6 cm with a mean of 67.5 ± 0.50 cm.

A total of 272 hatchlings from four nests were processed and measured (Table 6).

Hatchling SCL ranged from 36.50 to 44.85 mm with a mean of 41.50 mm ± 0.09, and

SCW ranged from 26.10 to 32.10 mm with a mean of 29.20 mm ± 0.07. Hatchling mass

spanned 12.7 to 19.6 g with a mean of 15.8 ± 0.4 g, and was positively correlated with

mean nest temperature (predicted slope = 0.61 ± 0.17, df = 2.8, t = 3.67, p = 0.04). Nest

success was defined as the percentage of eggs that hatched and survived until nest

excavation. Nest success values ranged from 61.9 to 75.4% with a mean of 69.8 ± 3.9%

(Table 6). Hatching success, defined here as the percentage of eggs that were at least

partially hatched (pipped), varied from 65.2 to 79.4% with a mean of 73.0 ± 3.3% (Table

6). Table 7 details data on hatchling emergence and stage of development at hatching.

Nest Temperature

Across the four nests with iButtons the mean temperature was 30.6 ± 0.5 °C, and

incubation periods ranged from 51 to 59 days with a mean of 54.8 ± 1.65 days. Two of

these nests, Nest A and Nest B, were laid by the same turtle. Nest A, which was partially

shaded, displayed temperatures from 28.0 to 33.3 °C with a mean of 30.6 ± 0.03 °C.

Nests B and C were located under the forest canopy and completely shaded. The

temperature range in Nest B was 26.9 to 32.4 °C with a mean of 29.8 ± 0.02 °C, and in

Nest C was 27.3 to 33.0 °C with a mean of 30.1 ± 0.03 °C. The final nest, Nest D, was

unshaded and exhibited the highest temperatures measured, ranging from 26.5 to 36.2 °C

with a mean of 32.0 ± 0.03 °C. All four nests experienced a mean temperature above the pivotal temperature of 29.2 °C during the thermosensitive (middle) portion of incubation (Nest A: 29.8 °C, Nest B: 29.3 °C, Nest C: 29.5 °C, and Nest D: 31.8 °C) (Fig. 11).
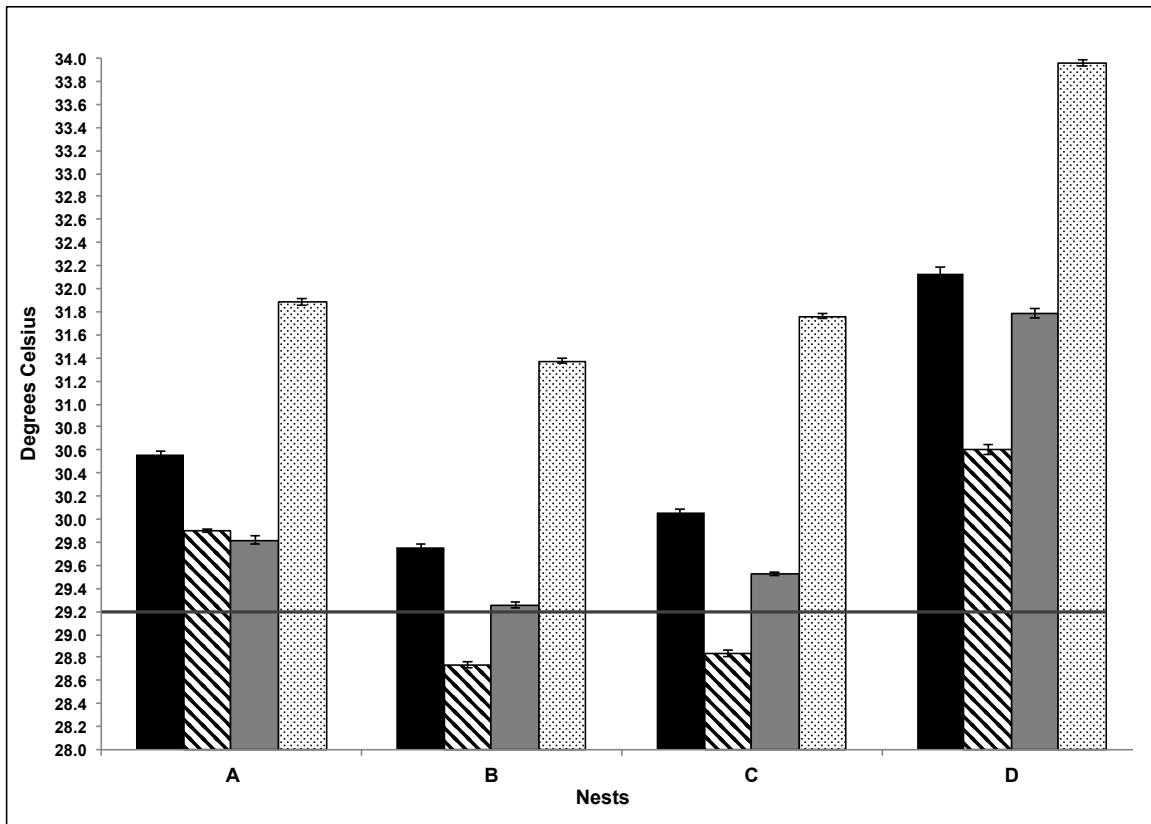

Figure 11. Mean nest temperatures over the incubation period. ■ = overall mean temperature, ▨ = first third of incubation, ▨ = middle third of incubation, and ▨ = final third of incubation. The grey line depicts the pivotal temperature of 29.2 °C. All four nests had mean temperatures above the pivotal temperature during the thermosensitive (middle) portion of incubation.

