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The influence of lunar phases, weather and tidal patterns on the nesting activity of adult female leatherbacks (*Dermochelys coriacea*) in Tobago, West Indies

Figure 1: Nesting female leatherback turtle (*Dermochelys coriacea)*

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Abstract

The leatherback turtle faces a number of global and local problems that have lead to significant declines in the majority of populations worldwide. Data on leatherback turtles' habitat use, spatial distribution and population status at a regional and local scale are important as it will be useful to know how much various environmental factors influence the nesting activities of leatherback turtles so conservation effort can be planned accordingly. Using data collected by Save Our Sea turtles (SOS) Tobago this study analysed the nesting events of female leatherback turtles from Tobago's three leatherback index beaches from 2005-09 to establish whether certain environmental factors influence nesting events or event outcomes. Leatherback nesting did not vary between lunar phases; weather had no biologically significant affect on nesting; leatherback emergence time was not correlated with the time of high tide; high frequencies of nesting events were observed at and after high tide, with high nesting frequencies continuing to low tide; leatherbacks appeared to be using time at night as a cue to initiate nesting; individual patterns of nesting were similar to nesting trends for Tobago's leatherback nesting population.

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1. Introduction

1.1. *Threats, conservation status and distribution of leatherback turtles*

The leatherback turtle (*Dermochelys coriacea*) is the only member of the family Dermochelyidae (Genus: *Dermochelys*) and is morphologically distinct from other sea turtles by the presence of leathery skin on its dorsal surface with large hydrodynamic ridges (Figure 1), rather than a shell overlaid by keratinous plates as found in the family Cheloniidae (Wyneken, 1996; Reina *et al*., 2002).

Leatherbacks face a number of problems on a global scale due to their migratory, pelagic life-history (Hendrickson and Balasingham, 1966). Commercial fishing equipment, such as long lines, shrimp nets and gill nets entangle and drown sea turtles that are then discarded as ‘incidental by-catch’; this is the main killer of leatherbacks worldwide (Sarti Martinez, 2000; Lewison and Crowder, 2007). Turtle Excluder Devices (TEDS) allow turtles to swim free from nets and are compulsory on US trawlers (Epperly, 1996), but lack of effective monitoring of pelagic fishing operations still causes significant by-catch mortality, especially in the Pacific Ocean (Sarti Martinez, 2000).

Local and regional pressures can also have devastating effects on leatherback populations e.g. egg harvesting by locals in Malaysia is believed to be the main reason for a crash from 10,155 to 37 clutches per annum over forty years (Sarti Martinez, 2000). Adult leatherbacks are viewed as a traditional food source in Tobago and are poached and eaten by locals (Clovis, 2005). The presence of an open season in Tobago (September to February) also does little to discourage local poaching of leatherbacks, green and hawksbill turtles (Lalsingh, 2008). Green turtle (*Chelonia mydas*) meat is preferred to leatherback meat in Tobago but with significant decreases in green turtles, poaching of leatherbacks may occur more often and opportunistically if nesting beaches are not monitored during the nesting season (Clovis, 2005). Coastal development and human recreational activities on local nesting beaches and feeding grounds may add further pressure on local numbers of nesting leatherbacks by destroying/disturbing large nesting and/or incubating nests. Artificial lights from beach developments can disorientate and deter adult turtles from nesting on these beaches; and if nesting does occur hatchling mortality may be high as hatchlings could move towards the artificial light source rather than the sea, therefore increasing the possibility of dying by exhaustion, dehydration or predation (Lutcavage, 1996).

The leatherback turtle's life history characteristics; slow, delayed sexual maturity, with high rates of egg and hatchling mortality further add to pressures at local and global scales and can cause populations to become depleted (Thorbjarnson, 2000; Seminoff and Shanker, 2008).

Leatherback turtles, as a species, are listed as critically endangered on the International Union for Conservation of Nature and Natural Resources (IUCN) red list and also included on Appendix 1 of the Convention on Trade in Endangered Species of Flora and Fauna (CITES), thereby preventing import or export of sea turtles and/or sea turtle products. Leatherbacks are also listed on Appendices I and II of the Convention on Migratory Species (CMS), which promotes and protects wildlife and habitats on a global scale. The Trinidad and Tobago Conservation of Wildlife Act (Chapter 67:01) bans turtle hunting from 1st March to 30th September and the Local Fisheries Act of 1975 (Chapter 67:51) states that no person shall catch, kill or sell turtles and/or turtle eggs during the nesting season. It is reported that Caribbean nesting populations of leatherbacks may be stabilising or increasing e.g. St Croix, US Virgin Islands. Atlantic leatherback populations show a similar trend e.g. an increase in the number of nests per annum in Suriname and French Guiana has been observed by Girondot *et al*. (2007), but Pacific leatherback populations have reportedly declined in regions such as Playa Grande [Costa Rica], Mexiquillo [Mexico] and possibly as much as 80% in Terengganu [Malaysia] (Sarti Martinez, 2000; Seminoff and Shanker, 2008). Although leatherbacks are described as being critically endangered due to an overall decrease in global nesting trends (IUCN Red List; Sarti Martinez, 2000) the existence of regionally distinct populations that are showing positive signs of recovery due to long-term conservation efforts may be referred to as 'conservation units' as these populations may not be in decline (Seminoff and Shanker, 2008). By identifying regional populations where leatherbacks are truly endangered greater conservation efforts can be allocated to protect these populations.

Leatherback turtles have a worldwide distribution being found in tropical and sub-polar regions (Figure 2). Leatherbacks grow much faster than other species of marine turtle, and reach large body sizes (Davenport, 1997); with a typical curved carapace length of 130-170 cm, and weigh up to 900 kgs (Zug and Parham, 1996; Meylan and Ehrenfeld, 2000). Leatherbacks' specialised diet of jellyfish, salps and other gelatinous organisms (Bjorndal, 1996) are spatially and temporally variable and unpredictable (Plotkin, 1996). As a result leatherbacks migrate large distances between nesting periods (~30-35 km/day (Hays *et al*., 2006)). They are able to exploit colder waters (< 20 degrees Celsius) that other sea turtles cannot survive in due to their unique anatomical and physiological adaptations i.e. a thick layer of subcutaneous blubber, counter-current heat exchangers in their flippers, specific compositions of lipids and thermal independence of muscle tissue metabolism; these specialisations allow leatherback turtles to thermoregulate and they are therefore considered endothermic (Davenport, 1997; Wallace and Jones, 2008).

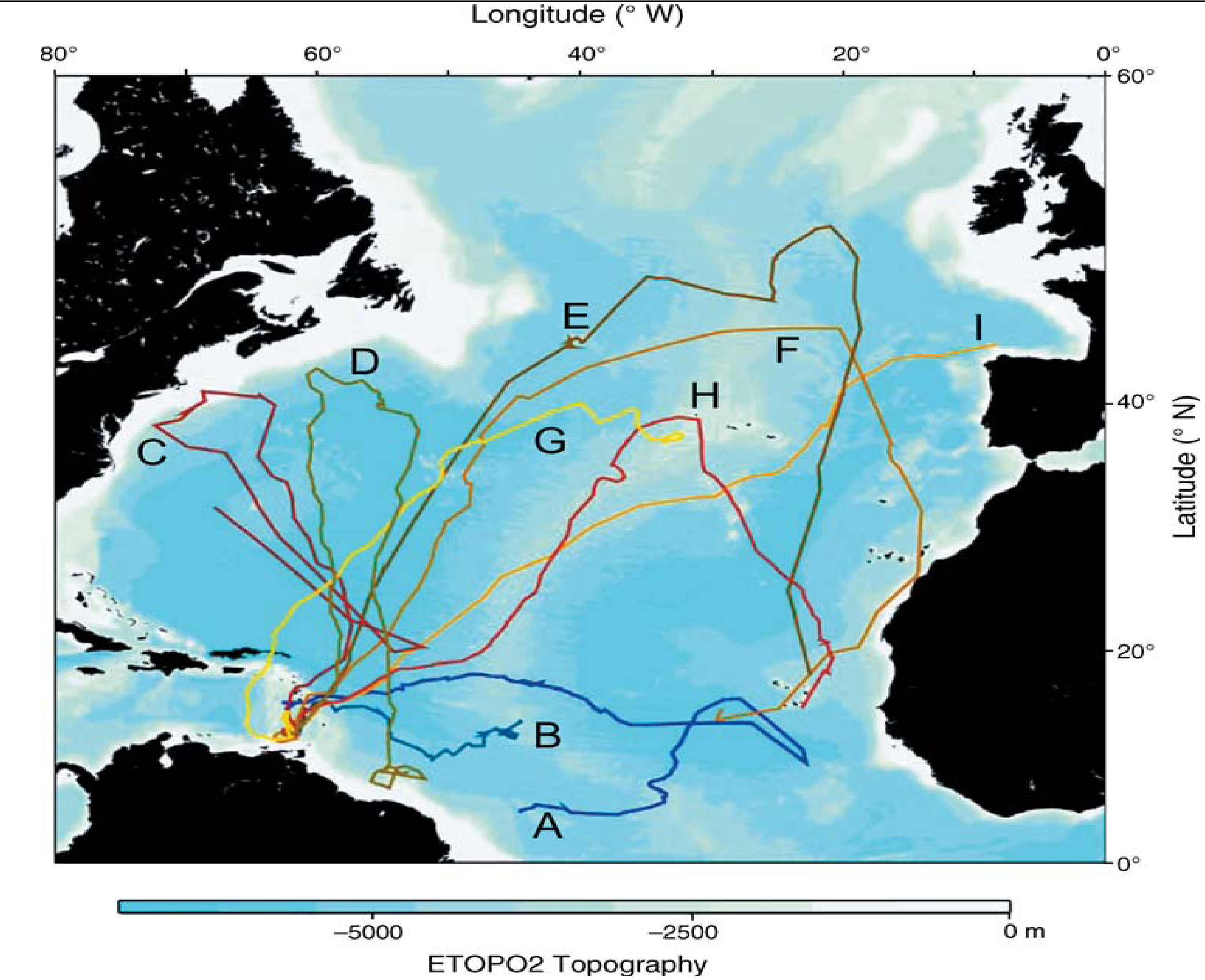


Figure 2: Movements over ~one year of nine satellite tracked leatherback turtles that nested and were tagged in Grenada, West Indies (Hays *et al*., 2006).

1.2. *Biology and processes involved in leatherback nesting*

Turtles will migrate from feeding areas to mating/nesting areas when they have accumulated sufficient fat reserves to support them throughout the nesting period; fat accumulation may take one to several years for leatherbacks (mean = 3 years) (Miller, 1996; Reina *et al*., 2002). Sea turtles find their way back to nesting regions using magnetite crystals located in their brain that can sense changes in the magnetic field due to the magnetite molecule being drawn towards the North Pole (Spotila, 2004). Mating occurs with one or several males in the month or two before the first oviposition cycle of the nesting season and the sperm are stored (Miller, 1996). Leatherbacks are less philopatric to nesting beaches than other sea turtles (Davenport, 1997) and often use many beaches within a region to nest (Sarti Martinez, 2000). After a successful nesting event the stored sperm are used to fertilise the next batch of eggs.

The majority of leatherback nesting takes place at night in order to avoid the potentially lethal temperatures that occur during the day in tropical nesting regions (Miller, 1996). Leatherback turtles can lay up to 11 clutches per season (mean = 6, mean range = 4-8) (Leslie *et al*., 1996; Reina *et al*., 2002) at nesting intervals of 6-15 days (mean = 9-10 days) (Girondot and Fretey, 1996), laying large numbers of fertile eggs (58-114) and yolkless eggs (21-56) (Caut *et al*., 2006). The main function of leatherback's unique yolkless eggs on incubating fertile eggs is unclear, but may be related to gas diffusion and egg hydration within the nest (Caut *et al*., 2006). Leatherback nesting takes around 1.5 hours to complete, during which they display characteristic behaviours seen in other sea turtle species (Miller, 1996). The stages in the nesting process are as follows:

- Approach - usually uphill away from the surf; although the direction may twist in order to reduce the uphill angle (Wyneken, 1996).
- Body pitting - select and clear an area with the front flippers which the turtle then moves forwards onto. A body pit is then created using the front flippers, the depth of which will be determined by the dryness of the sand i.e. the drier the sand the deeper the body pit, as firmer sand is needed to support the weight of a nesting turtle and prevent the nest from collapsing (Miller, 1996).
- Digging – using the back flippers alternately the leatherback will scoop sand out an approximately 1 meter deep chamber. When the turtle can dig no deeper a bowl shape is created at the bottom by scraping the walls of the chamber.
- Oviposition – digging ceases and a rear flipper hangs inside the nest chamber while the eggs are deposited. Tagging and measurements were carried out during this process as the turtles are less likely to abandon the nesting process at this point.
- Covering and camouflaging – the turtle covers and compacts the nest chamber with its rear flippers and then using its front flippers disguises the area surrounding

the nest and re-establishes the original beach environment surrounding the nest (Miller, 1996).

1.3. *Characteristics of leatherback nesting beaches*

Leatherback nesting colonies are associated with beaches where strong on-shore currents provide deep nearshore access with a steep (shelving) beach profile; this enables turtles to reach high nesting areas with minimal effort as the linear distance is short compared to gentle sloping beaches (Lamont and Carthy, 2007). The beach slope may also act as a barrier to high tides preventing water inundation of incubating nests (Lamont and Carthy, 2007). Nesting generally occurs on open/exposed sand areas near the water (Kamel and Mrosovsky, 2004). Other characteristics of the beach that determine whether the female will nest or not depend on:

- Temperature – turtles can sense the temperature difference between cool, moist sand and dry, warm sand further up the beach that is better suited for egg incubation (Miller, 1996).
- Moisture – when digging the nest must not be too moist or too close to the water table as the nest may be inundated at higher tides.
- Sand type –sand texture and quality may change throughout the beach and sand surrounding the nest must able to effectively facilitate gas diffusion (Hendrickson and Balasingham, 1966; Lamont and Carthy, 2007).

Beaches with desired characteristics that will ensure a greater hatchling and survival success will be selected for (Hendrickson and Balasingham, 1966; Hendrickson 1980; Lamont and Carthy, 2007).

In Tobago, Turtle Beach, Grafton Beach and Back Bay are the most active beaches for leatherback turtle nesting events and are considered nesting index beaches as they represent trends in island-wide leatherback populations due to regular monitoring (Clovis, 2005; Lalsingh, 2008). Turtle beach accounts for the majority of leatherback nesting events of all Tobago's index beaches from 2005-09 (66.1%); it has a steep beach profile, no corals immediately offshore and is the longest of the three (1.76 km). Grafton Beach (15.7% of total leatherback events from 2005-09) has large rock formations along the length of the beach (1km), has a gentle slope and the tide often creates sandbanks of approximately 30-80 cm. Back Bay also has rock formations throughout the length of the beach (1 km) and is inundated when high spring tides occur. 18.1% of total leatherback nesting events from 2005-09 occurred at Back Bay.

Data collection of leatherback nesting events in Tobago was carried out by Save Our Sea Turtles (SOS) Tobago head patrollers, local volunteers and international volunteers on Turtle Beach, Grafton Beach and Back Bay. SOS Tobago is a small, volunteer based organization formed in 2000 with a mission to conserve Tobago's sea turtle populations and their coastal and marine habitat through research, education and eco-tourism.

1.4. *Variables that may influence leatherback nesting patterns*

The terrestrial environment can be physically difficult for sea turtles to move (as well as increasing the chance of interactions with egg predators and/or poachers), so nesting females should try to minimise exposure to unfavourable environmental conditions by assessing conditions whilst still at sea (Pike 2008). Leatherback nesting processes will be affected by the environment and different cues (e.g. oceanic or atmospheric) may help to reduce the energetic and physiological stress of nesting (Pike 2008).

1.4.1. *Lunar and tidal patterns*

Lunar and tidal patterns are strongly linked. The Moon's gravitational pull will be directed towards its centre and will be greater on one side of Earth than the other (as points on the Earth are different distances away from the Moon); resulting in a tide-producing force. Tides move forward ~1 hour each day in coordination with each lunar day (24hrs 50 mins).

The Moon's orbit ranges to an inclined angle of 28 degrees that affects the tidal pattern e.g. semi-diurnal (two high tides a day) tides will show diurnal inequalities (one high tide a day) when the inclined angle is at 28 degrees from the equator. The Sun also has influence over the tide, and interacts with lunar tides. When the tide generating forces from the Sun and Moon are parallel or opposite to each other the tidal range is large; these spring tides (higher and lower than average) occur when the Moon is full or new (Figure 3A). When the tide generating forces of the Sun and Moon are out of phase i.e. the Sun and Moon are at right angles to each other (Figure 3B), the tidal range (high and low) is below average and are known as neap tides. Neap tides occur during the first and last quarter of the lunar phase. The response of the ocean to the force of the Earth, Sun and Moon will also depend on regional topography and the transient effects of weather patterns (Wright, Colling and Park, 1989). Tobago experiences mixed semi-diurnal tides due to it position near the equator, and tidal ranges within the Caribbean are generally small (~1 meter).

