Ecología de la nidificación, conservación y amenazas de la tortuga laúd, *Dermochelys coriacea*, en Pacuare Nature Reserve, Costa Rica

Nesting ecology, conservation and threats of leatherback sea turtle, Dermochelys coriacea, at Pacuare Nature Reserve, Costa Rica

Tesis doctoral realizada para la obtención del
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La doctorando Margarita López Rivas, los directores de la tesis Dr. Javier Diéguez Uribeondo, el Dr. Adolfo Marco y la tutora Dra. Carmen Zamora Muñoz garantizamos, al firmar esta tesis doctoral, que el trabajo ha sido realizado por el doctorando bajo la dirección de los directores de la tesis y hasta donde nuestro conocimiento alcanza, en la realización del trabajo, se han respetado los derechos de otros autores a ser citados, cuando se han utilizado sus resultados o publicaciones.

Granada, 29 de Julio de 2016

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Granada, España

2016

Los Dr. Javier Diéguez Uribeondo y Dr. Adolfo Marco

CERTIFICAN:

Que los trabajos de investigación desarrollados en la Memoria de Tesis Doctoral: “Ecología de la nidificación, conservación y amenazas de la tortuga laúd, *Dermochelys coriacea*, en Pacuare Nature Reserve, Costa Rica”, **son aptos para ser presentados por la MSc Margarita López Rivas ante el Tribunal que en su día se designe, para optar al Título de Doctora por la Universidad de Granada.**

Y para que así conste, en cumplimiento de las disposiciones vigentes, extiendo el presente certificado a 29 de Julio de 2016.

Granada, 29 de Julio de 2016

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Dr. Javier Diéguez Uribeondo Dr. Adolfo Marco

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"Esta tesis va dedicada a todos aquellos que aman la naturaleza y dieron su trabajo, esfuerzo y dedicación a la conservación de estas maravillosas criaturas"

A mi madre y mi padre,
a mi querida
hermana,
y mi amor Ferrer, por
ser todo en mi
vida

"Si todos ponemos nuestro granito de arena,
la conservación no será la utopía de unos pocos"

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Antecedentes

En el año 1989 D. John Denham adquirió a seis propietarios unos terrenos de 1050 Ha. en la costa de la provincia de Limón de Costa Rica. Poco después se establecería en dicha zona lo que hoy conforma la Reserva Natural de Pacuare, la cual se encuentra limitada en la costa por una playa de 5.7 kilómetros de longitud. A principios de los años 90 se descubriría que dicha playa albergaba un importante punto de nidificación de la tortuga baula o laúd, *Dermochelys coriacea,* además de una menor nidificación de la especie *Chelonia mydas* o tortuga verde y una esporádica de la tortuga carey, *Eretmochelys imbricata.*

En esos años Alexandra Denham y Stanley Rodríguez iniciarían el monitoreo de la playa junto a la asistencia de voluntarios y turistas. Lo que permitió identificar la existencia de un alto porcentaje de saqueo de nidos de tortuga laúd, la muerte y extracción de algunos ejemplares, y la necesidad de iniciar un proyecto que mitigase la continua extracción de huevos y ejemplares de varias especies. Históricamente, al igual que en otras partes del mundo, en Costa Rica se ha consumido la carne de tortuga y sus huevos: a éstos últimos se les han atribuido efectos afrodisiacos entre otros, por lo cual, su saqueo y consumo ha sido popularmente aceptado desde decenios. Por todas estas razones, es en este momento cuando surge la idea y necesidad de establecer un proyecto focalizado en la conservación de estas especies en crítico peligro de extinción (*Dermochelys coriacea y Eretmochelys imbricata*) y en peligro de extinción (*Chelonia mydas*); y es fundada la ONG Endangered Wildlife Trust (EWT), organización no gubernamental sin fines de lucro, encargada de establecer el proyecto de conservación de tortugas marinas, y de llevar la gestión y funcionamiento de la Reserva Natural de Pacuare hasta el día de hoy.

Inicialmente tras el establecimiento del proyecto se comenzaron a realizar monitoreos esporádicos a lo largo de playa por algunos voluntarios, pero sería a partir del año 1991 cuando se tomarían registros más exhaustivos a lo largo de cada temporada de nidificación. Sin embargo, son considerados los datos obtenidos a partir del 1994 ya que eran de mayor fiabilidad, al estandarizarse la metodología de los registros.

El proyecto ha ido aumentando en tamaño y complejidad durante los 25 años de funcionamiento, donde voluntarios, biólogos asistentes de campo y coordinadores realizan cada año registros exhaustivos de la nidificación de la tortuga laúd entre otras especies, y cuyos esfuerzos se han visto reflejados cada temporada.