We observed metabolic heating in all nests, as differences between mean nest and pseudo-nest temperatures were statistically significant (t = 7.490, df = 3, d = 3.745, p = 0.005). When incubation periods were divided into thirds, mean temperature differences between nests and pseudo-nests were not significantly different during the first third (p =

0.38), but were during the middle (p = 0.03) and final (p = 0.001) thirds. All four nests exhibited a similar pattern of metabolic heating, with small amounts in the first third of incubation, steadily increasing throughout the middle third of incubation, and reaching peak amounts in the final third of incubation.

Recording temperature hourly allowed us to correlate changes in nest temperature with changes in the environment. Of particular note, temperature profiles of Nests A – C (Fig. 12A, 12B, and 12C) showed a sharp drop in temperature corresponding with rain events from Hurricane Ernesto. Nest D lacked this drop because it was laid after the storm period, and exhibited greater periodic diel fluctuations than the other nests (Fig. 12D). The amount of rainfall experienced by each nest is shown as total rainfall, and rainfall divided into incubation thirds, in Figure 13.

A time series analysis using a linear cross-correlation function was used to determine the degree to which changes in nest temperature corresponded to changes in ambient air temperature and amount of rainfall. In all cases, changes in ambient air temperature produced changes in nest temperature after a 1-day lag, and rainfall caused changes in nest temperature with a 0-day lag. These significantly correlated changes in nest temperature occurred only during specific periods of incubation. In Nest A, changes occurred during the middle third of incubation, from air temperature (r = 0.620, p = 0.008) and rainfall (r = -0.714, p = 0.0009) (Fig. 14A). In Nests B (air r = 0.671, p = 0.0023, rainfall r = -0.713, p = 0.0006) and C (air r = 0.665, p = 0.0036, rainfall r = -0.741, p = 0.0004) changes occurred during the first third of incubation (Fig. 14B and 14C). In Nest D, changes in air temperature affected nest temperature during the final

third of incubation ($r = 0.517$, $p = 0.0401$), but rainfall was not a significant factor during