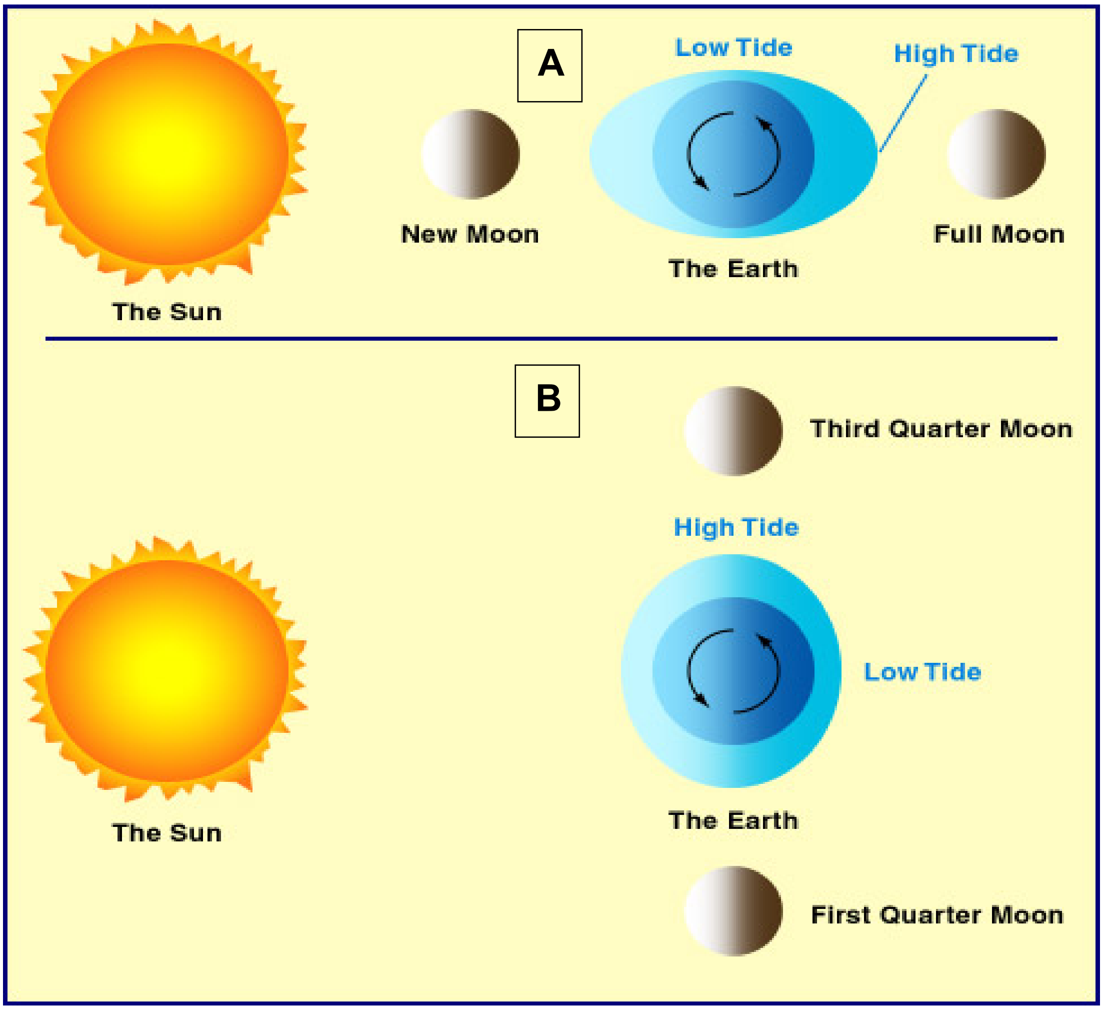


Figure 3: Diagram of the interactions between the tide generating forces of the Sun and Moon and their effects on Earth's tidal patterns (Website 3). (A) Parallel or opposite gravitational pulls resulting in spring tides. (B) Perpendicular gravitational pulls resulting in neap tides.

The lunar cycle causes a number of environmental changes that may be perceived by animals (e.g. amphibians, reptiles, birds and fish) e.g. change in the brightness of lunar light, gravitational changes (i.e. tidal patterns) and geomagnetic fields may be moderated; these changes could be used as temporal cues by animals (Grant *et al*., 2009). Solar, lunar and tidal cycles are believed to influence leatherback nesting activities because the turtles generally nest above the high tide line, so emerging when tides are at their highest will minimise the distance and duration of crawls. The greater the vertical distance between high and low tides, the greater the advantage of emerging at high tides; although beach profile will affect this potential advantage (Frazer, 1983). Emerging when tide is low could make nesting difficult due to the large size of leatherbacks and resultant slow terrestrial locomotion. Leatherbacks have a 'swing and stance' pattern of movement where the front and rear flippers are simultaneously swung forward (Wyneken, 1996). The body is then raised up on its front flippers and pushed forward with the back flippers (Miller, 1996; Wyneken, 1996). The carrier effect of the rising tide could facilitate the arrival of the turtles and Fretey and Girondot (1989) observed peak leatherback nesting occurring at and around the nightly high tide on beaches in French Guiana. The tide's influence on sea turtles is also apparent in foraging patterns e.g. movement is highly influenced by currents with respect to speed and direction in green turtles (Brooks, Harvey and Nichols, 2005).

The lunar phase may also affect leatherback nesting visually. On clear nights where the Moon is full, visual ability may be increased and the presence of tourists and egg predators may discourage turtles from emerging. Alternatively on clear nights where the Moon is not bright (e.g. new moon), artificial lights and dark silhouettes may be more apparent and discourage nesting.

1.4.2. *Weather patterns*

Weather patterns may also affect nesting events in a number of ways; on clear nights visibility may be greater and could result in more false crawls if visible distractions or deterrents are present, or alternatively there may be more confirmed lays if there are no visible deterrents present. The weather condition may also affect leatherback nesting events as rain may act to cool the turtles during the nesting process. Leatherbacks have a resting metabolism that is three times greater than green turtles resting metabolism (Paladino, O'Connor and Spotila, 1990) and therefore heat production will be greater. The ratio of surface area to volume decreases as size increases so leatherbacks will have a greater excess of heat produced when nesting compared to smaller turtles. Rain may increase the rate of evaporative cooling and on nights when it rains leatherbacks may be encouraged to nest. Wetness (and temperature) of the sand is known to contribute to the decision of whether to nest or not (Miller, 1996), if rainfall is heavy for a long duration turtles may be deterred from nesting.

1.5. *Individual patterns of nesting*

The evolutionary potential of successful individual nesting patterns is that more offspring will survive, and therefore nesting patterns where offspring survive to reproduce should be under strong selection; successful nesting patterns and habits should be consistent within and between populations.

Leatherbacks move around within nesting regions and nest on different beaches within nesting seasons and so any consistent adaptations to nesting may be at a regional level rather than a local level, so choosing consistent nest sites could be an example of stabilising selection e.g. different populations of turtles show similar nesting patterns in different environments and therefore gene flow may be high between different populations preventing local adaptation (Kamel and Mrovosky, 2004). If stabilising selection occurs with choice of nest site then it may be possible that there may be selection of specific environmental conditions in which individuals choose to emerge.

1.6. *Aims*

All species of sea turtles are listed as threatened, endangered or critically engangered so data on their habitat use, spatial distribution and population status at a regional scale are important (Sarti Martinez, 2000; Witt *et al*., 2009). From a local conservation perspective it would be useful to know how much influence various environmental factors have on the nesting activities of leatherback turtles so patrols can be planned accordingly. This study analyses the nesting events of female leatherback turtles from Tobago's three index beaches from 2005-09 to observe if environmental factors influence nesting. The following questions were tested:

- Do the numbers of nesting leatherback turtles vary between lunar phases?
- Does the weather influence the number of leatherbacks nesting or nesting outcome?
- Is leatherback turtle emergence time correlated with the high tide time for Tobago's index beaches?
- Is leatherback turtle emergence influenced by tidal stage?
- Does the time at night influence leatherback turtle emergence?
- Are nesting patterns from an individual leatherback turtle consistent over nesting seasons or consistent with the leatherback nesting population in Tobago?

2. Materials and Methods

2.1. Study Site and data collection

Nesting data for leatherback turtles were collected from three index beaches on the south-west Caribbean coast of Tobago, West Indies from 2005-2009 (Figure 4). Tobago's beaches receive mixed semi-diurnal tides; two high and two low waters each day, or one tidal cycle per day depending on the Moon's incline to the Earth.

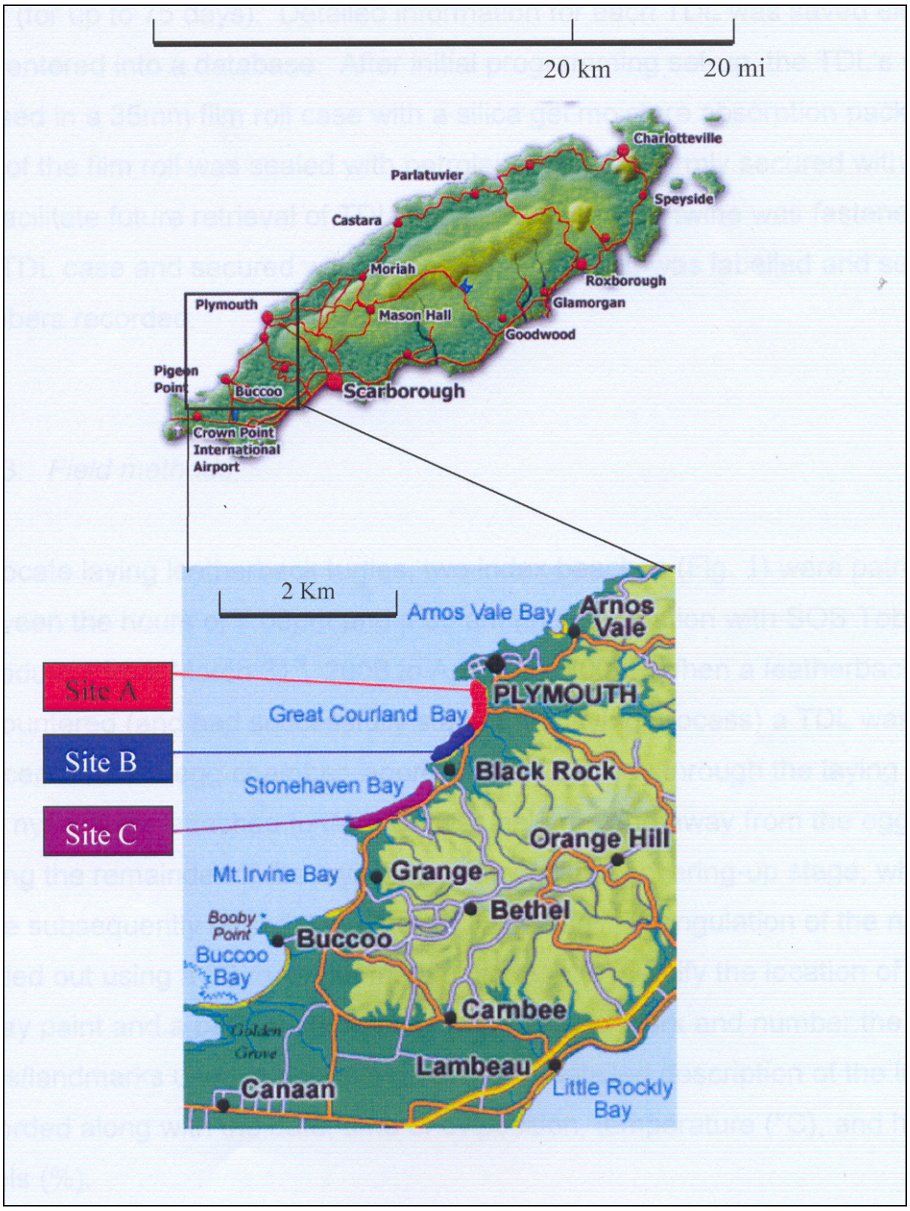


Figure 4: Map of Tobago's three leatherback index nesting beaches; Site A – Turtle Beach, Site B – Grafton Beach and Site C – Back Bay.

During the leatherback nesting season in Tobago (March-August) nightly patrols were carried out on the three index beaches between 8pm and 4am by SOS Tobago head patrollers and volunteers. When sea turtles were encountered the beach, zone, date, time, weather (2009 season only), species and activity were recorded on a standard data sheet (Appendix 1). Turtles that successfully dug a nest chamber and laid their eggs were measured (length and width of carapace in centimetres), checked for physical damage or distinct markings, their rear metal flipper tags read and recorded, and Passive-Integrated Transponder (PIT) tags scanned and recorded from each turtle's shoulder area. If rear flipper tags or PIT tags were not present the head patroller or volunteer would fit these. Head patrollers or volunteers would remain with the turtle and confirm the nesting event outcome. The numbers of tourists and locals were also recorded and whether or not the turtle was disturbed by the presence of tourists/locals or beachfront lighting.

Each nesting event was categorised by the eventual outcome:

- Confirmed lay – successful nest excavation, oviposition, covering and camouflaging of the nest, and return to the sea.
- False crawl – the turtle emerged from the surf but did not successfully dig; possibly due to disturbance or individual preference not being met.
- False crawl with body pit – after emergence from the surf the turtle does not successfully dig a nest chamber; possibly due to the quality, texture or temperature of the sand or disturbance.
- Estimated lay – where two tracks are found in opposite directions with an area of camouflaging apparent, or where the turtle is found covering or leaving a nest area.

Information from data sheets was transferred to a computerised data-base by Tanya Clovis and Giancarlo Lalsingh of SOS Tobago and kindly made available to the author.

2.2. Analysis

2.2.1. *The effect of lunar phases on all leatherback nesting events combined*

To analyse whether nesting events are even between lunar quarters, months during the nesting season were divided into lunar quarters i.e. plus and minus 3 days from the date of the first quarter, full moon, last quarter or new moon, giving 7 days per quarter. When a nesting date was outwith plus or minus 3 days from the date of a lunar phase it was not included in the analysis. Moon phases and dates were obtained from http://kalender-365.de/lunar-calendar.php# (Website 1) accessed on 1st July 2009.
Turtles disturbed by tourists or lights and where the nesting event outcome was unknown were also not included in the analysis.
All nesting activities were included in the first analysis of the effect of lunar phase i.e. confirmed lays, estimated lays, false crawls and false crawls with body pits. As the data was binomially distributed it was analysed using a Kruskal-Wallis test with multiple comparisons in Minitab version 15. The second analysis examined the effect of lunar patterns on confirmed lays within nesting years also using a Kruskal-Wallis test with multiple comparisons. Other nesting activities were not individually analysed with lunar phase as the numbers were low.

2.2.2. *The effect of weather on all leatherback nesting events combined*

Weather conditions during leatherback nesting events were recorded only in 2009. Firstly all leatherback nesting activities and secondly nesting event outcomes were analysed using a Kruskal-Wallis test with multiple comparisons (due to the bimodal distribution of the data). Nesting events where the event outcome was unknown or estimated were not included in the analysis.

2.2.3. *The relationship of high tides to leatherback emergence time*

Time data from female leatherback turtles observed on approach, body pitting and digging from were analysed for each nesting year (2005-09) using a Pearson's Correlation. Observed time is used in figures rather than emergence time as turtles were often found digging or body pitting i.e. not emerging from the surf; these nesting events are within the first twenty minutes of the nesting process. Only confirmed lays were used in the analysis. Times of high tides for Tobago in years 2005-09 were obtained from www.mobilegeographics.com accessed on 1st July 2009 (Website 2).

2.2.4. *The relationship of tidal patterns to leatherback nesting activity*

Data were only used in this section where turtles were first seen on approach, body pitting or digging with the time seen recorded. Data where turtles were first seen when covering, camouflaging or leaving were not included in the analysis. All nesting event data were analysed in the first section; the second section analysed confirmed lays only.

Tides were divided into eight categories/phases:

1. Low tide (L)
2. Low tide rising (LR)
3. Mean sea level rising (MR)
4. Rising to high tide (HR)
5. High tide (H)
6. High tide falling (HF)
7. Mean sea level falling (mF)
8. Falling to low tide (LF)

Tidal charts were obtained from www.mobilegeographics.com (Website 2) accessed on 1st July 2009 and the data were analysed using a chi-squared test. The data was then categorised by the beach where nesting occurred and analysed using a chi-squared test.

2.2.5. *Time of leatherback observation at night*

For the hours when the three index beaches were patrolled (8pm-4am) the shift was divided into eight time categories to observe if leatherbacks choose a particular time to emerge.

The time categories are:

1. 20:00 – 20:59
2. 21:00 – 21:59
3. 22:00 – 22:59
4. 23:00 – 23:59
5. 00:00 – 00:00
6. 01:00 – 01:59
7. 02:00 – 02:59
8. 03:00 – 03:59

Only data were the leatherback was seen on approach, body pitting or digging were used in this analysis. Differences in leatherback observed time were analysed using a chi-squared test for 2005-2009 and all years combined.

2.2.6. *Individual leatherback nesting activity over three seasons*

As leatherback turtles nesting on index beaches in Tobago are tagged with PIT and metal rear flipper tags, it is possible to identify individual turtles over seasons if or when they return. A female leatherback with right flipper tag number 33077 (nick named Diana Ross) was tagged in 2005 and subsequently returned in 2007 and 2009. The effect of high tide on emergence time, the effect of tidal phase of emergence time and the time of emergence at night were investigated for this individual for the seasons in which she returned.