Debido al conocimiento de este proyecto, en 2008 entré a formar parte del equipo de asistentes de investigación de la Reserva Natural de Pacuare, donde tras haber tenido experiencia monitoreando en playa otras especies, como la tortuga lora de la costa pacífica de Costa Rica, *Lepidochelys olivacea,* inicié mi formación en el monitoreo de la nidificación de las tortugas laúd o comúnmente conocidas en Costa Rica como baulas.

Posteriormente, trabajé junto a la investigadora Cristina Ordoñez en la coordinación del proyecto de playa Soropta, localizada cerca del límite fronterizo entre Costa Rica y Panamá. Durante mi estancia en este proyecto tuve la oportunidad de ampliar mi conocimiento sobre la ecología y biología de esta especie y además, trabajar con jóvenes asistentes procedentes de la comunidad Gnöbe del norte de Panamá: lo cual me enriqueció enormemente y donde pude adquirir un mayor conocimiento sobre las amenazas a las que se enfrentan estas tortugas milenarias.

Con estas experiencias adquirí una profunda admiración por unos de los seres primitivos más apasionantes que existen y nunca antes había tenido la oportunidad de conocer. Dichas experiencias me llevaron a hacerme muchas preguntas relacionadas con su biología, ecología y conservación, y debido a mi interés en responder a algunas de ellas he seguido investigando, dedicando mi trabajo y disfrutando todos estos años. Por todo ello, dedico esta tesis a mi búsqueda personal en contestar algunas de esas preguntas, siempre teniendo como objetivo profundizar en el conocimiento de esta maravillosa especie y nunca olvidando mi principal motivación: su conservación.

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Chapter 1. Introducción general

1.1. Características ecológicas de la tortuga laúd y amenazas

Se estima que las tortugas marinas habitan en los mares desde hace al menos 100 millones de años, cuyas especies se engloban en dos familias: Cheloniidae y Dermochelyidae. La especie *Dermochelys coriacea,* comunmente llamada tortuga laúd o baula (Fig.1A), es la única especie perteneciente a la Familia Dermochelyidae existente en la actualidad y sus poblaciones se encuentran catalogadas por la lista roja oficial de especies amenazadas de la Unión Internacional para la Conservación de la Naturaleza desde en peligro crítico de extinción hasta vulnerable según la zona de nidificación en la que se encuentre localizada (Wallace et al., 2013). Se ha detectado la existencia de poca variabilidad intraespecífica en esta especie con respecto al resto de tortugas marinas pertenecientes a la Familia Cheloniidae (Bowen and Karl, 2007). Su origen se podría datar en 900.000 años, siendo baja la variabilidad genética de las poblaciones del Océano Atlántico y Pacífico, y con leves diferencias interpoblacionales (Dutton et al., 1999). Sin embargo, mediante técnicas con mtDNA y microsatélites se ha identificado en los últimos años la existencia de poblaciones demográficamente diferentes: una de ellas conformaría la metapoblación atlántica (Dutton et al., 2013).

Las poblaciones de tortuga laúd presentan el rango geográfico de distribución más amplio conocido dentro de los reptiles. Estas tortugas se caracterizan por ser muy buenas navegadoras y sus migraciones transoceánicas pueden alcanzar miles de kilómetros entre las zonas de nidificación en áreas tropicales y las de alimentación de aguas más frías (Hays et al., 2004). Sin embargo, dichas migraciones podrían variar según las condiciones ambientales presentes (Price et al., 2006). El límite norte de distribución de esta especie se corresponde con temperaturas superficiales marinas del Atlántico norte de entre 10 y 12°C (Witt et al., 2007). Además, su alimentación está especializada en la ingestión fundamentalmente de medusas (Bjorndal, 1997), sobretodo de especies del género *Rhyzostoma*. Por lo que su distribución puede estar condicionada por la localización de agregaciones de estas especies.

La tortuga laúd se caracteriza por anidar en casi todos los continentes, exceptuando Europa y la Antártida (Eckert et al., 2012). Respecto a la población de América Central, donde se centra este estudio, podemos destacar que se considera la cuarta zona de nidificación más importante del mundo, después de la zona de nidificación de Gabón, Guayana francesa y Suriname (Turtle Expert Working Group, 2007; Patiño-Martinez et al., 2008) y Trinidad y Tobago (Eckert et al., 2012). En particular, la población de Costa Rica y norte de Panamá constituyen las más abundantes de Centroamérica (Chacón- Chaverri and Eckert, 2007; Rivas et al., 2016a).