any period of incubation in this nest (Fig. 14D).
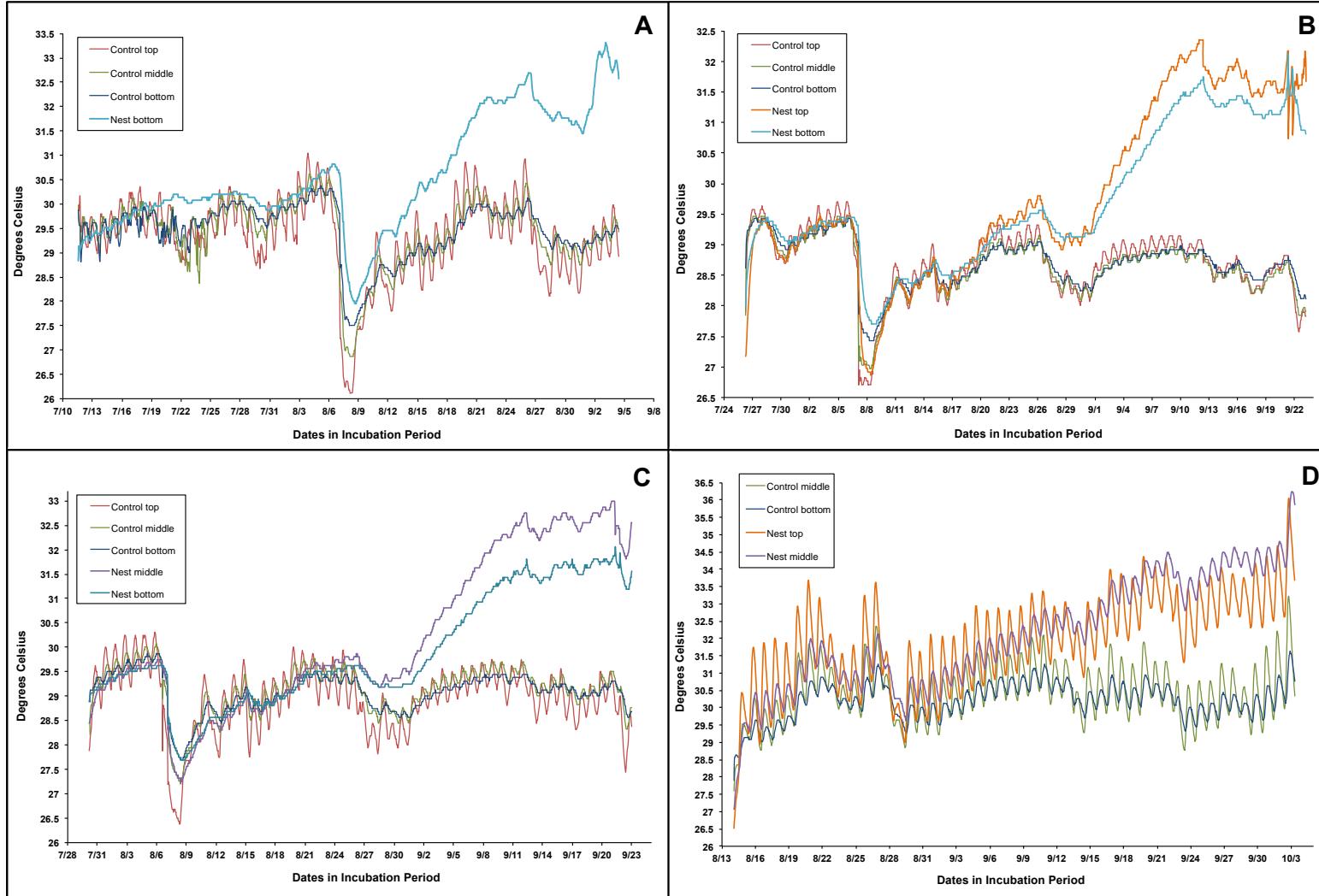
Figure 12. Temperature profiles from viable iButtons in nests A – D and their corresponding pseudo-nests throughout incubation. Temperatures from nest and control iButtons are graphed together for comparison, with each line denoting data from one iButton.
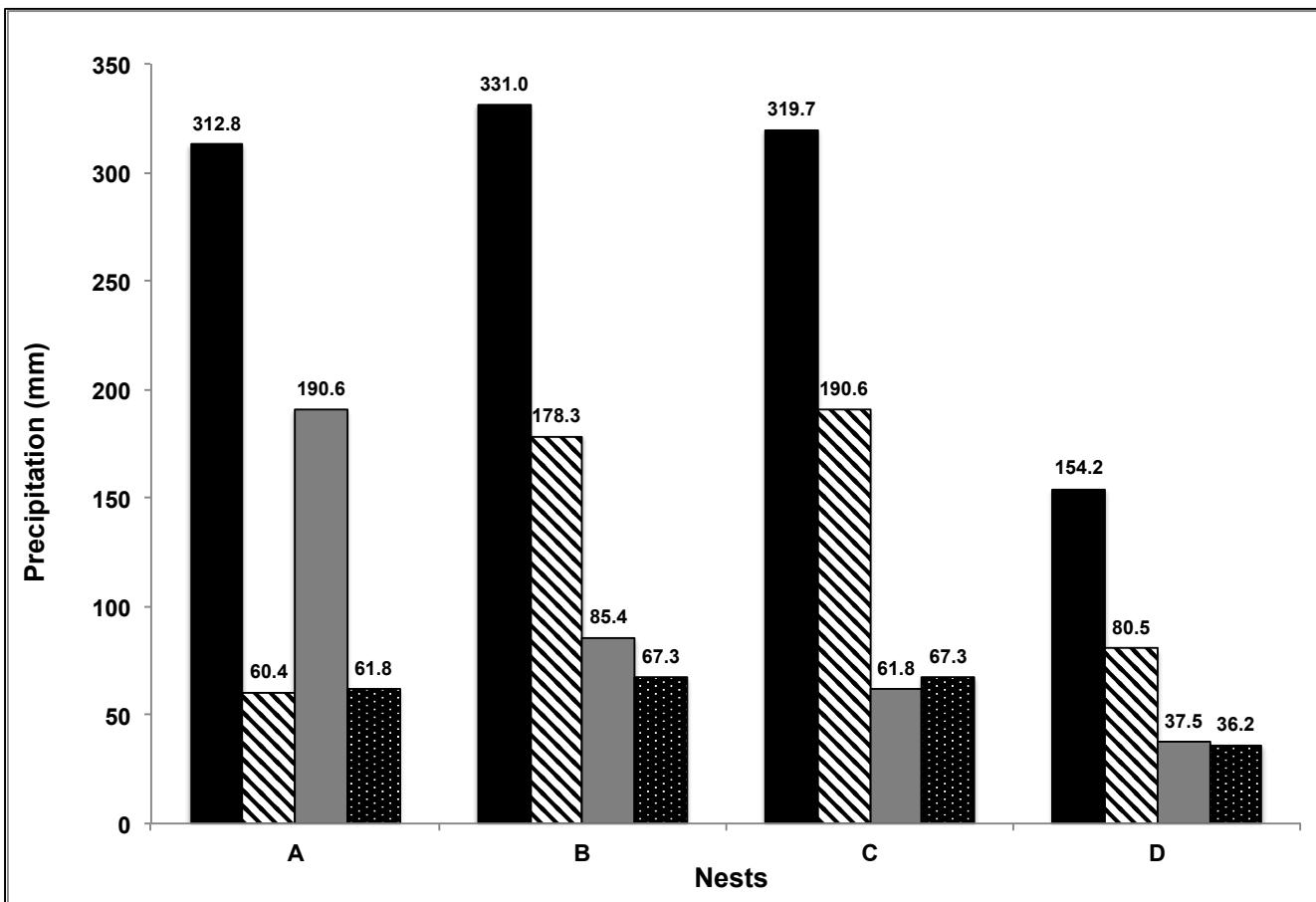
Figure 13. Rainfall amounts by nest over the incubation period. ■ = total rainfall, ◩ = first third of incubation, ▦ = middle third of incubation, and ▨ = final third of incubation.
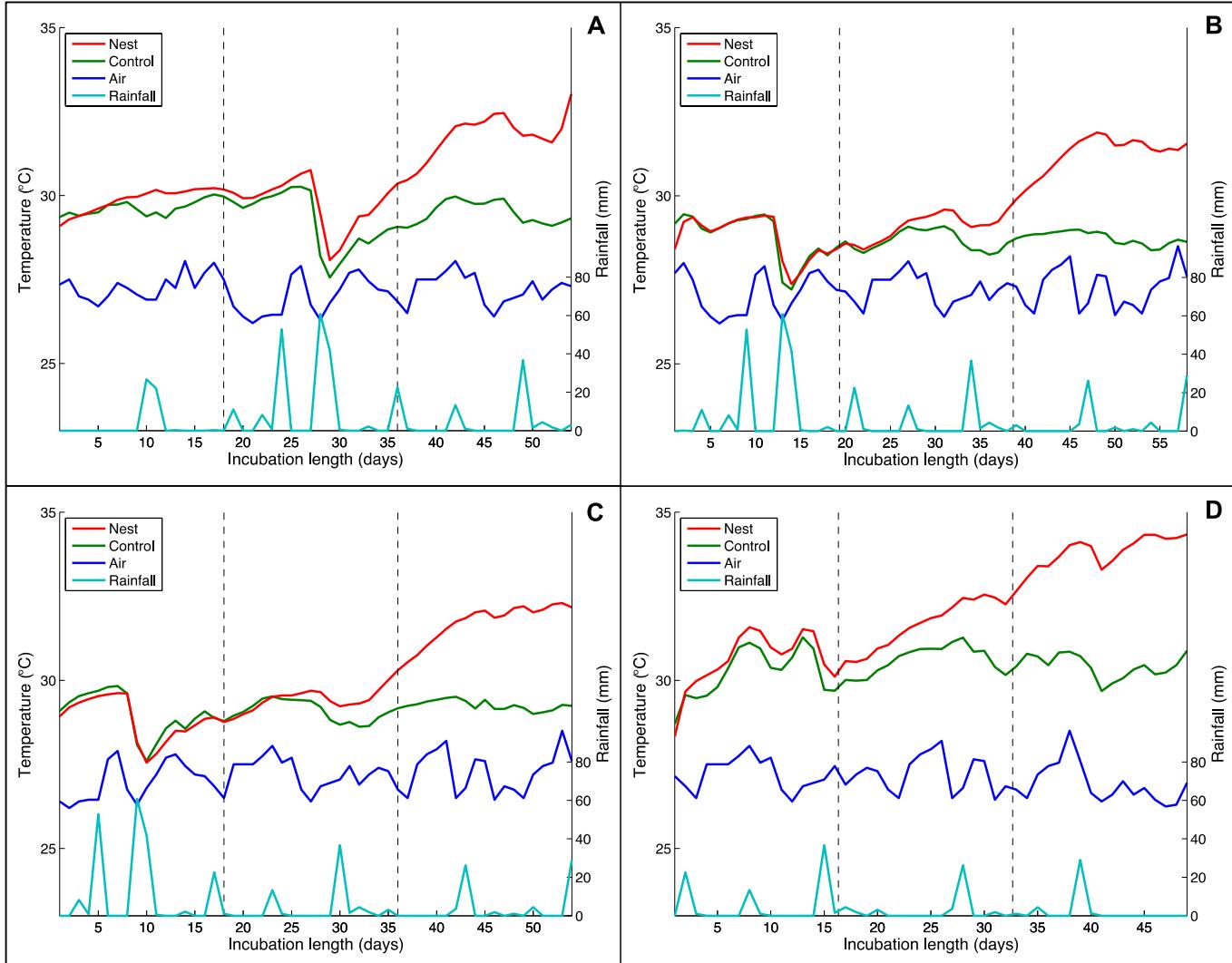
Figure 14. Time series analysis for nests A − D showing correlation between temperature and rainfall during incubation. Red line = nest temperature, green line = pseudo-nest temperature, dark blue line = ambient air temperature, and light blue line = rainfall.