3. Results

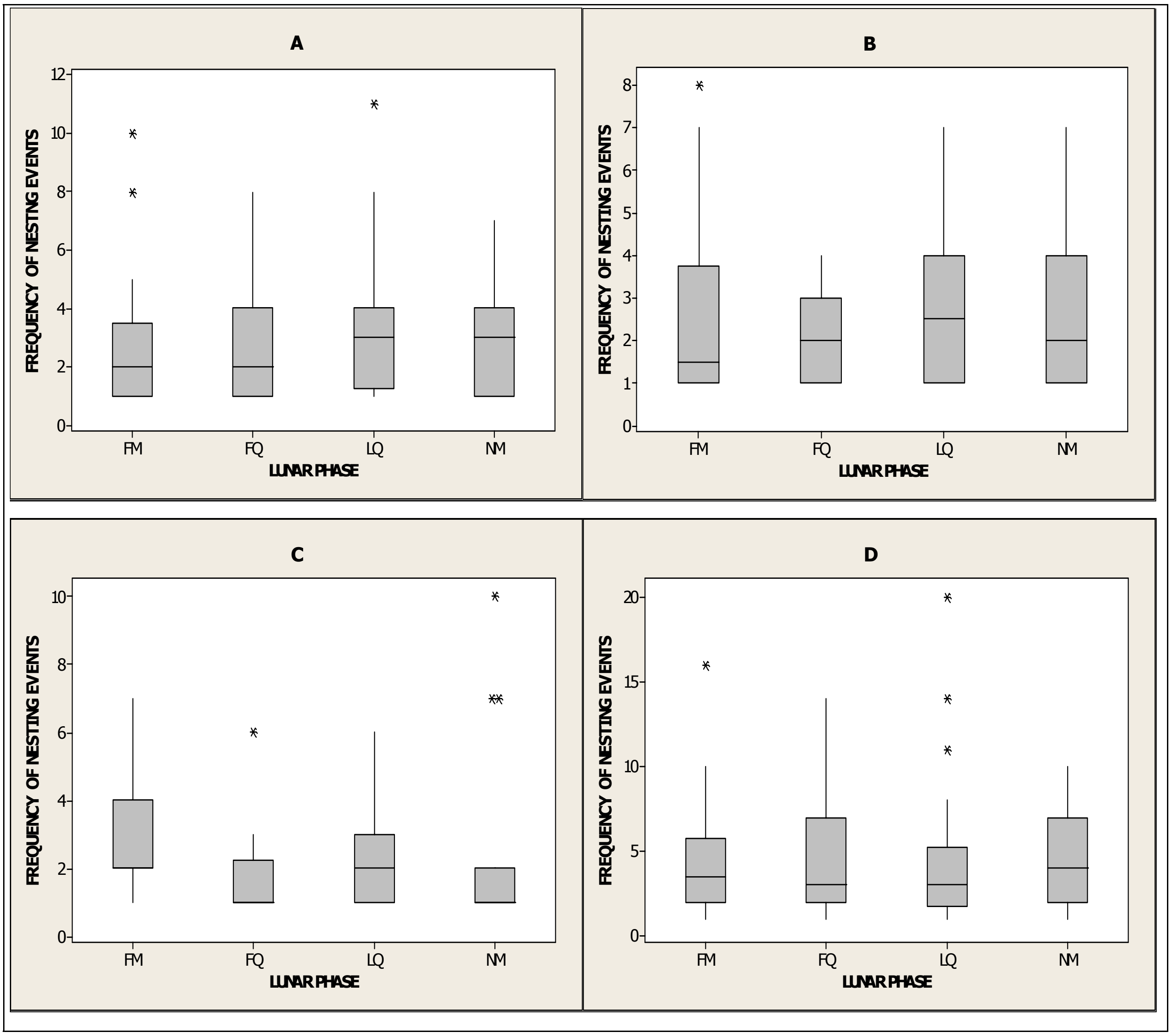
The total number of female leatherback nesting event outcomes from 2005, 2006, 2007, 2008 and 2009 from Tobago's index nesting beaches are presented in Table 1.

Table 1: Summary of female leatherback nesting event outcomes from 2005-2009 for Tobago's three index beaches.

	Confirmed lays (% of total)	False crawls	False crawls with body pits	Estimated lays	Unknown	**Total**
2005	216 (76.4%)	7	6	45	9	283
2006	173 (71.5%)	17	4	6	42	242
2007	123 (64.4%)	22	10	33	3	191
2008	345 (78.1%)	24	13	31	29	442
2009	317 (65.9%)	74	34	44	12	481
Total	1174 (72%)	144	67	159	95	1639

3.1.1. *The effect of lunar phases on all leatherback nesting events combined*

The frequency of nesting events (Figure 5.1) does not significantly differ between lunar phases for 2005, 2006, 2008 and 2009 as the p-values are greater than 0.05 (Table 2.1). In 2007 (Figure 5.1 C) there is a significantly higher frequency of nesting events during the full moon phase compared to the first quarter and new moon lunar phases (Table 2.2). For all years combined (Figure 5.1 F) the frequency of nesting events during the first lunar quarter is significantly less than the median from the full moon and last quarter lunar phases (Table 2.3).



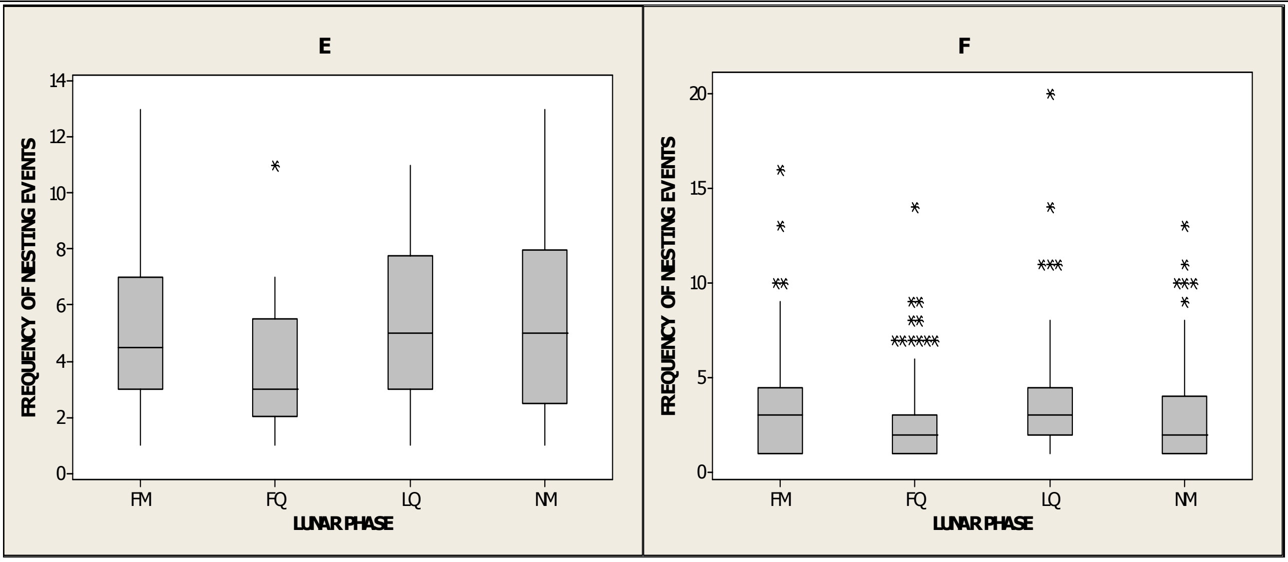


Figure 5.1: The frequency (number of nesting events per night) of female leatherback nesting events for each lunar phase for (A) 2005, (B) 2006, (C) 2007, (D) 2008, (E) 2009 and (F) all years combined.

Key: FM – full moon; FQ – first quarter; LQ – last quarter; NM – new moon

Each plotted box displays the interquartile range box (containing 50% of the nesting frequency data); box whiskers represent the frequency data range; the median is represented by the black line in each box and data outliers are represented by asterisk symbols.

Table 2.1: Results of the Kruskal-Wallis test; H-statistics, degrees of freedom and probability values for female leatherback nesting events during lunar phases in 2005, 2006, 2007, 2008, 2009 and all years combined from Tobago's index nesting beaches.

	2005	2006	2007	2008	2009	All years
H-statistic	2.50	3.2	12.17	0.9	5.64	7.94
DF	3	3	3	3	3	3
P-value	0.475	0.362	0.007	0.827	0.13	0.047

Table 2.2: Lunar phase comparisons and probability values for nesting events in 2007.

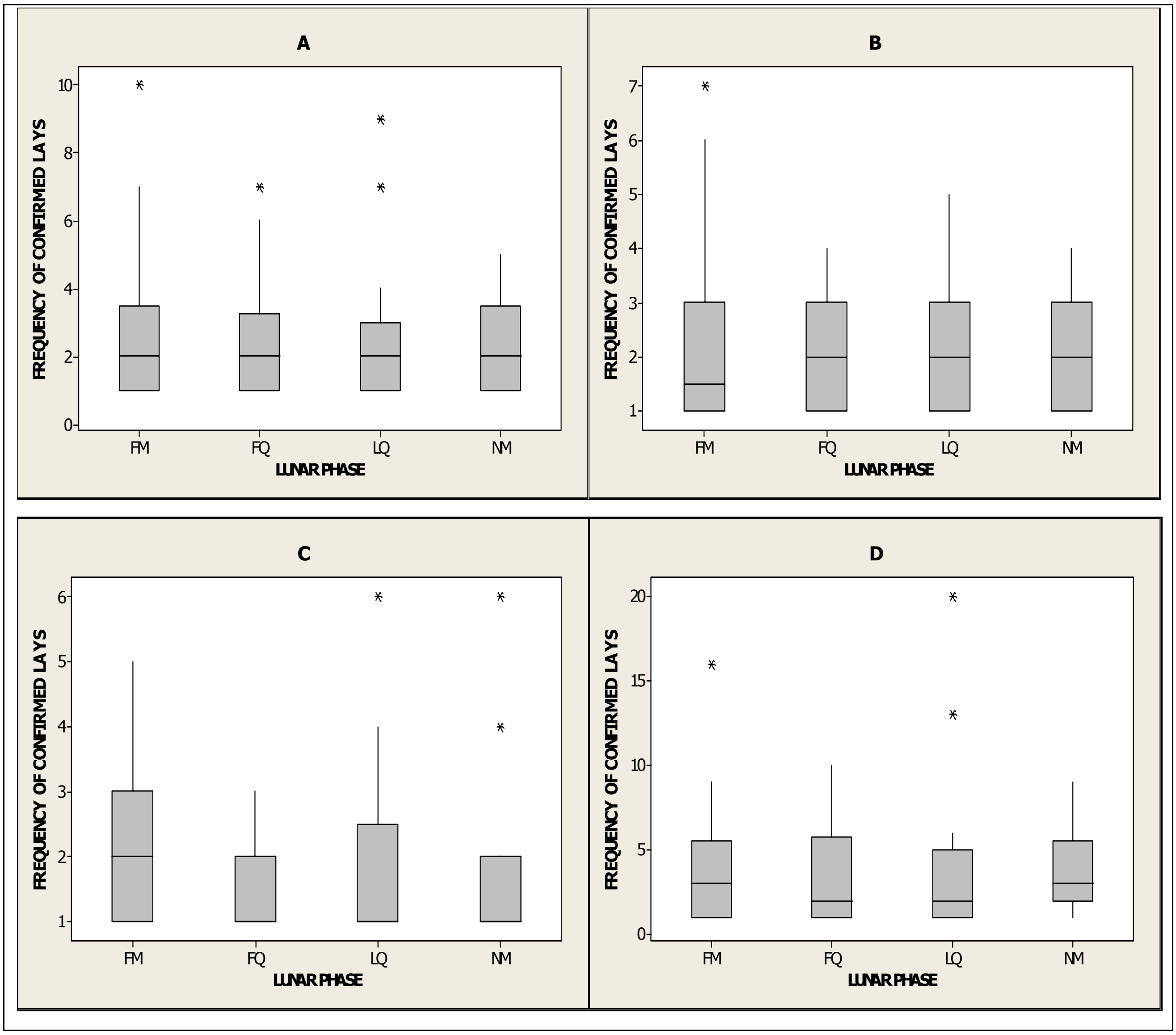
Groups	P-value
NM vs. FM	0.0031
FQ vs. FM	0.0038

Table 2.3: Lunar phase comparisons and probability values for nesting events when all years are combined.

Groups	P-value
FQ vs. LQ	0.01
FQ vs. FM	0.0277

3.1.2. *The effect of lunar phases on leatherback confirmed lays*

When the frequencies of confirmed lays are visually examined in relation to lunar phase (Figure 5.2 A-E) it is clear that the numbers of confirmed lays are evenly distributed between lunar quarters for leatherback index nesting beaches in Tobago for seasons 2005-09. There are no significant differences between the frequencies of confirmed lays and different lunar phases (Table 3).



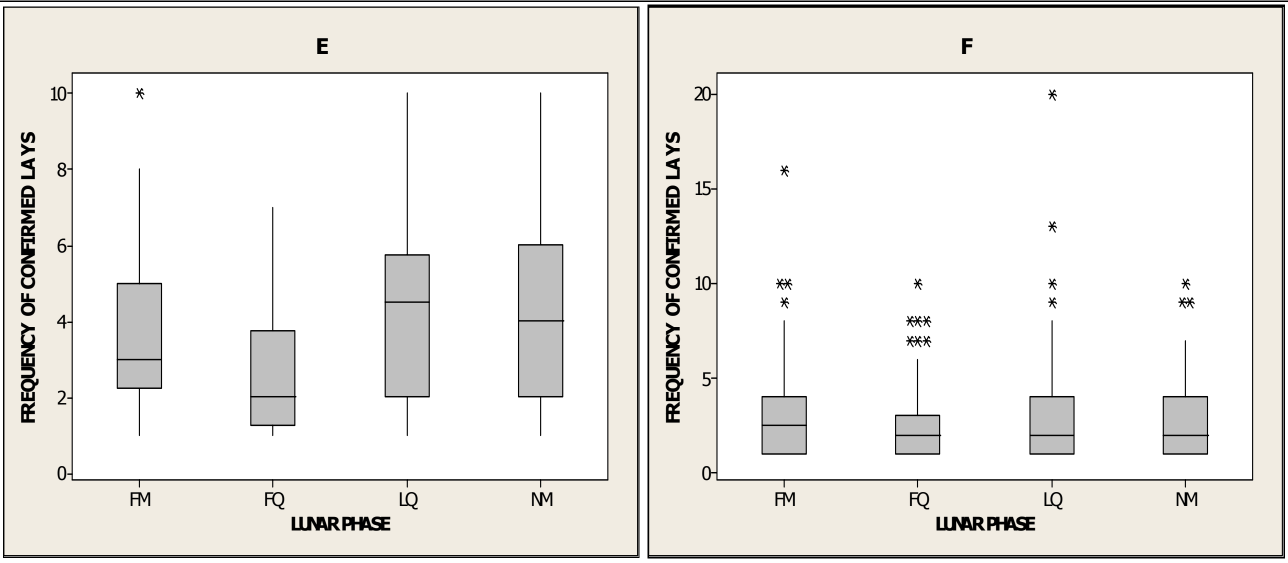


Figure 5.2: The frequency (number of confirmed lays per night) of female leatherback confirmed lays for each lunar phase for (A) 2005, (B) 2006, (C) 2007, (D) 2008, (E) 2009 and (F) all years combined.

Table 3: Results of the Kruskal-Wallis test; H-statistics, degrees of freedom and probability values for female leatherback confirmed lays during lunar phases in 2005, 2006, 2007, 2008, 2009 and all years.

	2005	2006	2007	2008	2009	All Years
H-statistic	0.62	0.11	4.43	0.31	4.66	3.26
DF	3	3	3	3	3	3
P-value	0.892	0.99	0.218	0.957	0.199	0.353

3.2.1. *The effect of weather on all leatherback nesting events combined*

A summary of female leatherback nesting events during different weather conditions for Tobago's index nesting beaches in 2009 is presented in Table 4. The total number of nesting events in Table 4 is less than the total number of nesting events for 2009 in Table 1 as the weather conditions for 6 female leatherback nesting events was not recorded, and therefore not included in this section.

Table 4: Summary of weather and nesting event data for Tobago's index beaches in 2009.

Weather (No. of days)	Confirmed lays (% of total)	False crawls	False crawls with body pits	Estimated lays	Unknown	**Total**
Clear (103)	243 (64.6%)	61	29	34	9	376
Overcast (42)	58 (71.6%)	9	5	7	2	81
Rain (10)	13 (72.2%)	2	0	2	1	18
Total	314	72	34	43	12	475

On inspection Figure 6.1 shows there is more leatherback nesting activity on clear nights than on overcast or rainy nights in 2009. This is statistically significant (Kruskal-Wallis test; H = 24.65, DF = 2, P = 0.001) with the significant comparisons between weather groups shown in Table 5.

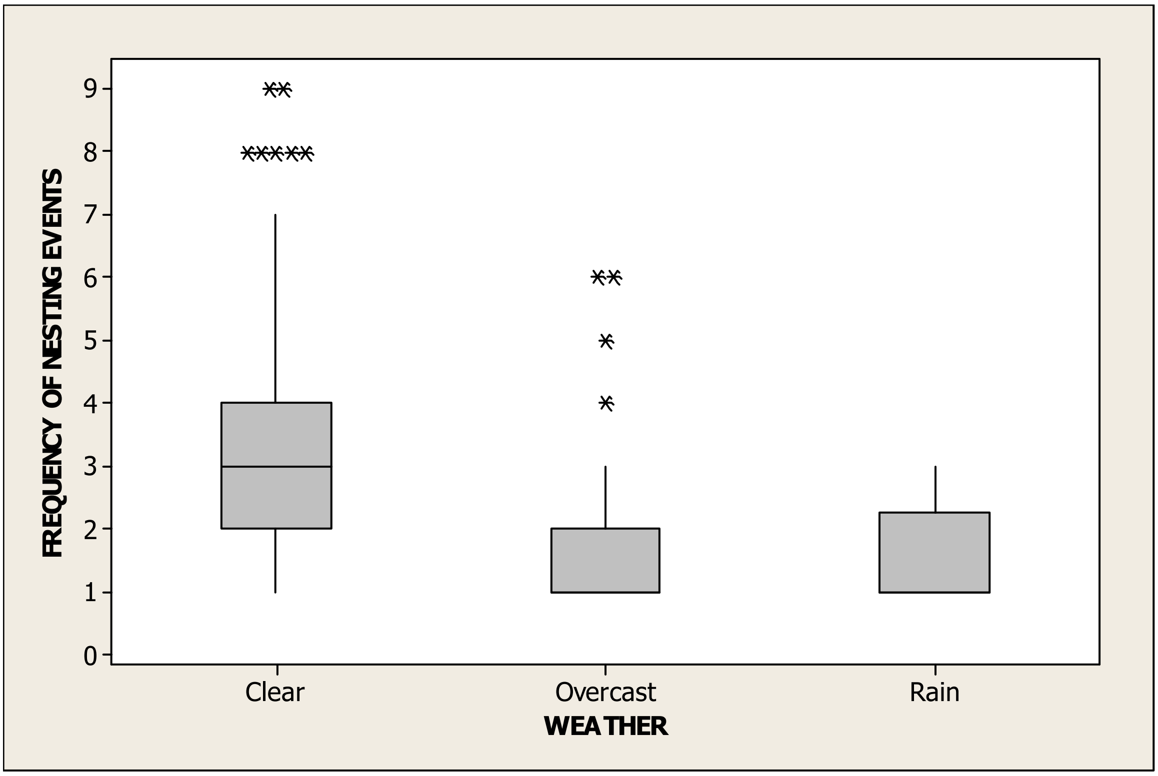


Figure 6.1: The frequency (number of nesting events per night) of all female leatherback nesting events related to the weather for 2009.