Discussion

Beach Profiling

We found hawksbill nests were grouped together at similar elevations at the westernmost end of Pumpkin Hill Beach. The tendency to nest at certain elevations has also been documented in hawksbills on Shidvar Island, Iran by Zare et al. (2012) and in Barbados, West Indies by Horrocks and Scott (1991). Vegetation species documented in other hawksbill nesting studies, such as *Ipomoea pes-caprae* (Horrocks and Scott 1991) and *Coccoloba uvifera* (Horrocks and Scott 1991; Kamel and Mrosovsky 2006a), were also prominent on Pumpkin Hill Beach. Our findings that hawksbills nested among vegetation are consistent with other studies, and although our sample size was comparatively small, the percentages of 57.2% within the forest or at the forest border and 100% within vegetation were similar to other reported values. For example, in Australia, Loop et al. (1995) found 67.2% of hawksbill nest sites were located under trees. In Guadeloupe, French West Indies, Kamel and Mrosovsky found hawksbills consistently nested among vegetation as seen in multiple studies: 58.5% within the forest or forest border and 91.8% within vegetation (2005), 58.4% within the forest or forest border and 91.4% within vegetation (2006a), and 58.4% inside the forest or forest border and 96.9% within vegetation (2006b). An eight-year study by Kamel and Delcroix (2009), also from Guadeloupe, found 62.2% of hawksbill nest sites were in the forest or at the forest border, and 94% were located among vegetation. In the current study, the combination of high elevation and forest cover available to nesting hawksbills on the small westernmost area of beach likely explain the preferential nesting on this section.

Additional study into the importance of this section of beach is necessary, as few beaches on the island have such extensive forest. If this location is indeed the primary nesting beach on Utila (as it so far appears to be), additional monitoring and protection efforts are warranted. Our work in this study is in keeping with the urgings of Mrosovsky and Godfrey (2010) to investigate thermal profiles on hawksbill nesting beaches that contain intact littoral vegetation before it is destroyed.

Nesting Turtles and Hatchlings

Overall, morphometric data of nesting turtles and hatchlings were within values reported worldwide for hawksbills, although nesting turtle mean CCL_{max} and CCW were smaller than other Caribbean and Atlantic populations. For example, Beggs et al. (2007) found nesting hawksbills to have a maximum CCL of 89.7 cm in Barbados, and in Brazil a CCL_{max} of 97.4 cm and CCW of 89.6 cm were described by Marcovaldi et al. (1999). However, our values were similar to reports from the Pacific Ocean, such as 81.6 cm CCL_{max} recorded by Liles et al. (2011) from El Salvador, and 81.7 cm described by Loop et al. (1995) from Australia. While nesting turtles in the current study were smaller than Caribbean counterparts, their hatchlings were heavier, with a mean of 15.8 g. Miller (1997) reported a mean hatchling mass of 14.8 g for hawksbills, which is the same number van Dam and Diez (1998) described from Puerto Rico. Mean hatchling mass in the current study was also greater than conspecifics from the Pacific and Indian oceans, for example 14.5 g by Hitchins et al. (2004) from the Seychelles, and 13.3 g described for hatchlings in Australia by Loop et al. (1995).

We found a positive correlation between hatchling mass and mean nest temperature, which conflicts with several recent studies. In their work with leatherbacks, Mickelson and Downie (2010) found a higher mean incubation temperature produced hatchlings with lower mass. Booth and Evans (2011) reported hatchling mass and mean nest temperature were not correlated in green turtles, and a similar lack of correlation was found in olive ridleys by Maulany et al. (2012). However, working with loggerheads, Reece et al. (2002) found that hatchlings incubated at warmer temperatures during the final third of incubation had greater mass than same-sex hatchlings from cooler nests. It is possible hawksbills are similarly affected by high temperatures during the final period of incubation, resulting in greater mass at hatching. One potential benefit of hatchlings having a greater mass is the presence of a larger residual yolk store, which could sustain hatchlings for longer periods of time during their initial foray offshore (Ischer et al. 2009). To our knowledge, however, no study has yet been conducted with hawksbills correlating hatchling mass and nest temperature. Thus, the relationship between nest temperature and hatchling phenotype requires further study in this species.

Mean hatching success in the current study was low compared to some values for hawksbills in the Caribbean. Kamel and Mrosovsky (2005) reported $86.5 \pm 12.4\%$ from Guadeloupe, and Horrocks and Scott (1991) reported a success value of 84.5% from Barbados. However, our hatching success was similar to the value for hawksbills of 72.6% reported by McIntosh et al. (2003) from Antigua. While investigating factors affecting hatching success of hawksbills in Antigua, Ditmer and Stapleton (2012) found that increased vegetation cover was associated with reduced hatching success. In the current study, hatching success was highest in the unshaded nest and decreased with

increasing amounts of vegetation cover, thus the high degree of nest shading may be a factor in the lower hatching success on this beach.

Nest Temperature

In the current study, the fully and partially shaded nests (Nests A – C) had mean temperatures greater than 29.2 °C during the middle third of incubation, while their corresponding pseudo-nests had mean temperatures less than 29.2 °C. The unshaded nest (Nest D) and pseudo-nest had mean temperatures of at least 30 °C during the entire incubation period. Based on mean nest and pseudo-nest temperatures, it appears nest temperatures are being maintained above the pivotal temperature during the sex-determining phase of incubation. If that is the case, then Pumpkin Hill Beach may have produced primarily females during this particular nesting season.

However, the pivotal temperature calculated by Mrosovsky et al. (1992) was based on constant-temperature experiments conducted in a laboratory. In natural nests, fluctuations in temperature create complications for predicting sex ratios. This is highlighted by Georges et al. (2005), who modeled reptile embryo development under fluctuating temperatures. They concluded that, when natural stochastic events are taken into account, the thermosensitive period of embryonic development does not necessarily correspond to the middle third of incubation. One such event mentioned was sudden changes due to rainfall. This type of abrupt occurrence can be clearly seen in our temperature profiles, and was established in the correlation analysis that demonstrates the immediate effect large amounts of rainfall can have on nest temperature. Changes in ambient air temperature caused changes in nest temperatures with a lag of 1 day, whereas

rainfall had a more immediate effect on nest temperatures, with a lag of 0 days. Nest A temperature was significantly affected in the middle third of incubation, corresponding to a substantial drop in air temperature and an increase in rainfall. The same relationship between falling nest and air temperature and increased rainfall was seen in Nests B and C, except it occurred during the first third of incubation. All three of these substantial temperature changes corresponded to rainfall events from Hurricane Ernesto. Nest D was laid after Hurricane Ernesto occurred and received substantially less rainfall. The co-occurrence of the air temperature change on nest temperature with the rainfall change on nest temperature suggests the ambient air temperature change was a direct result of the increased rainfall, and thus it would be misleading to conclude that air temperature alone was affecting nest temperature. Therefore, taking into account the natural stochastic events that can decouple the thermosensitive period from the middle third of incubation – in this case, rainfall events from Hurricane Ernesto – makes it difficult to accurately estimate a hatchling sex ratio in this study.