Table 5: Weather group comparisons and probability values for nesting events in 2009.

Group	P-value
Clear vs. Overcast	0.0001
Clear vs. Rain	0.0072

3.2.2. *The effect of weather on leatherback nesting event outcome*

In 2009 there are significantly more confirmed lays than false crawls and false crawls with body pits on clear nights (Figure 6.2 A). On overcast (Figure 6.2 B) and rainy nights (Figure 6.2 C) there are no significant differences between the frequency of nesting events and nesting event outcome (Table 6).

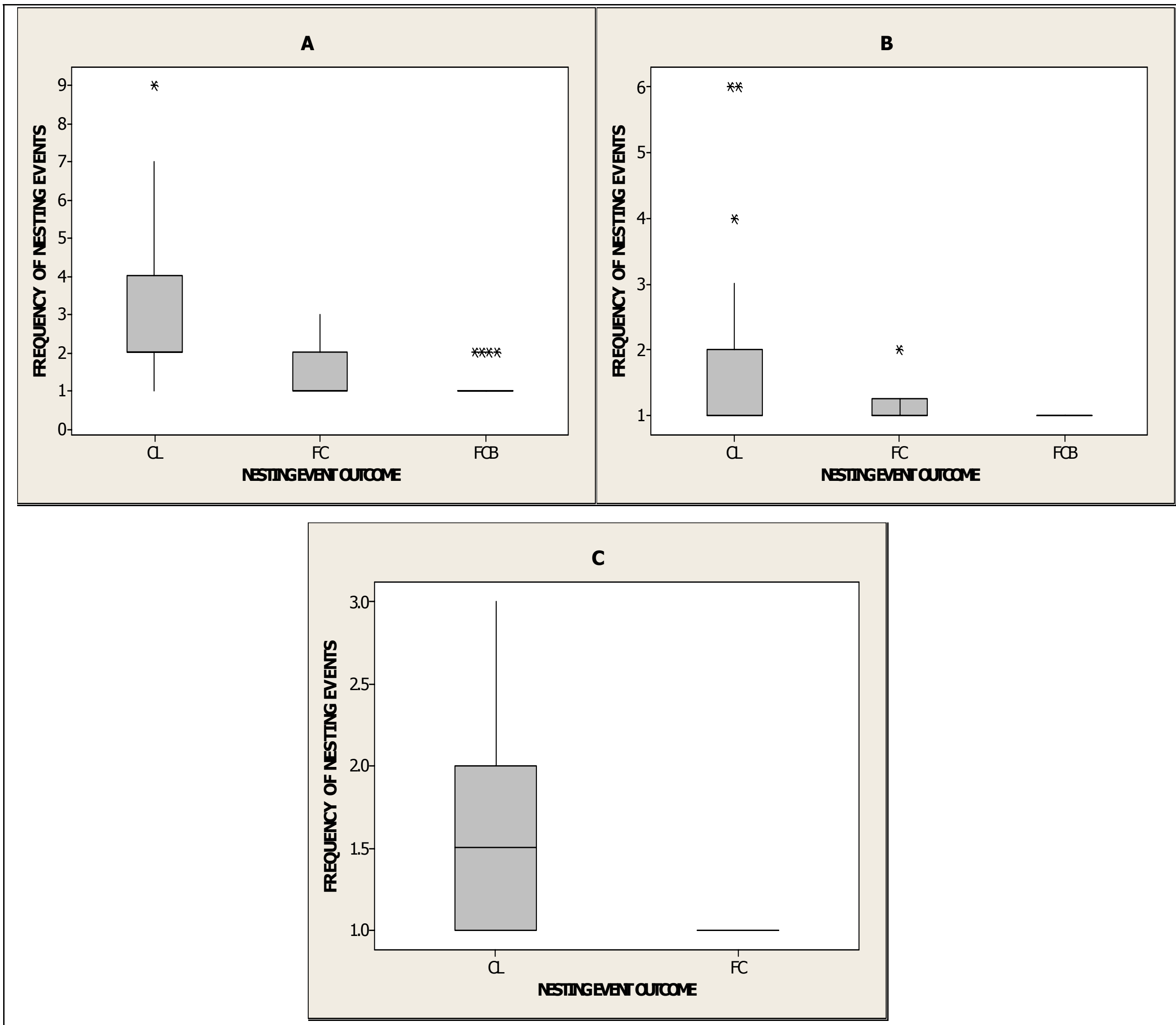


Figure 6.2: The frequency of nesting events against each nesting event outcome for 2009 for (A) clear, (B) overcast and (C) rainy nights.

Key: CL – confirmed lays; FC – false crawls; FCB – false crawls with body pits.

Table 6: Results of Kruskal-Wallis test; H-statistics, degrees of freedom and probability values for female leatherback for the frequency of nesting events against nesting event outcome for clear, overcast and rainy nights in Tobago 2009.

	Clear	**Overcast**	**Rain**
H-statistic	45.54	4.89	0.75
DF	2	2	1
P-Value	> 0.001	0.087	0.386

Table 7: Nesting event outcome group comparisons and probability values for 2009

Groups	**P-Value**
Confirmed lays vs. false crawls	> 0.001
Confirmed lays vs. false crawls with body pits	> 0.001

3.3. *The effect of high tides on leatherback emergence time*

Visually Figures 7.1, 7.2, 7.3, 7.4 and 7.5 do not appear to show any relationship between the time of high tide and leatherback observed time for Tobago's index beaches in 2005, 2006, 2007, 2008 and 2009. The relationship between high tide time and leatherback observed time is not significantly correlated for any nesting year (Table 8). If there was a close relationship exists between high tide time and leatherback observed time, most blue circles would cluster along the black lines.

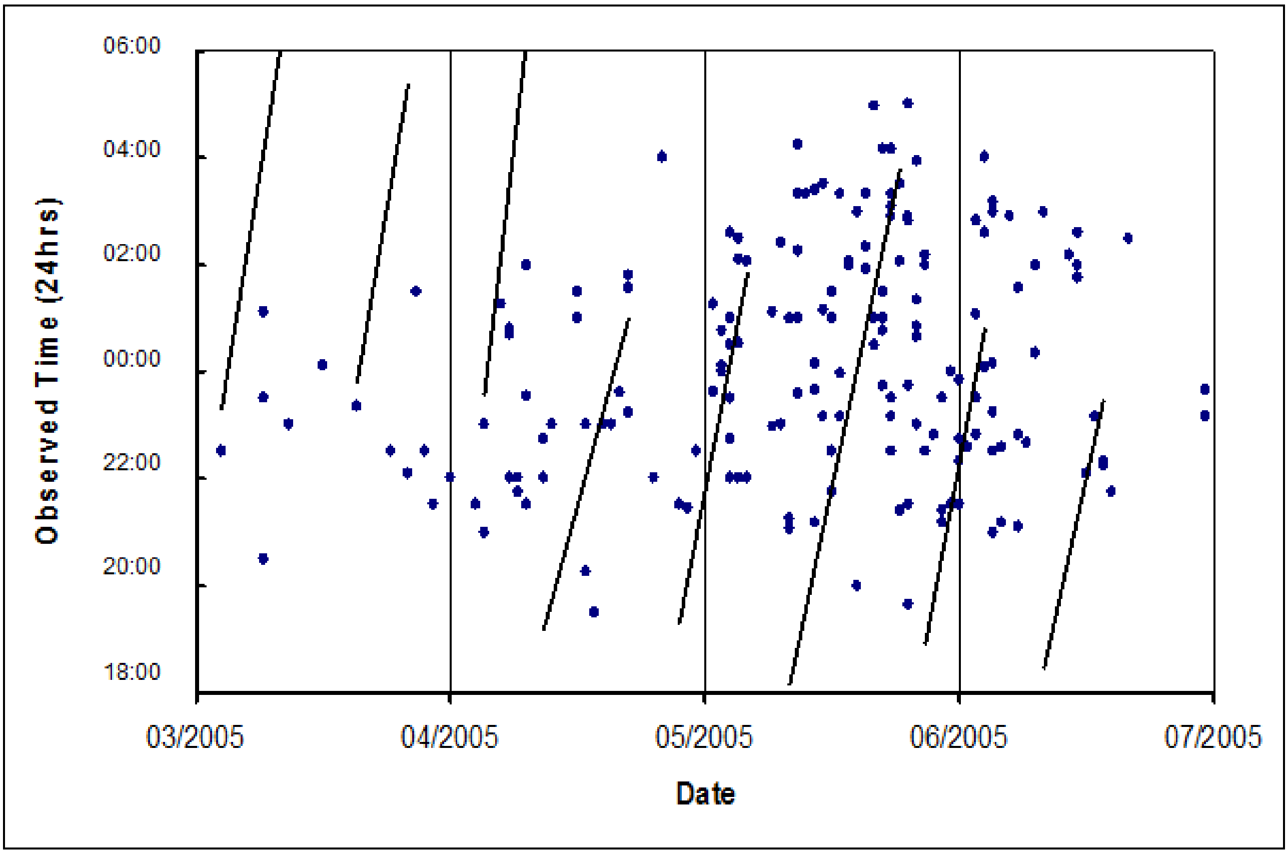


Figure 7.1: Leatherback observed time (solid blue circles) against high tide time (black lines) from three index beaches in Tobago from March (03) to July (07) 2005.

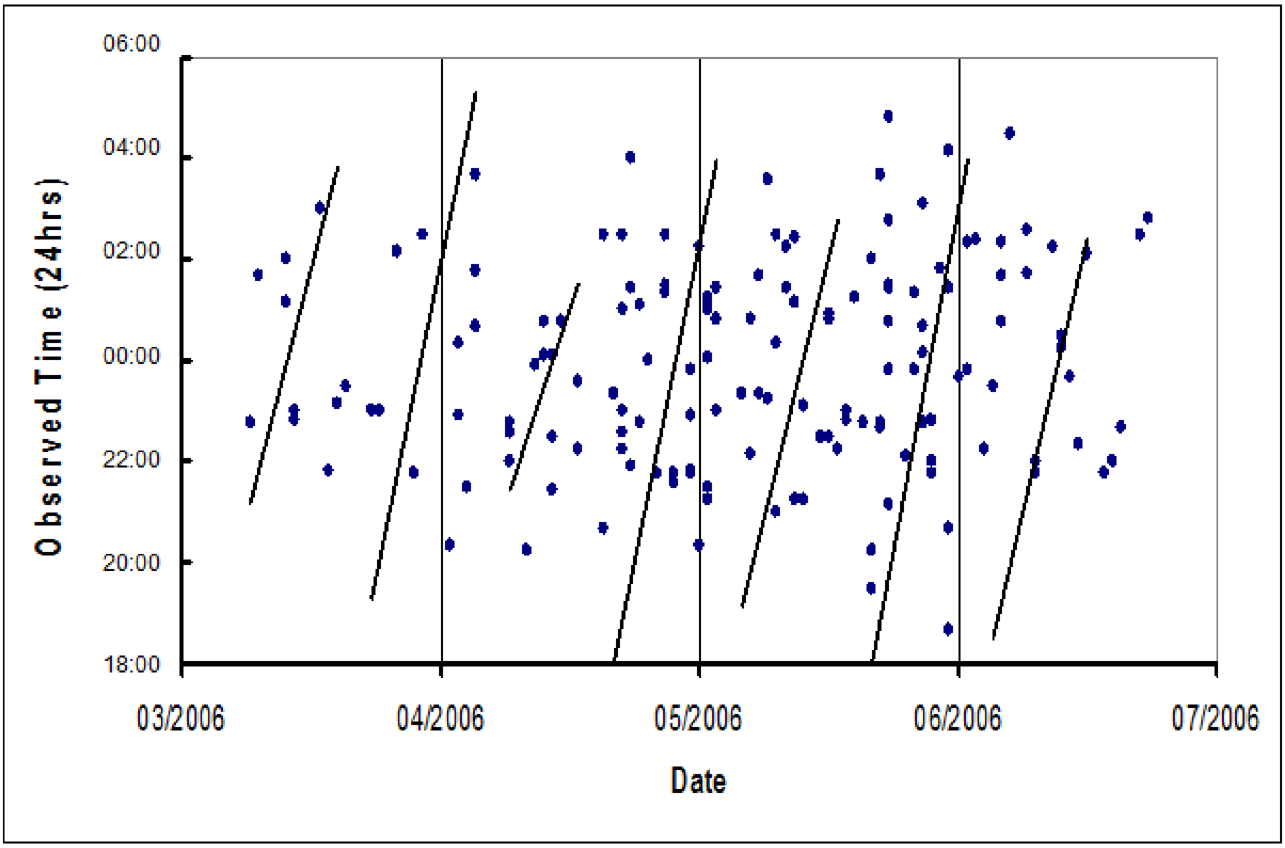


Figure 7.2: Leatherback observed time (solid blue circles) against high tide time (black lines) from three index beaches in Tobago from March to July 2006.

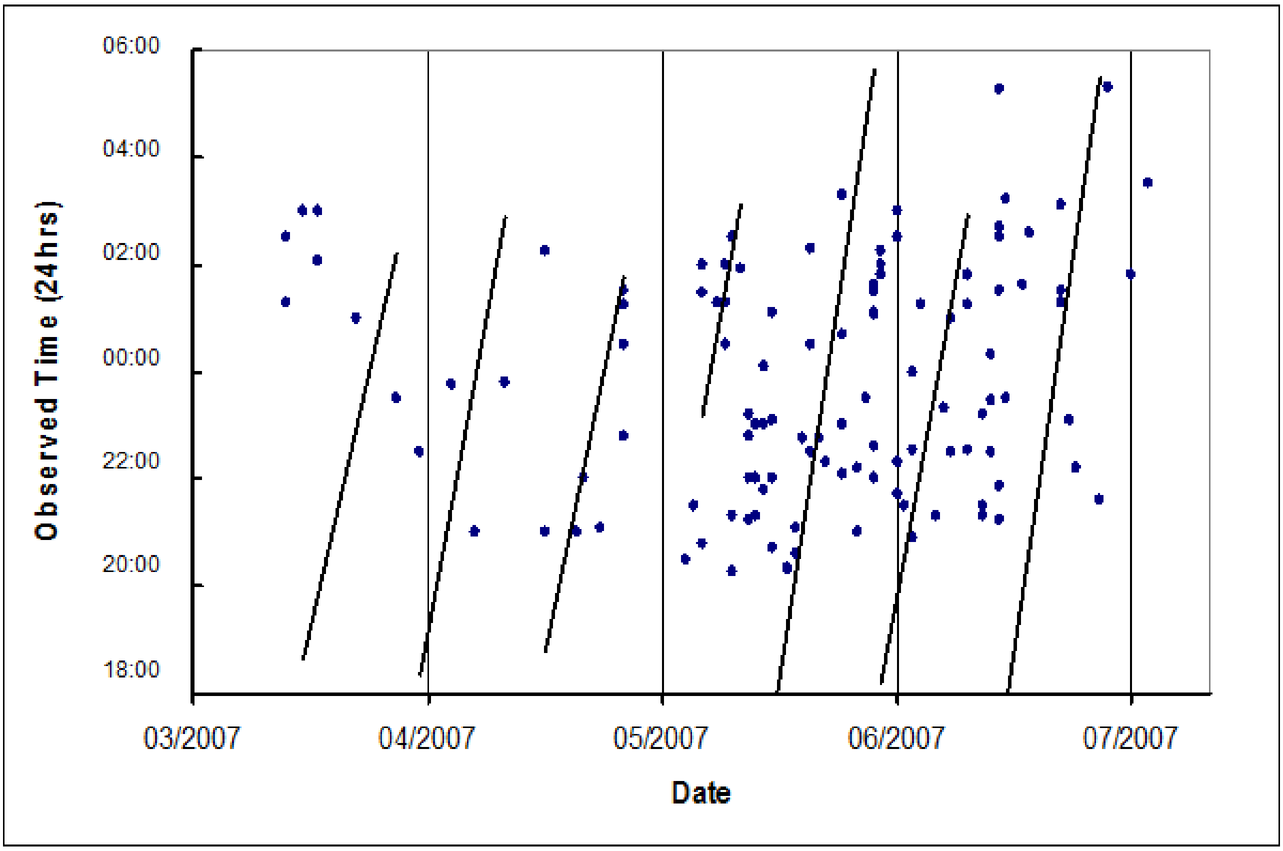


Figure 7.3: Leatherback observed time (solid blue circles) against high tide time (black lines) from three index beaches in Tobago from March to July 2007.