Defining metabolic heating as the temperature difference between nest and pseudo-nest is standard practice, but attributing that difference entirely to metabolic heating does not account for physical parameters that differ between the nest and sand. The heat capacity of sand is given by Garrison (2012) to be 837 J/kg/°C (although it should be noted that the heat capacity of sand will vary somewhat depending on its water content and precise mineral composition). Sandoval et al. (2011) calculated the heat capacity of sea turtle eggs to be 2,200 J/kg/°C. These approximations indicate that the nest has considerably higher heat capacity than the surrounding sand. By definition, a higher heat capacity means that for a given heat transfer, the temperature will change by a

smaller amount. In a dynamic temperature system the heat capacity will act similarly to inertia in a dynamic mechanical system. Thus, we refer to the qualitative effect of the increased heat capacity on the nest temperature relative to the sand as thermal inertia.

This thermal inertia was seen in our data as smaller day-to-day fluctuations in the nest temperature compared to the pseudo-nest temperature, and as a slower response time in the nest compared to the pseudo-nest to large temperature fluctuations such as those that resulted from the rainfall during Hurricane Ernesto. This implies that an increased heat capacity of the eggs relative to the sand will result in the dampening of temperature fluctuations caused by meteorological changes.

While we were unable to determine what proportion of the temperature difference was due to metabolic heating and what was due to thermal inertia, our data suggest that thermal inertia in the nests help insulate them from extreme drops in temperature, such as those experienced during unusually heavy rainfall. Metabolic heating was clearly seen in our study as the systematic increase in nest temperature over control temperature, and may be maintaining nest temperatures above the pivotal temperature during the thermosensitive period of incubation. However, due to thermal inertia within the nest it is difficult to determine precisely how much metabolic heating is occurring. In addition, naturally occurring temperature fluctuations combined with large fluctuations due to stochastic rain events may serve to decouple the thermosensitive period from the middle third of incubation, making it unclear at what point during incubation the thermosensitive period occurs.

To our knowledge, this is the first study to place three thermocouple data loggers at precise, known intervals in a sea turtle nest. Due to the failure of some nest loggers, we

were unable to conduct comparisons between iButtons located at the same level in nests and control nests. However, our data did show a difference in temperature recorded by data loggers that were only a few centimeters apart in both nests and control pseudo-nests. Because hawksbills dig relatively shallow nests and often nest under vegetation, further study into temperature variances within the nest is warranted.

Conservation Implications

Effectively protecting sea turtles requires understanding sex ratios at the population level, which may be impacted by changes in rainfall patterns on both seasonal and long-term scales (Hamann et al. 2013). The current study illustrates the effect such rainfall events can have on nest temperatures, and underscores the need to further investigate the impacts of stochastic events on hatchling development. In addition, this study confirms the presence of nesting hawksbills in Caribbean Honduras, and is the first to characterize a hawksbill nesting beach in this country. Due to its designation as a historically significant hawksbill nesting location, furthering our understanding of nesting patterns in this region is essential to creating and implementing appropriate conservation strategies. The current study is an important step forward, and data from future nesting seasons will add to our knowledge regarding the status of this critically endangered species in the country of Honduras.

Acknowledgements

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CHAPTER FOUR

CONCLUSIONS

Study

The purpose of this study was to collect data on nesting beach characteristics and nesting ecology of the hawksbill turtle in Honduras. We affixed platform transmitter terminals (PTTs) to two nesting hawksbills to determine potential migration pathways and the location of their foraging sites, conducted transit surveys of the beach to create a topographic map depicting elevation and substrate type, and placed thermocouple data loggers in hawksbill nests to obtain thermal profiles.

I successfully achieved my first objective of affixing PTTs to two nesting hawksbills. I hypothesized that hawksbills would migrate to distant foraging grounds, and the data supported this. The first turtle, Chel, spent 15 days in Utilan waters and nested again, then left Utila and moved northwest toward Belize. The turtle traveled along the southern-most peninsula of Quintana Roo, Mexico, staying near the coast until she ended her migration just south of Cozumel, Mexico. The entire migration covered a straight-line distance of 403 km, with a total recorded distance of 1,029 km. The second turtle, Ginger, left Utila immediately following nesting and set off in a northwest direction. After entering the waters of Belize, she navigated through the southern cays, then changed to a due north course and ended her migration just south of Belize City. Ginger migrated a straight-line distance of 181 km, and covered 325 km total distance before signal transmission ceased. Thus, the nesting population on Utila supports turtles that utilize

foraging grounds in a variety of countries. The finding that Honduran hawksbills originate from different countries is supported by recent work on the island of Roatán, where Wingers and Dunbar sampled mitochondrial DNA from hawksbills in their foraging grounds, and found 10 different haplotypes. They concluded that Roatán hawksbills have wide-spread source rookeries, ranging from Mexico to Brazil (Wingers and Dunbar, pers.comm.).