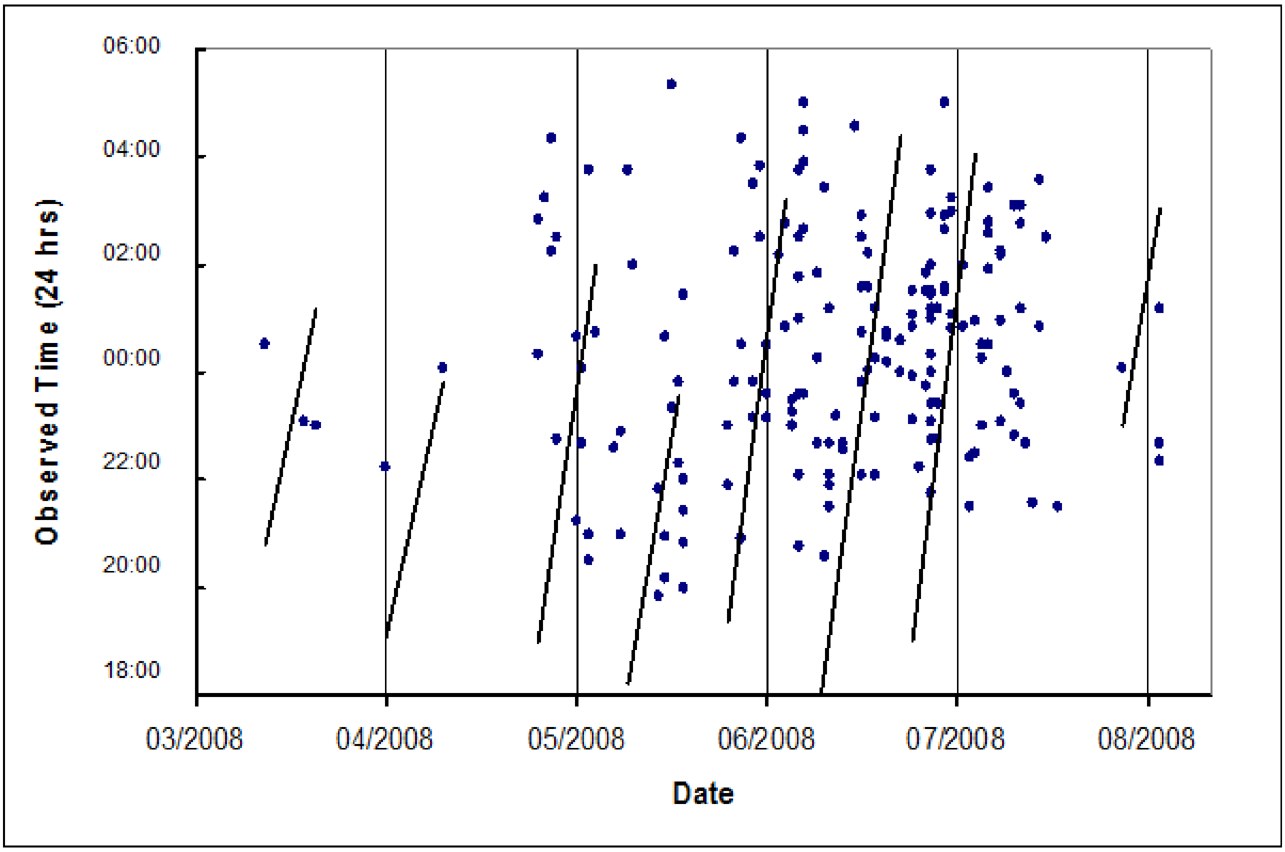


Figure 7.4: Leatherback observed time (solid blue circles) against high tide time (black lines) from three index beaches in Tobago from March to August 2008.

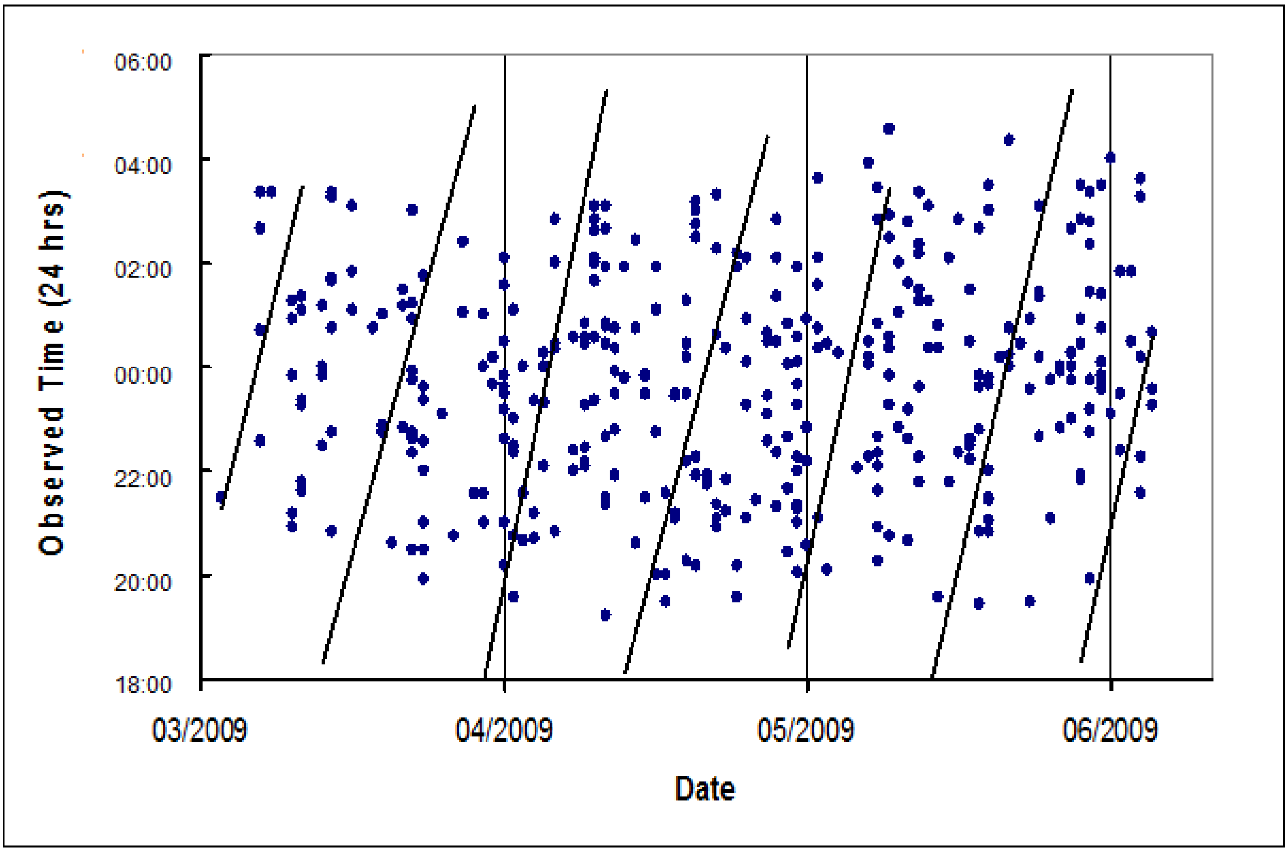


Figure 7.5: Leatherback observed time (solid blue circles) against high tide time (black lines) from three index beaches in Tobago from March to June 2009.

Table 8: Results of the Pearson's Correlation; correlation coefficients and probability values for leatherback observed time against high tide time.

	2005	**2006**	**2007**	**2008**	**2009**
R-statistic	0.154	-0.094	-0.031	0.073	-0.076
P-value	0.182	0.411	0.802	0.556	0.496

3.4.1. *The relationship of tidal patterns to leatherback nesting events*

In 2005 the majority of female leatherback nesting events took place from the high tide (tidal stage 5) falling to low tide (tidal stage 1) for all nesting events and for confirmed lays for Tobago's leatherback index nesting beaches. There was a distinct lack of nesting events and confirmed lays when the tide is rising from low tide i.e. tidal stages 2 and 3. Using a null hypothesis that there is no relationship between nesting events and tidal stage, chi-squared tests showed that there is a significant relationship (Figure 8.1 A; $X^2 = 36.2$, DF = 7, $P < 0.001$, Figure 8.1 B; $X^2 = 34.2$, DF = 7, $P < 0.001$) with more activities than expected during tidal stages 1, 5, 6, 7 and 8 with fewer activities during tidal stages 2, 3 and 4.

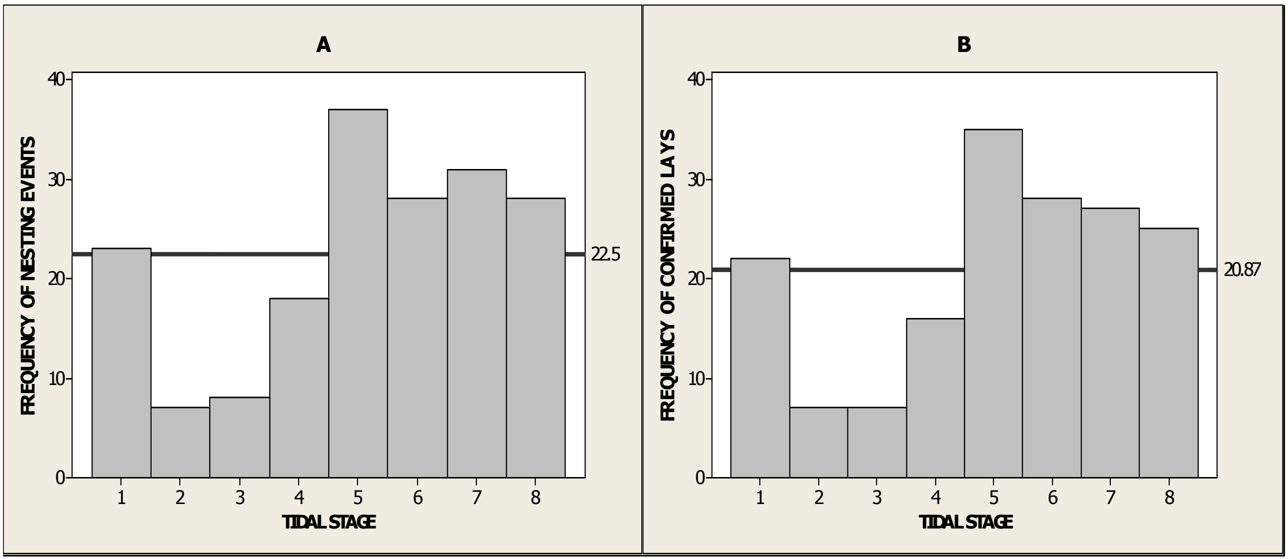


Figure 8.1: Histogram of (A) all nesting related events and (B) confirmed lays against tidal stage with the expected value shown (black line) for leatherback index beaches in Tobago from 2005.

Key: 1 – low tide | 2 – low tide rising | 3 – mean sea level rising | 4 – rising to high tide | 5 – high tide | 6 – high tide falling | 7 – mean sea level falling | 8 – falling to low tide

In 2006 the frequency of nesting events (Figure 8.2 A) and confirmed lays (Figure 8.2 B) are relatively low in tidal stages 2, 3 and 4 (low tide rising, mean sea level rising to high tide) when compared to nesting frequencies after high tide i.e. tidal stages 6-8 (high tide falling). Observed nesting frequencies at tidal stages 6, 7 and 8 differ significantly from expected values for both nesting event ($X^2 = 35.9$, DF = 7, $P < 0.001$) and confirmed lays ($X^2 = 35.8$, DF = 7, $P < 0.001$) for Tobago's leatherback index nesting beaches.

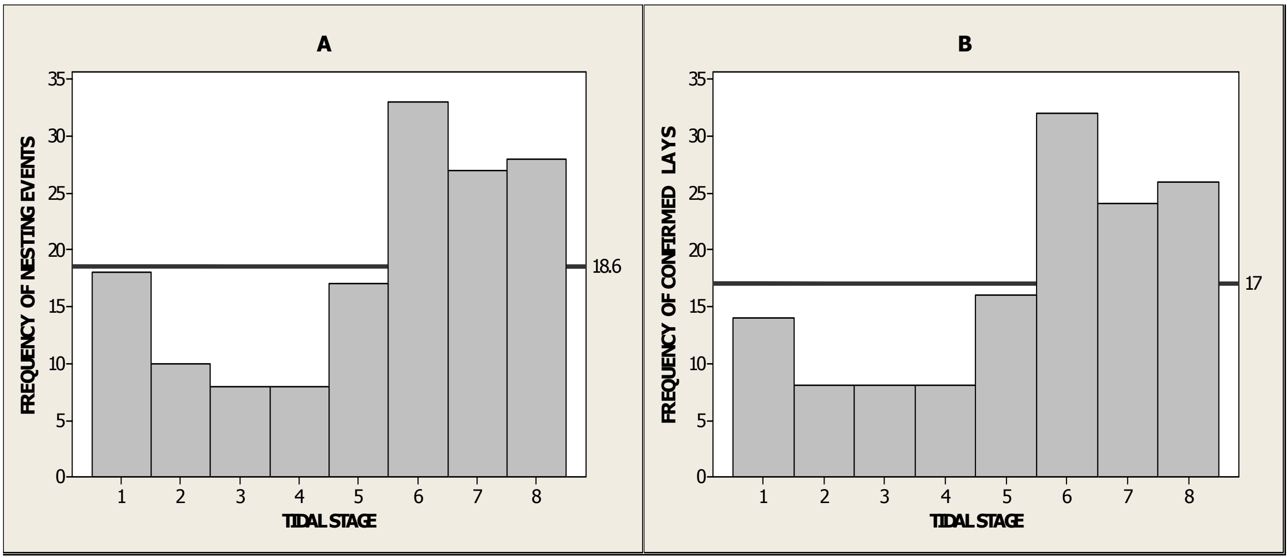


Figure 8.2: Histogram of (A) all nesting related events and (B) confirmed lays against tidal stage with the expected value shown (black line) for leatherback index beaches in Tobago from 2006.

In 2007 the frequencies of nesting events and confirmed lays (Figure 8.3 A and B) show the majority of nesting events at stages 5, 7, 8 and 1 (high tide, mean sea level falling, falling to low tide and low tide). Frequencies of leatherback nesting events is uneven between tidal stages for (A) all nesting related events ($X^2 = 28.8$, DF = 7, $P < 0.001$) and (B) confirmed lays ($X^2 = 23$, DF = 7, $P > 0.01$) for Tobago's index nesting beaches.

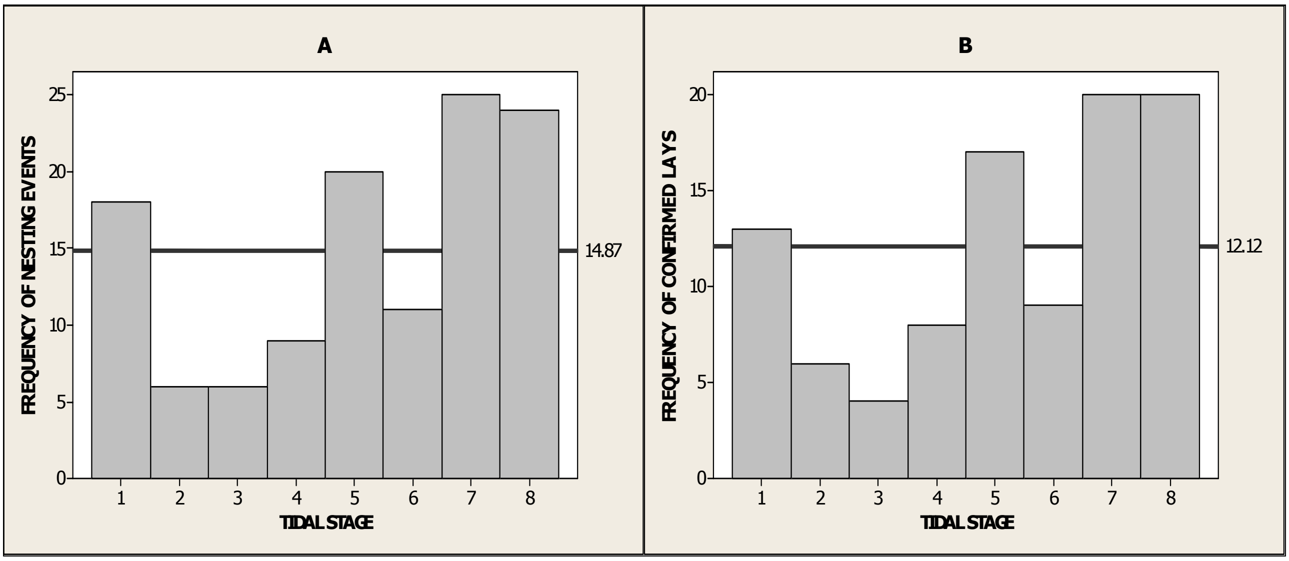


Figure 8.3: Histogram of (A) all nesting related events and (B) confirmed lays against tidal stage with the expected value shown (black line) for leatherback index beaches in Tobago from 2007.

In 2008 frequency of nesting events (Figure 8.4 A) and frequency of confirmed lays (Figure 8.4 B) both show an increase from tidal stages 2 to 6, with a slight decrease at stage 7 (mean sea level falling) then the highest frequency of nesting events at stage 8 (falling to low tide) and also high activity at low tide (stage 1). Frequency of nesting events ($X^2 = 47.9$, $DF = 7$, $P < 0.001$) and frequency of confirmed lays ($X^2 = 36.4$, $DF = 7$, $P < 0.001$) are significantly different between tidal stages for Tobago's leatherback index nesting beaches.

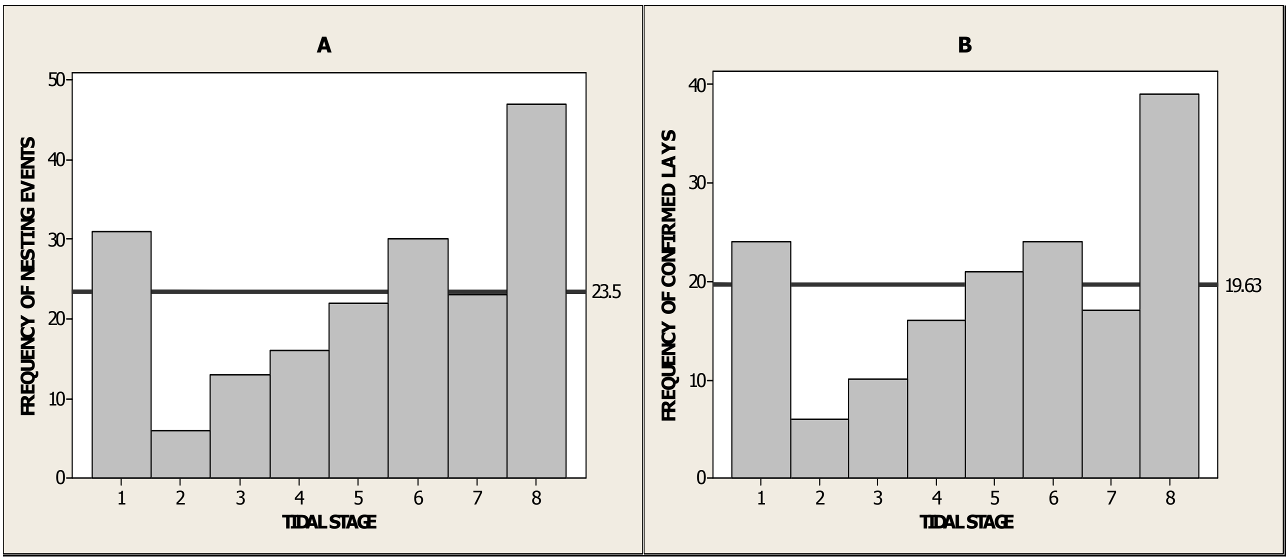


Figure 8.4: Histogram of (A) all nesting related events and (B) confirmed lays against tidal stage with the expected value shown (black line) for leatherback index beaches in Tobago from 2008.

In 2009 the greatest frequency of nesting events (Figure 8.5 A) and confirmed lays (Figure 8.5 B) occurs at tidal stage 4 (rising to high tide). Nesting is significantly different between tidal stages (A) $X^2 = 44.8$, $DF = 7$, $P < 0.001$, (B) $X^2 = 32.4$, $DF = 7$, $P < 0.001$, as observed values for tidal stages 4 and 6 are significantly greater than expected nesting values.

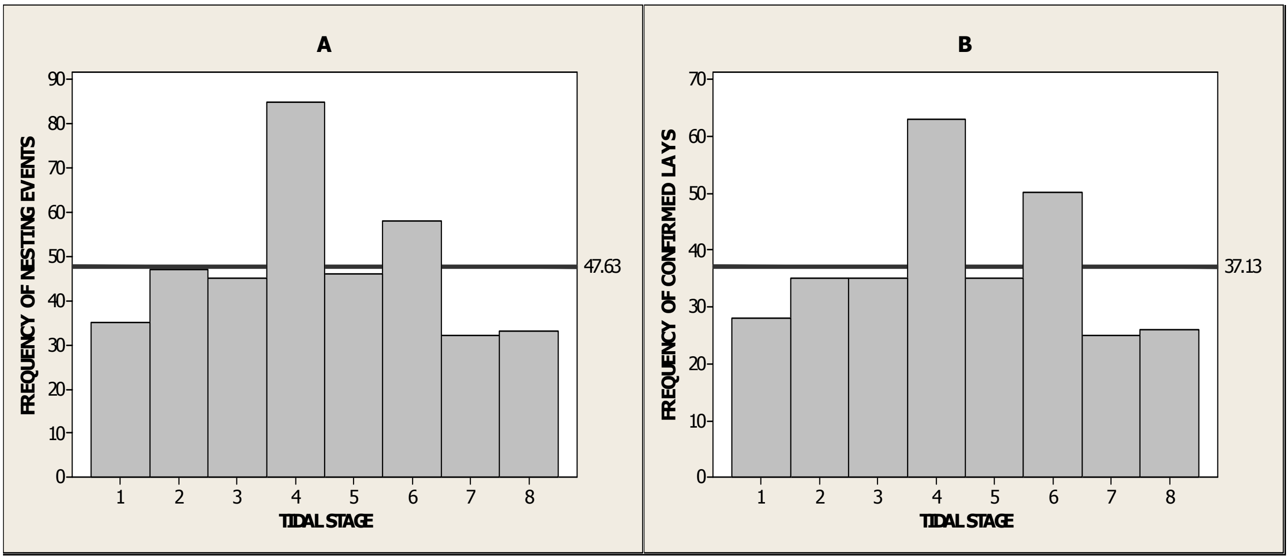


Figure 8.5: Histogram of (A) all nesting related events and (B) confirmed lays against tidal stage with the expected value shown (black line) for leatherback index beaches in Tobago from 2009.

Frequencies of nesting events for all years combined (Figure 8.6 A) and all years confirmed lays (Figure 8.6 B) show observed values in tidal stages 5, 6, 7 and 8 are greater than the expected values (Table 8). Figure C and D do not show significant deviations from the expected values of nesting events (Table 9).

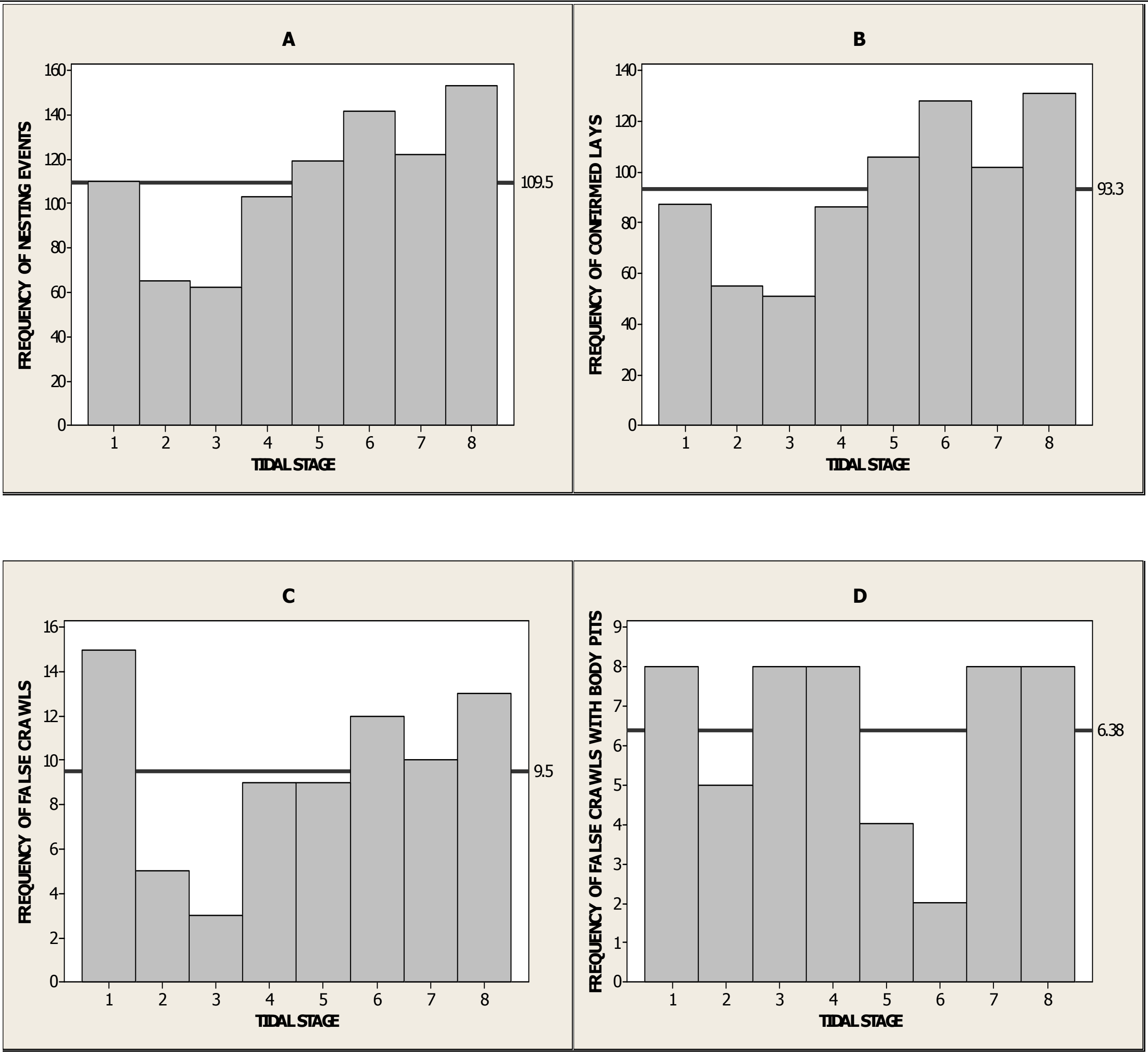


Figure 8.6: Histogram of (A) all nesting events, (B) confirmed lays, (C) false crawls and (D) false crawls with body pits against tidal stage with the expected value shown (black line) for leatherback index beaches in Tobago from 2005-2009.

Table 9: Chi-squared values, degrees of freedom and probability values for the frequency of each nesting event against tidal stage.

	All nesting events	Confirmed lays	False crawls	False crawls with body pits
X^2	68.26	66.6	11.79	6.25
DF	7	7	7	7
P-value	> 0.001	> 0.001	> 0.2	> 0.7

3.4.2. *The relationship of tidal patterns to leatherback nesting events on different beaches*

The trend in the frequency of nesting events for Turtle Beach (Figure 9.1 A and B) is similar to nesting trends seen in section 3.3.1; i.e. a low nesting frequency for tidal stages 2 and 3 (low tide rising and mean sea level rising) with most of the nesting events and confirmed lays occurring at and after high tide and also with high frequencies of nesting activity during low tide. Frequency of nesting frequency (X^2 = 51.7, DF = 7, P < 0.001) and confirmed lays (X^2 = 53.5, DF = 7, P < 0.001) indicate nesting patterns for leatherbacks were significantly different between tidal stages for Turtle Beach, Tobago in years 2005-2009.

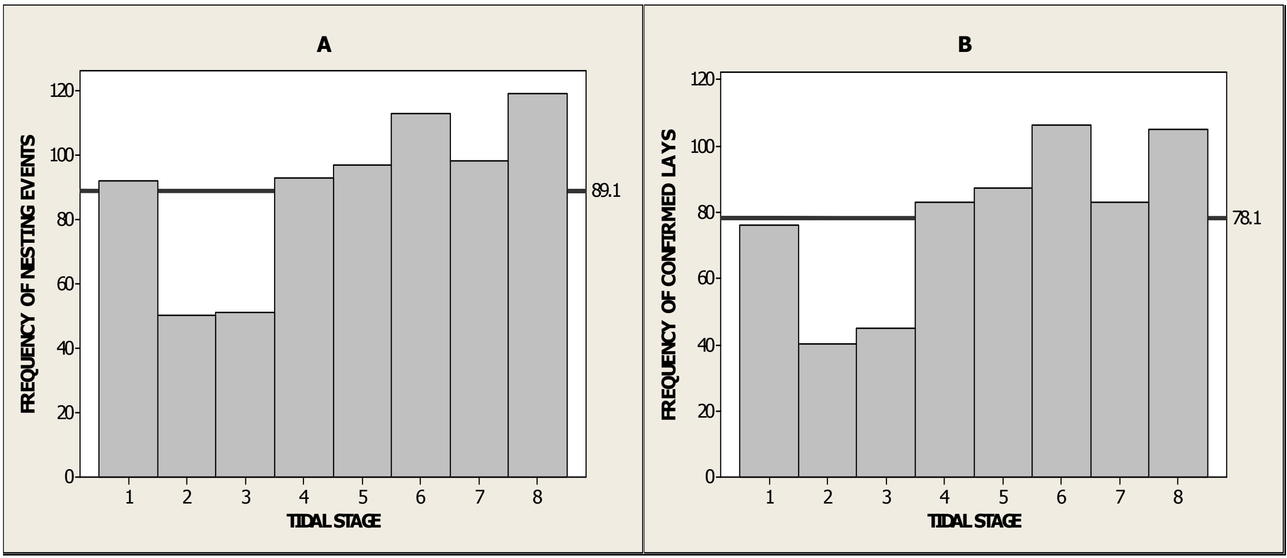


Figure 9.1: Histogram of (A) all nesting related events and (B) confirmed lays against tidal stage with the expected value shown (black line) for Turtle Beach, Tobago from 2005-2009.

Leatherback nesting frequency data for Grafton Beach (Figure 9.2 A and B) showed peak leatherback nesting events at stages 5 and 6 (high tide and falling high tide); however these frequencies did not significantly differ from expected values for all nesting events (X^2 = 11.8, DF = 7, P > 0.2), or confirmed lays (X^2 = 13.8, DF = 7, P > 0.1).

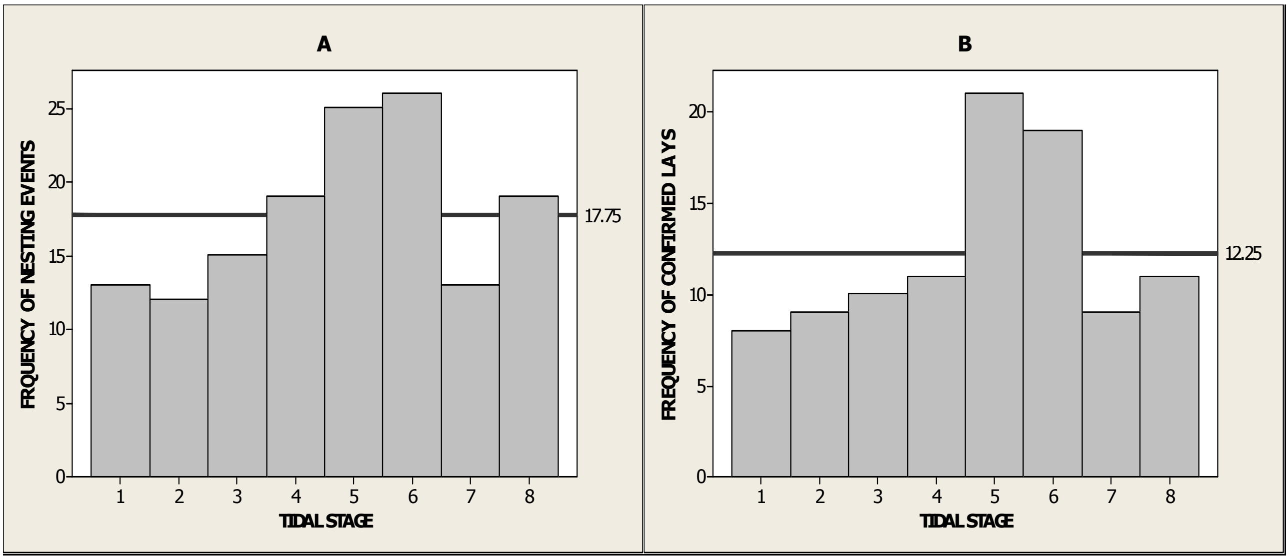


Figure 9.2: Histogram of (A) all nesting related events and (B) confirmed lays against tidal stage with the expected value shown (black line) for Grafton Beach, Tobago from 2005-2009.

Leatherback nesting activity for Back Bay also showed the trend of a low frequency of nesting events at tidal stages 2 and 3. For both frequency of nesting events (Figure 9.3 A) and frequency of confirmed lays (Figure 9.3 B) tidal stage 7 contains the highest level of nesting events, although these values are not significantly different from expected values for frequency of nesting events ($X^2 = 5.8$, DF = 7, $P > 0.7$) or frequency of confirmed lays ($X^2 = 6$, DF = 7, $P > 0.7$).

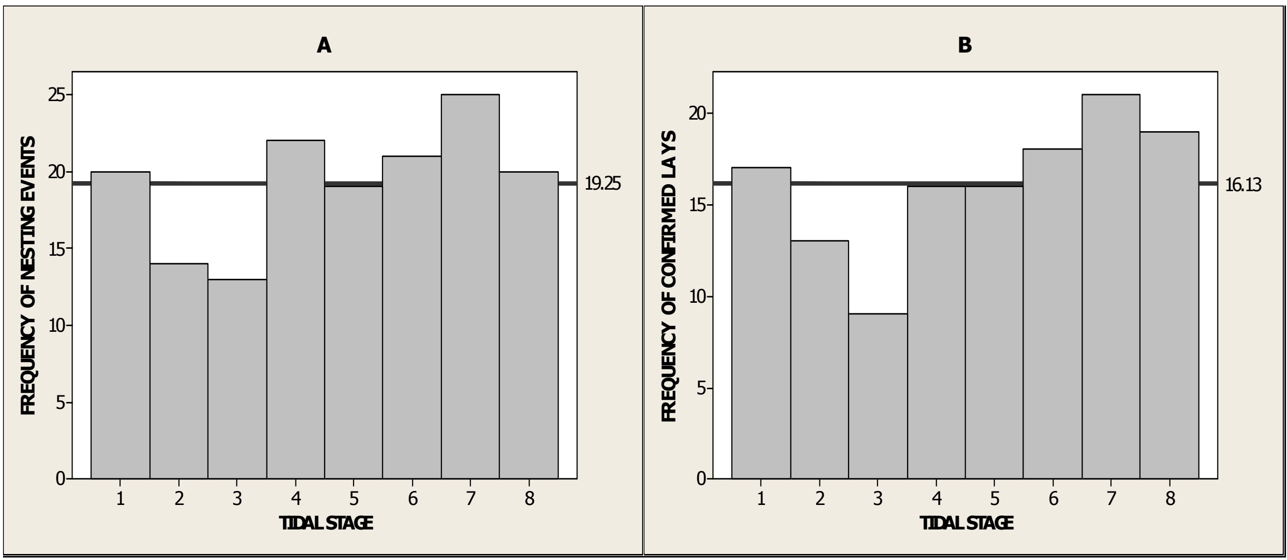
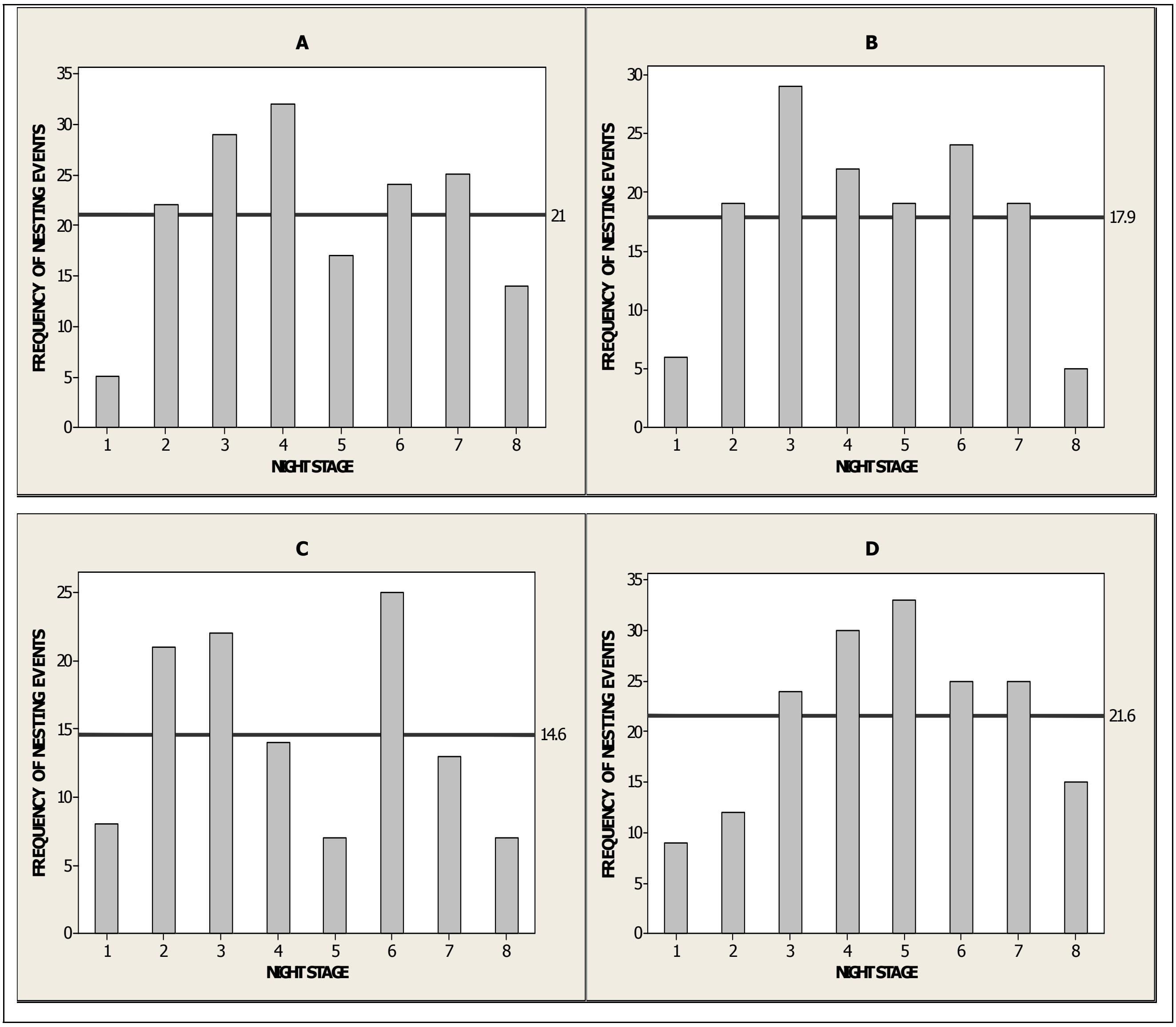


Figure 9.3: Histogram of (A) all nesting related events and (B) confirmed lays against tidal stage with the expected value shown (black line) for Back Bay, Tobago from 2005-2009.