My second objective, to obtain a topographic and habitat profile of the beach, was completed successfully. We determined Pumpkin Hill Beach was 475 m long and contained 14 vegetative species. My hypothesis that the beach section hosting the most nesting hawksbills would have different characteristics than the remainder of the beach was correct with regard to elevation and tree cover. Hawksbills preferentially nested on an 80-m section of beach that was at a higher elevation and backed by extensive forest.

My final objective to measure nest temperatures by placing three thermocouple data loggers (iButtons) in each of four nests and control pseudo-nests was also accomplished. Of the 24 iButtons deployed, 18 provided data. My hypothesis that a significant difference in temperature would exist between *in situ* nests and control pseudo-nests was supported by the data. Mean nest temperatures were above the pivotal temperature, while control pseudo-nests were below, suggesting that metabolic heating is a possible factor affecting sex ratio on this beach. However, temperature fluctuations that occur in natural nests make it difficult to ascertain at what point during incubation the thermosensitive period actually occurs (Georges et al. 2005). The time series cross-correlation analysis conducted on nest temperature data highlighted the strong effect

unusually high amounts of rainfall can have on nest temperatures, as large temperature fluctuations were especially prominent after extensive rainfall from Hurricane Ernesto.

Applications to Conservation

Hawksbills are critically endangered throughout their range, and their numbers in the Caribbean have been drastically reduced (Dampier 1968; Meylan and Donnelly 1999). The Caribbean coast of Honduras, and in particular the Bay Islands region, have been described as a historically important nesting area for this species (McClenachan et al. 2006). However, almost nothing is known about the status of nesting hawksbills in that country (Meylan 1999). Dunbar and Berube (2008) and Dunbar et al. (2013) report some hawksbill nesting activities on Roatán, Utila, and associated cays. Nevertheless, the current study is an important step in our efforts to research nesting hawksbill populations in Honduras, as this is the first regular nesting population to be reported from this area.

Studies suggest that migrating sea turtles often follow established corridors when migrating between their nesting and foraging grounds. Griffin et al. (2013) found that female loggerheads followed migration pathways between nesting and foraging areas off the southeastern coast of the United States. Marcovaldi et al. (2010) demonstrated similar behaviors in post-nesting loggerheads along the northern coast of Brazil, where the turtles followed pathways of up to 2,400 km between nesting and foraging areas. In a subsequent study in the same region, Marcovaldi et al. (2012) reported migration corridor fidelity in hawksbills, with turtles that traveled north using the same corridor as loggerheads in their previous (Marcovaldi et al. 2010) study. Working on the north coast of Australia, Pendoley et al. (2014) found that flatbacks traveled along specific pathways

in their migrations. A corridor of 30,800 km^2 was defined, of which 52% was within established marine reserves. In addition, the primary corridor area coincided with the migration pathways of a number of other marine vertebrates, including olive ridleys (*Lepidochelys olivacea*) (Pendoley et al. 2014). This finding of sea turtles utilizing marine protected areas in their travels is encouraging, as it supports efforts to address threats to migrating sea turtles.

Currently, the most detrimental human impact on sea turtle populations is fisheries bycatch (Lewison et al. 2013). While large-scale commercial fisheries do immense damage, research suggests that small-scale fisheries may produce as much bycatch as industrial fleets (Lewison and Crowder 2007). These small-scale fisheries are particularly prevalent in developing countries (Bene 2006), such as Honduras. Current strategies to reduce sea turtle bycatch are being designed based on insights into sea turtle ecology gained from satellite telemetry (Lewison et al. 2013). Our data from satellite tracking, along with the work of researchers in Belize, suggests that the Gulf of Honduras may be a migratory corridor for hawksbills. Determining the location of migration pathways, as well as the timing of migration in this region, will enable researchers to work more effectively with local communities and small-scale fisheries in reducing sea turtle bycatch. For this strategy to succeed, a cooperative international effort will be required. Managing the protection of marine vertebrates that travel through international waters and use resources in multiple countries may be both complicated and challenging (Moncada et al. 2012). However, this type of cooperation will be necessary to address threats to sea turtles in the Gulf of Honduras.

Another significant threat to sea turtle populations is global climate change. The warming of the earth's climate system was declared unequivocal by the Intergovernmental Panel on Climate Change (IPCC) (IPCC 2007). Sea turtles will be affected by changes to numerous climatic processes (including precipitation and storm activity) at all life stages. However, the changes likely to be most readily detected are those found during the terrestrial reproductive phases, such as egg laying, egg incubation, and hatchling success (Hamann et al. 2013). These aspects of reproduction are particularly susceptible to climate change because of their relationship to temperature.

The IPCC predicts that severe weather events, such as tropical storms, are likely to increase (IPCC 2007). In order to develop the knowledge required for accurate predictions of sex ratios at the population level, it is essential that we determine the effects that changes in precipitation patterns may have both seasonally and long term (Hamann et al. 2013). Reductions in nest temperature due to rainfall, as seen in the current study, highlight the need to better understand the effects of large temperature fluctuations within the nest, especially those caused by stochastic events such as unusually high amounts of rainfall from tropical storms.