3.5. *Time of leatherback observation at night*

From Figure 10 (A-F) the majority of leatherback nesting events takes place in night stages 3 – 6 (22:00 – 02:00), with frequency of nesting events being significantly different from the expected nesting values for all years individually (2005-2009) and all years combined (Table 10).



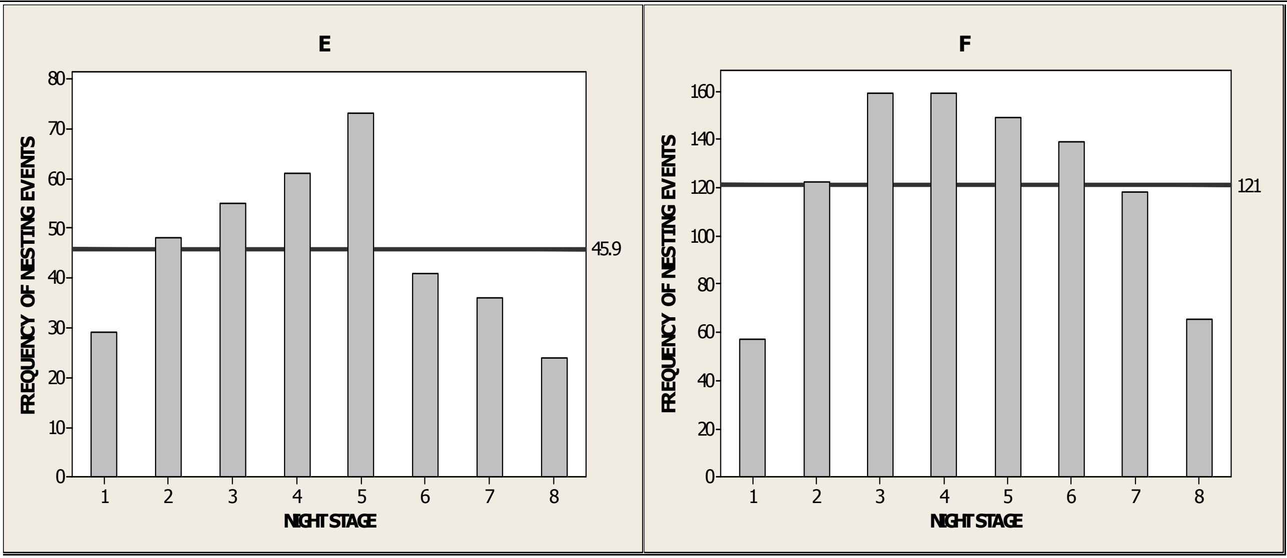


Figure 10: Histograms of the frequency (number of nesting events for each season) of nesting events for (A) 2005, (B) 2006, (C) 2007, (D) 2008, (E) 2009 and (F) all years combined. Expected number of nesting events per night stage is shown by the black line.

Key: 1 - 20:00 – 20:59; 2 - 21:00 – 21:59; 3 - 22:00 – 22:59; 4 - 23:00 – 23:59; 5 - 00:00 – 00:00; 6 - 01:00 – 01:59; 7 - 02:00 – 02:59; 8 - 03:00 – 03:59.

Table 10: Chi-squared values, degrees of freedom and probability values for the frequency of nesting events against night stage.

	2005	**2006**	**2007**	**2008**	**2009**	**All years combined**
X^2	25.33	27.35	25.02	24.23	42.22	92.88
DF	7	7	7	7	7	7
P-value	> 0.001	> 0.001	> 0.001	> 0.01	> 0.001	> 0.001

3.6. *Individual leatherback nesting activity over three seasons*

There does not appear to be any visual trend for high tide against leatherback observed time (Figure 11.1); although the trend line is slightly positive. The correlation is not significant ($R = 0.287$, $P = 0.365$).

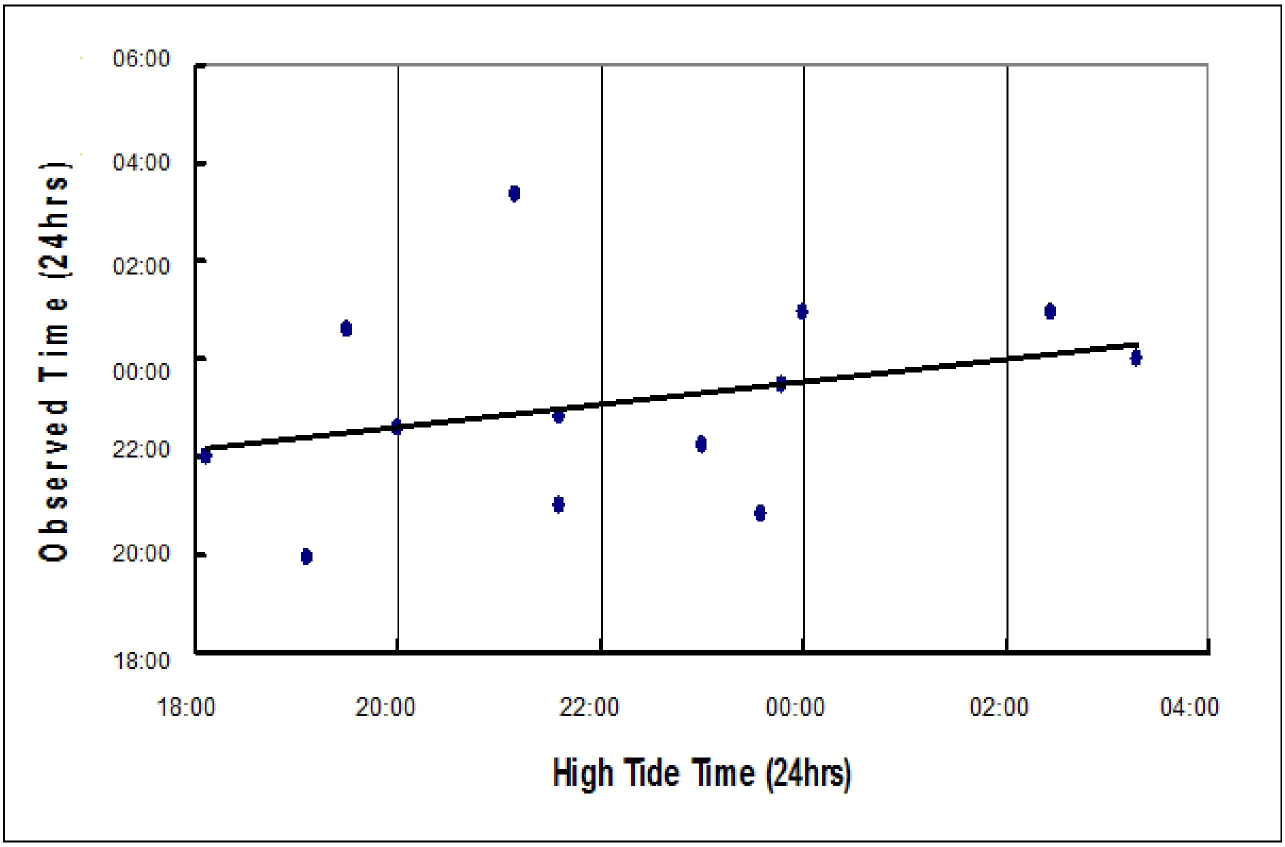


Figure 11.1: Correlation of an individual leatherback ('Diana Ross') observed times against high tide time from 2005, 2007 and 2009 Turtle Beach, Tobago.

Figure 11.2 shows nesting activity frequency highest at tidal stages 1, 4 and 5 (low tide, rising to high tide and high tide), but observed frequency numbers are low, and not significantly different from expected nesting values ($X^2 = 2.29$, $DF = 7$, $P > 0.95$).

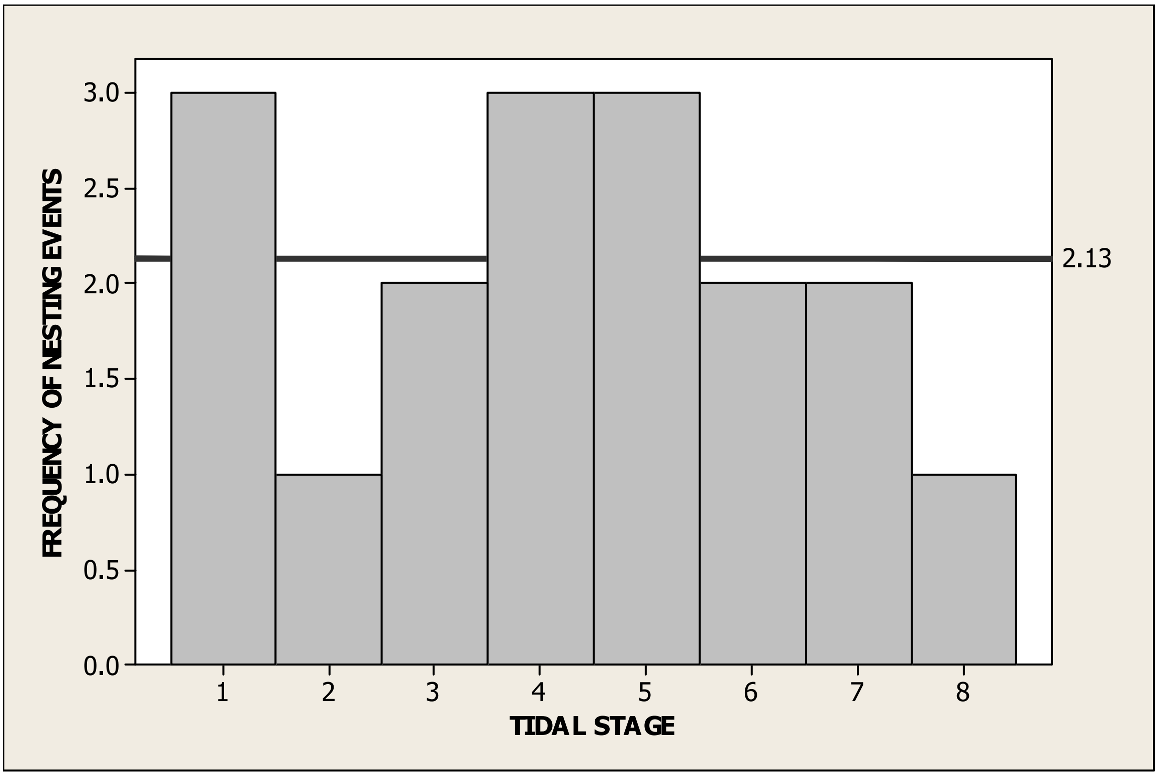


Figure 11.2: Histogram of nesting events for 'Diana Ross' from seasons 2005, 2007 and 2009 combined, with the expected nesting events value shown (black line).

Figure 11.3 displays similar trends of emergence for each night stage to the population trend i.e. emerging after 10pm (night stage 3). This is statistically significant ($X^2 = 17$, DF = 7, $P > 0.05$).

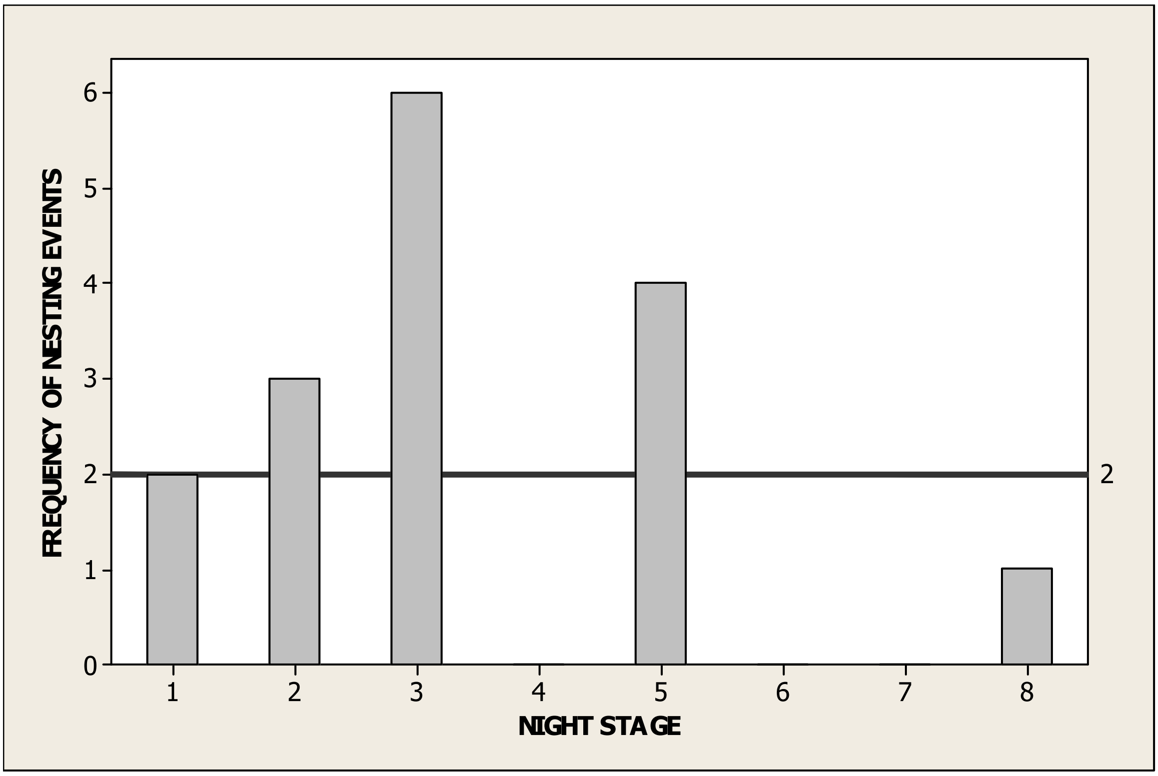


Figure 11.3: Histogram of nesting events for 'Diana Ross' against stage at night when observed, with the expected nesting events value shown (black line).

4. Discussion

This study looked at a number of oceanic and atmospheric variables that may affect leatherbacks nesting patterns; each measured variable will be discussed in the following sections.

4.1 *The effect of lunar phases on all leatherback nesting events combined*

There was a significant difference between the number of nesting events at full moon compared to the first quarter and new moon for all nesting events in 2007. A difference in the number of nesting events between full moon and first quarter could be expected as during the full moon phase the high tides are at their highest point for that lunar month; whereas tides in the first quarter have the lowest tidal range for the lunar month. But there is also a significant difference between the number events at full moon compared to nesting events at new moon. Both full and new moon tidal patterns are similar and occur when the Sun and Moon's gravitational pulls are aligned to each other (Figure 3 A), resulting in a high tidal range. The median values of frequency of nesting activity of the full moon, first quarter and new moon phases equal the lower quartile values for each respective plotted box in Figure 5.1 C and the numerical difference between the medians of full moon and new moon is one [nesting event]. Although this difference is statistically significant it is very unlikely to be biologically significant as the numbers of leatherbacks nesting in 2007 is less than other nesting years and the statistical power of the test may be affected by this. In 2007 when the number of confirmed lays per lunar phase are analysed there is no significant difference between any lunar phase and the number of confirmed lays. This would suggest that the lunar phase is not influencing the number of observed nesting events or nesting outcome for Tobago's index beaches.

For combined nesting data from all years (Figure 5.1 F) the full moon and last quarter phases have a greater frequency of nesting events than the first quarter lunar phase. The first and last quarter have similar tidal patterns as a result of the solar and lunar gravitational pulls acting perpendicular to each other resulting in neap tides (where the tidal range is lower than average). It is therefore unusual for there to be a difference in the total number of nesting events between these lunar phases as environmental conditions, as a result of lunar influence, will be similar. The number of other nesting events (e.g. estimated lays, false crawls and false crawls with body pits) may have influenced the statistical test outcome, as there are no observed differences in frequencies of nesting activity when analysing confirmed lays for all years combined (Figure 5.2 F). Combining the total number of nesting events for all years would assume that the total numbers of nesting events are consistent across seasons, but the numbers of nesting events were highly variable between seasons (Table 1). Any result taken from the combined data from all years should be interpreted carefully, as years where a greater number of nesting events occurred may influence the statistical significance of each test.