In addition, due to connections between sex ratio and nesting beach characteristics, ascertaining the function of nest beach selection and nesting site fidelity has been identified as a research priority in order to allow researchers to develop conservation protocols in response to increased climatic temperatures (Hamann et al. 2010). Our findings of the intraseasonal fidelity shown by nesting hawksbills to a small section of Pumpkin Hill Beach underscore the need to determine the reasons this section

of beach is favored by hawksbills. Results from the current study, such as the topographic profile of the beach, provide a foundation for acquiring these important types of data.

Limitations of This Study and Recommendations

This study provided new information on Honduran hawksbill nesting ecology. However, beach monitoring was limited to a single nesting season. To gain a more complete picture of the importance of this nesting beach to the region, beach monitoring should continue. Hawksbills nest every 2 to 3 years; thus, a long-term study would be beneficial, providing further information regarding the size of this nesting population.

Although 18 of the 24 data loggers successfully recorded data, no nest had all three data loggers survive, and none of the nests had the same combination of data loggers survive (e.g., one nest had the top and bottom, whereas another had the middle and bottom, etc.) Data loggers fared better in pseudo-nests, suggesting a mechanical reason for logger failure, perhaps resulting from the movement of hatchlings. Providing a protective shield for the data loggers could allow for better logger survival.

The prohibitive cost of the PTTs limited the number in this study to two, and while they provided useful data, more nesting hawksbills should be tracked to develop a better idea of the international status of the population. Also, PTTs should be programmed to record additional data, such as diving depth and duration, as well as sea surface temperature. These types of behavioral and environmental data may allow for a better understanding of the factors influencing turtle behaviors during migration.

Future Directions

The current study is the first report of a small but regular nesting population of hawksbills in Caribbean Honduras. The nation of Honduras does not currently have a published national plan for the study and protection of sea turtles (Dunbar and Salinas 2013). Research and conservation protocols developed from the studies on Utila may provide a basis for management strategies that could be implemented throughout the country. Additional study into hawksbill life history could allow for the development of site-specific protective measures, which local communities could develop and enforce. Ideally, this would lead the community to view themselves as caretakers of an important population of endangered turtles.

To build on results from the current study, future research could include further expansion of the techniques used, as well as additional procedures in both tracking and nesting beach studies.

1. Tracking Hawksbill Internesting and Post-Nesting Movements

Nesting hawksbills should continue to be fitted with PTTs for long-distance tracking to ascertain the location of their foraging sites and migration routes. In addition, it would be advantageous to employ finer-scale GPS tracking to establish turtle movement patterns around the island during internesting periods. This information would be particularly useful in establishing local fishing and recreation guidelines to better protect hawksbills during the nesting season.

To augment fine-scale tracking of internesting hawksbills, it would be informative to survey the habitat in the regions they frequent. This would address the question of whether or not internesting hawksbills in this population feed between oviposition events.

First-hand observation of internesting turtles would provide valuable information, and if turtles are noted to be feeding, then a detailed transect survey of the reef identifying available species would help elucidate attributes of the internesting diet.

2. Factors Affecting Nest Site Selection and Embryo Development on a Hawksbill Nesting Beach

To better understand how the nest behaves thermodynamically and how it is affected by abiotic factors, thermocouple data loggers need to be placed in a greater number of nests. Ideally, this would allow for pairwise logger comparisons between nests, which may establish the presence of temperature differences at varying nest depths. Additionally, given the importance of moisture in the nest for successful embryo development, it would be worthwhile to use data loggers that also measure humidity. This would allow for the creation of both a thermal and a hydro profile within the nest.

In addition to the egg and nest measurements taken in this study, further nest measurements could include depth from the nest bottom to the top of the sand, and from the top of the egg mass to the top of the sand. This could provide an accurate picture of how far the nest is below the sand surface, which would be useful when analyzing nest temperature fluctuations and diel changes in air temperature.

The amount of shade cover provided by vegetation should be quantified at each nest site to enable more thorough analyses of nest temperature data. Overhead vegetation could be quantified with a densiometer, and the degree of nest shading should be noted at intervals throughout the day.

In tandem with nest temperature data, abiotic factors affecting the beach need to be characterized. On-site meteorological data should be collected at varying times of the

day. Weather measurements could include amount of precipitation, wind speed, and air temperature. This information could be correlated with nest temperatures, providing a better understanding of the interaction between biotic and abiotic factors that affect nest temperature and hatchling development.

In regard to nest site selection, two other useful factors to measure are sand grain size and salinity levels in the sand. Taking measurements at the nest site, along the turtle crawl, and at non-nesting sites along the beach would help establish whether or not significant variations in these traits exist on the preferred section of nesting beach.

Finally, ambient light from the town of Utila was noted on the eastern section of beach, but was not noticeable on the forested western end where turtles preferred to nest. Thus, nighttime light levels should be measured at different sections of the beach to determine if this affects hawksbill nesting site selection.

Conclusion

As ecosystems continue to be modified as a result of global climate change, it will be imperative that researchers adequately comprehend the factors affecting sea turtle nesting behavior and hatchling development in order to develop appropriate management strategies. Further research remains to be done, but the current study provides an important foundation for hawksbill research in Honduras, a region where as yet we have insufficient knowledge to successfully protect this critically endangered species.

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