Each nesting event outcome could not be analysed separately to observe the influence of lunar phases as there were not enough data for false crawls, false crawls with body pits and estimated lays for each nesting seasons.

The number of nesting events occurring in each lunar phase can be affected by a number of variables; the effect of lunar illumination and the resultant high and low tides occurring due to solar and lunar gravitational forces. Vision is the primary sea-finding sensory mechanism for both adult and hatchling leatherbacks on land (Bartol and Musick, 1996) and this will be affected by lunar phase (Salmon and Witherington, 1995), provided the weather is clear. There is evidence that artificial lights will have a greater impact on nights near the new moon (where the unilluminated portion of the Moon faces almost directly toward Earth, so that the Moon is not visible to the naked eye) as they will appear brighter (Lohmann *et al*., 1996). On nights where the moon is brighter i.e. the full moon, the influence of artificial lights on navigation will be diminished and adults and hatchlings will rely on shape and silhouette cues to guide them (Salmon and Witherington, 1995; Lohmann *et al*., 1996). Pinou *et al*. (2008) report a negative correlation between lunar illumination and nesting for sea turtles nesting on Teopa Beach, Jalisco, Mexico, suggesting peak nesting does not occur during the full moon phase due to the increased illumination. Per lunar month gravitational pulls peak twice (full and new moon) whereas lunar illumination only peaks once (full moon), as there is no difference between frequencies of nesting events (excluding 2007) or confirmed lays for any year between the

full and new moon, I can conclude that lunar illumination is not having a discernable affect on leatherback nesting or nesting outcome for Tobago's index beaches.
Ya:lima:po Beach in French Guiana displays peaks of nesting every 15 days during spring tides (full and new moon), contradicting the observation that nesting occurs on average every 9-10 days due to the turtles biological patterns (Girondot and Fretey, 1996). Girondot and Fretey (1996) found that leatherback turtles can adjust their nesting day as a function of lunar phase, by timing emergence with spring tides (presumably at high tides). Pike (2008) states oviparous freshwater turtles and Olive Ridley (*Lepidochelys olivacea*) sea turtles have short-term control over the timing of egg oviposition; this may allow gravid females the opportunity to wait for optimal environmental conditions to lay and therefore minimise the physical and physiological effort required for terrestrial nesting. Witt *et al*. (2009) observed that the tidal phase had influences on leatherback nesting at all three beaches they monitored, with an increase in nesting on neap days (first and last quarter) for monitored nesting beaches in Gabon.
Opposing trends on the effect of lunar phase and sea turtle nesting activity are indicted by Girondot and Fretey (1996) and Witt *et al*. (2009). The influence of lunar phase on sea turtle's nesting patterns differs between regions and the total influence will depend on local beach topography, tidal patterns (e.g. diurnal, semi-diurnal or mixed tides) and weather. Any literature that claims sea turtle nesting is affected by lunar phase has to take the relevant environmental factors into consideration i.e. tidal phase, weather conditions and geographic location.

This study cannot distinguish between the effect of lunar phase on visual cues and/or tidal cues on leatherback nesting events; although it is clear that the tidal and/or lunar influence on leatherback nesting events in Tobago is absent among the nesting populations for each season.

4.2. *The effect of weather on all leatherback nesting events combined*

As stated in section 4.1 the potential benefits of nesting on clear nights could be influenced by lunar illumination i.e. visibility may be greater on clear night but this could be a disadvantage if distinct silhouettes deter nesting activity. The potential benefits of nesting on rainy nights are debated by Pike (2008); rainfall may act to wash away scents or tracks from freshly laid nests, therefore making it difficult for predators to locate nests, loosening the sand so digging is easier, slowing the nesting female's water loss and being able to crawl easier on moist sand. The rate of evaporative cooling may also increase as a result of rainfall. For nesting events combined and when nesting events are categorised there are significantly more nesting events and confirmed lays on clear nights than rainy or overcast nights.

Three months nesting data from 2009 were used in the analysis (April, May and June); April and May are in Tobago's dry season, whereas June is in the wet season (Murphy, 1997). Leatherback nesting trends from 2005-2009 in Tobago show the majority of nesting events occur throughout May and early June. This is the leatherback's nesting season in the Caribbean and as a result most activity will take place in months during the dry season. If rainy or overcast nights do have an influence on leatherback nesting events it is very unlikely it will be observed at Tobago's index beaches, unless weather data from June-August were to be collected over several years and analysed. Leatherbacks possess mechanisms which they use during nesting to avoid overheating regardless of the weather e.g. blood flow changes (increased blood flow to insulating layers) and the skin turns pink and appears flushed with blood (Paladino, O'Connor and Spotila, 1990).

The effect of weather on leatherback nesting event outcome may be unreliable in this analysis as the sample number of overcast and rainy nights is very small compared to number of nesting events on clear nights. There are also low observed numbers of false crawls, false crawls with body pits and estimated lays for 2009; this is not uncommon amongst nesting leatherback populations. Reina *et al*. (2002) observed ~92.4% of nesting attempts by leatherbacks resulted in confirmed lays in Parque Nacional Marino Las Baulas, Costa Rica. In Tobago percentages of confirmed lays have a range of 64.4 - 76.4%, with a mean of 72% from 2005-09. Trying to detect trends in number of false crawls or false crawls with body pits will be extremely difficult to correlate with any environmental variable for leatherbacks due to the low number occurring within this species.

Although there are significant differences between leatherback nesting events on clear nights compared to overcast/rainy nights this is unlikely to be biologically significant i.e. we cannot predict there will be more or less of a certain nesting event depending on the weather for Tobago’s nesting leatherback population.

4.3. *The effect of high tides on leatherback emergence time*

The relationship between lunar patterns and tides are intrinsically linked; there was no clear pattern between the number of nesting events and lunar phase, so we may also expect there is no clear pattern between high tides and leatherback observed time. For each year (2005-09) there are no significant correlations between the time of high tide and the leatherback observed time. If a positive correlation were present the blue circles (observed time) would be closely distributed around the black lines (high tide time), but as the blue circles are randomly distributed around these lines there is no relationship present and therefore leatherback emergence time is not influenced by the time of high tide for Tobago’s index beaches.

The geography, location and tidal pattern (i.e. diurnal, semi-diurnal or mixed tides) of the nesting beach will greatly influence the difference in the vertical and horizontal distance of the high tides. Little Cumberland Island, Georgia has a tidal range of 2m with a horizontal distance of ~63m between low and high tide lines, a slope of 1.71 degrees (gentle sloping) and shows a high frequency of emergences at high tidal stages (Fraser, 1983). Cape Canaveral, Florida has a tidal range of 1.1m with a horizontal distance of ~33m between high and low tide lines (Frazer, 1983; Pike, 2008), but does not show any significant differences between frequencies of emergences at different tidal stages. At Playa Grande, Costa Rica (on the Pacific coast) the vertical distance between low and high tide can be 4m resulting in a horizontal distance of 50-100m depending on lunar phase (Reina *et al*., 2002). This could add almost an hour onto the leatherback’s terrestrial migration time, placing an increased oxygen demand and energetic cost on the nesting female (Reina *et al*., 2002). On the Pacific coast of Costa Rica there is a loose association with emergence

time and high tide, but when tides were high during the afternoon and early morning, turtles emerged to nest throughout the night regardless of the tidal stage (Reina *et al*., 2002). On the Caribbean coast of Costa Rica (Tortuguero) vertical tidal distances are only around 1m and there is no relationship apparent between leatherback emergence and tidal stage (Leslie *et al*., 1996; Reina *et al*., 2002). Tobago also has tidal range of around one meter with the horizontal distance between high and low tide is no greater than 20-30 meters (personal observation) for all three of Tobago's index beaches. There may be no correlation between high tide time and leatherback emergence time in Tobago as there is no major benefit emerging at high tide rather than low tide i.e. the increased horizontal distance that leatherbacks face on Tobago's beaches at low tide does not deter them from emerging to nest.
As leatherbacks nest on other beaches within the Caribbean region (Girondot *et al*., 2007) it would be interesting to observe emergence times from several individuals from different beaches to observe whether emerging regardless of high tide is an individual preference or Caribbean leatherback preference. As tidal ranges are small throughout the Caribbean the author would expect that nesting is not correlated with high tides throughout the Caribbean, as there is no selection pressure on populations to emerge at or around high tide.

Data were not used for turtles first observed covering, camouflaging and gone as the length of each nesting process is variable between individuals (personal observation) and therefore an estimated arrival time may not be reliable; Fretey and Girondot (1989) estimate arrival time and include this in their analysis between high tide and leatherback arrival time. Other nesting events such as false crawls were not used in the analysis because the observed numbers were low, but also because if a turtle false crawls on one beach it may appear on the same beach or another index beach later that evening resulting in pseudo-replication. Only confirmed lays were used in the analysis.

4.4. *The relationship of tidal patterns to leatherback nesting events*

When leatherback nesting events for all beaches are combined there is a general trend of a higher frequency of nesting observed at and after the high tide, with high nesting frequencies continuing to low tide. For most years there is also a distinct lack of nesting events when the tide is rising from low tide to high tide. As nesting frequencies are high at low tides the potential benefit of emerging at high tides (where the distance to crawl on the beach is less than low tide) is not apparent for Tobago's index beaches as the difference in vertical and horizontal tidal range is low, so there may be other factors influencing the observed trend of emergence at specific tidal stages e.g. tidal velocity. Gravid nesting female leatherbacks can weigh up to 435kg (range = 250-435kg, mean = 346.8kg) (Leslie *et al*., 1996), but a proportion of their weight will be supported by salt water when in the marine environment and so tidal velocities will affect them. Watanabe, Seino and Uda (2004) conclude that turtles tend to emerge from the sea where the across shore current velocity decreases. The state of a tidal current where the velocity is near zero is known as slack water and this occurs when the current changes. Emerging at high and low tides could be when tidal velocity is at its lowest and therefore the nesting leatherbacks are timing there emergence low velocity of currents in order to reduce energy expelled on the approach to the beach. Their must be no advantageous carrier affect of approaching when the tide coming in as the observed numbers of leatherbacks emerging at these stages (2 and 3) are consistently lower than the expected values for all seasons.

Leatherbacks do not have strongly developed behavioural patterns for nesting beyond the tide's reach, possibly due to the range of different beaches where they nest and also due to changing beach dynamics on beaches where they may have previously laid (Mrosovsky, 1983; Kamel and Mrovosky, 2004) e.g. in Trinidad (where many of Tobago's leatherbacks are PIT-tagged (personal observation)) the available nesting habitat changed markedly from week to week (Bacon, 1970; Leslie *et al*., 1996). If nesting were to occur further down the beach as a result of emerging during low tides this may increase the amount of nests inundated with water when tides rise, but for Tobago's index beaches only a handful of nests are relocated each year because of marginal location below the upper tidal line (personal observation). This could be due to the small horizontal distance between high and low tides and/or due to the 'scatter nesting pattern' adopted by leatherbacks when choosing nest sites i.e. hedging their bets by scattering nests throughout a nesting beach where some nests will be too far away from the sea, some will be too close to the sea but some will located at an ideal place (Mrosovsky, 1983).

Turtle Beach and Back Bay both display similar tidal emergence trends to the graphs where all beach data are combined (Figure 8.6 A); nesting frequencies are highest at and after high tide, with high nesting frequencies continuing to low tide. Grafton Beach does not show any significant differences between observed and expected nesting values, but there are a large number of nesting events at high tide compared to any other tidal stage; this reflects the differences in beach profiles between Tobago's index beaches. Grafton Beach has a more gentle slope on and off shore compared to Turtle Beach and Back Bay, and as a result at low tide the tide goes out further thereby increasing the horizontal distance a turtle would have to crawl. Leatherback nesting beaches commonly have steep sloping banks and shelves created by strong on-shore currents. It is possible on-shore currents are strongest when the tide is rising and this may deter leatherback nesting at these tidal stages as they prefer to nest where across-shore currents are low (Watanabe, Seino and Uda, 2004). Turtle Beach has the steepest beach slope compared to Grafton Beach and Back Bay. On-shore currents are possibly not as strong on Grafton Beach and Back Bay compared to Turtle Beach; this could be a reason why there is no significant differences observed between the frequency of leatherback nesting events and tidal stage for Grafton Beach and Back Bay. Strong on-shore currents may also explain why nesting frequencies at stages 2 and 3 are particularly low for Turtle Beach (Figure 9.1 A).

Nesting frequencies vary from year to year e.g. in 2008 there were a high frequency of leatherbacks nesting at low tidal stages, whereas in 2009 the highest nesting frequencies were at high tidal stages with low nesting frequencies at low tides. There may be a number of reasons for this. Firstly, onshore and offshore beach dynamics will vary annually, and this could be a reason for differences observed in nesting events between years if the available nesting habitat changes between years. Secondly, trends in leatherback emergence time and tidal stage could also vary between years as leatherbacks do not lay annually, they return to nest every 2-3 years on average after a nesting season, so on consecutive nesting years there are different population of turtles nesting, and also many transient turtles nesting in Tobago. Third and finally, the tidal stage at the time of emergence will also vary from year to year as a result of individual choice.

4.5. *Time of leatherback observation at night*

The time of leatherback observation time at night is almost consistent between seasons, so we can conclude this is not only a population trend, but a species trend for leatherbacks nesting on index beaches in Tobago. Leatherbacks do not generally emerge during the day due to potentially lethal temperatures that may exhaust the nesting turtle, and so they suppress emergence till night, regardless of high tides during the day (Reina *et al*., 2002). As leatherback nesting occurs mostly throughout Tobago's dry season where temperatures will be greater than the wet season, this may have contributed to selection for nesting activity to occur nocturnally when the coolest temperatures occur. The nesting process takes around 1.5 hours to complete so by emerging between 10pm and 2am (when most of the turtles emerged in this study) reduces the probability that turtles will be exposed to higher sand and air temperatures and therefore heat gain will not be a serious problem. Sunset occurs around 7pm and sunrise around 5am in Tobago. Leatherback turtles may be using the time at night (hours of darkness) as a cue to signal when to commence the nesting process.

As turtles may be counted nesting several times during one season there is a danger of pseudoreplication, but the average number of times a turtle will be recorded is only between one and three within a season (personal observation) and the sample number is large (nesting event range = 168-367, nesting event mean = 193.6). There are only a few turtles that return to nest several times within and between seasons e.g. 'Diana Ross' nested 8 times in 2009, but this is rare for leatherbacks nesting on Tobago's index beaches. As these trends of emergence occur for the whole population throughout several seasons the observed high frequencies of nesting between 10pm and 2am cannot be due to counting the same turtles several times.

4.6. *Individual leatherback nesting activity over three seasons*

Apart from one nesting event, all other nesting events recorded of ‘Diana Ross’ were on Turtle Beach (n = 16), clearly showing an individual beach preference for a turtle species that does not always return to the same or natal beaches (Davenport, 1997). There is no correlation between high tide time and leatherback observed time for this individual, but this is expected as there is no population/species trend of high tide emergence for Tobago’s index beaches, and because the vertical and horizontal distance between high and low tides is low. Diana Ross’s emergence at certain tidal patterns is similar to the trends observed for leatherback populations over seasons i.e. emerging at and around high tides and also at low tides. This individual preference of emergence at certain tidal patterns is consistent to the leatherback nesting populations over seasons so it’s likely that leatherbacks are responding the same environmental cue e.g. tidal velocity. There is also a higher frequency of nesting after 10pm for Diana Ross; the same trend observed for the population, but nesting observations of ‘Diana Ross’ are low. Bell *et al*. (2009) states that ‘behaviours that are more sensitive to the environment are less repeatable’, but if the environmental variation is reasonably stable (e.g. tidal patterns) the behaviour may be consistent.

“Given that the level of investigation concerning the nesting process, it seems odd that no one has been able to define the process by which the turtle (any species) selects its nesting beach or the site for the nest on the beach” (Miller, 1996). For leatherbacks it is unlikely that a defined, definite nesting process will be described as leatherbacks nest on different beaches within regions that may be variable in topography and tidal patterns. For one leatherback (Diana Ross) it is hard to observe any individual patterns of statistically significant consistent nesting emergence as the number of times observed per year is low (excluding 2009). This problem will occur in any project trying to identify and define individual nesting patterns in leatherbacks as they do not always return to the same beaches; identification tags may fall off between nesting seasons; patrols may miss nesting events; there may have been selection for behavioural traits that are most suited for nesting on different and variable beaches e.g. scatter nest positions. In fact, it may be more beneficial not to have a rigid, definite nesting process for leatherbacks as the beaches in which they are nesting will vary it may be useful to posses an adaptable nesting process.

Conclusions drawn from Figure 11.2 and Figure 11.3 are to be interpreted with caution as the expected values are less than 5.

5. Conclusions

This study looked at a number of variables that may influence leatherback nesting and found that:

- The number of leatherback nesting events did not vary between lunar phases.
- Weather did not influence leatherback nesting or nesting outcome.
- Emergence time of leatherbacks is not correlated with high tides.
- Leatherbacks in Tobago displayed a trend of nesting at and after high tide, with high nesting frequencies continuing to low tide. Leatherbacks did not nest in high numbers when the tide low rising to high tide.
- The highest frequency of leatherback nesting events took place between 10pm and 2am.
- Nesting patterns of an individual leatherback seem consistent with trends observed in populations.

The impact of a conservation effort on the health i.e. numbers and physical wellbeing, of a population is difficult to judge in the short term, especially with long-lived, slow maturing turtles such as leatherbacks. Any information on consistent nesting trends within a nesting region will be helpful as conservation effort can be coordinated more efficiently. Due to the geographic location, structure of each beach and amplitude of the tide, Tobago's beaches are not heavily influenced by environmental processes, and as a result leatherback nesting is not overly affected by environmental processes. Peak leatherback emergence and nesting activity is more closely associated with the time at night.

Further work may include accurately profiling Tobago's three index beaches i.e. angle (slope of the beach), tidal amplitude, the difference between high and low tides per lunar phase and how tidal velocities change within the tidal cycle.

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