Biología reproductiva

Esta especie se caracteriza por su alta longevidad (Musick et al., 1999) y por desarrollar la mayor parte de su vida en el mar. Diferentes estudios, tanto en cautividad como en libertad, han determinado mediante análisis de tendencia poblacional, histología y esquelotocronología, que la edad de maduración para esta especie oscilaría entre 5 – 30 años (Zug and Parham, 1996; Dutton et al., 2005; Jones et al., 2009; Jones et al., 2011). Cuando alcanzan la edad adulta, tras el primer episodio reproductivo, presentan un crecimiento muy lento alrededor a 0.2-0.3 cm por año (Price et al., 2006; Rivas et al., 2016a), aunque el tiempo de crecimiento hasta alcanzar la maduración sexual parece ser de los más rápidos de todas las tortugas marinas exceptuando las del género *Lepidochelys* (Eckert et al., 2012).

Tras la maduración sexual vuelven a anidar en sus playas de nacimiento, sin embargo, esta especie no presenta una filopatría natal muy acusada en comparación a otras especies de tortugas marinas (Witt et al., 2007; Hawkes et al., 2009). Durante la época de apareamiento se ha detectado que los machos también se dirigen a las playas de nidificación, viajando entre colonias de anidamiento, y pueden permanecer cerca de la costa para aparearse con las hembras durante la temporada de nidificación (Eckert et al., 2006; James et al., 2005). Esto ha sido observado en la costa Pacífica Costa Rica donde se han observado machos de esta especie en las inmediaciones de la costa de playa grande (Reina et al., 2005). Su estrategia reproductiva es de poliginia y poliandria (Stewart and Dutton, 2011), sin embargo la monogamia es la estrategia de apareamiento más observada (Crim et al., 2002), ya que mediante microsatélites se ha visto que la paternidad múltiple entre sucesivas ovoposiciones en esta especie es bastante infrecuente (Dutton et al., 1999).

Las hembras salen de forma aislada a la playa, sin embargo se han detectado frecuentemente salidas sincronizadas (Obs. Personal). Existen intentos fallidos donde la hembra no ovoposita debido a diferentes factores como pueden ser: nido en contacto con la marea, taludes de gran altura, vegetación, etc.; a estas actividades se les considera como salidas falsas (Rivas et al., 2016a).

Los tamaños medios de caparazón registrados entre las hembras nidificantes de la población del Caribe de Costa Rica varían entre 150 y 160 cm (Chacón, 1999). Sin embargo, los mismos datos para la población de la costa Pacífica oscilan en valores medios de 145 cm (Reina et al., 2002).

En esta especie no existe un aparente dimorfismo sexual (James et al., 2005), sin embargo, existe una distinción sexual entre hembras y machos: la cola del macho adulto es mucho más larga que la de la hembra y la cloaca se localiza más allá de la parte posterior del caparazón (Eckert et al., 2012). El espécimen más grande registrado fue el de un macho capturado en la costa de Gales de 916 kg (Morgan, 1990).

El periodo de nidificación varía entre poblaciones: la población de la región atlántica del Caribe inicia su periodo de nidificación en febrero y termina en junio, anidando esporádicamente en julio. Los picos máximos de nidificación se dan en abril y mayo (Chacón, 1999; Rivas et al., 2016a). Los intervalos interanuales de nidificación en el Caribe suelen ser mayoritariamente de entre 2-3 años, aunque también se han detectado puestas en años consecutivos por algunas hembras (Obs. personal). Sin embargo, en el Pacífico, se ha detectado una frecuencia de reproducción más baja que en el Atlántico (Bailey et al., 2008). Dentro de cada estación reproductiva las hembras pueden anidar de 3 a 11 veces cada 9 - 11 días (Chacón, 1999). La zona de nidificación tendrá gran influencia en los éxitos de eclosión, además de las condiciones ambientales del nido (Garrett et al., 2010). La zona de mayor frecuencia de nidificación será la media y las de menor: la intermareal y de vegetación (Chacón, 1999).

La profundidad media de los nidos suele variar entre 60 y 80 cm, y la anchura superficial entre 40 y 60 cm (Wallace et al., 2004). Los huevos de esta especie son los más grandes de todas las tortugas marinas y es de los más grandes de todas las especies ovíparas. En cada ovoposición la hembra deposita una media de entre 60 y 100 huevos fértiles y posteriormente una cantidad variable de huevos vanos, que suele representar el 31. 03% del total de la puesta. Estos huevos son más pequeños, irregulares y contienen sólo albúmina, y la masa total de estos huevos constituye el 20% de la masa total de los huevos de cada nido (Chacón et al., 1999; Wallace et al., 2006). El período medio de incubación para esta especie es de 60 días y el éxito de eclosión de los nidos es el menor conocido de todas las especies de tortugas marinas: alrededor del 50% (revisado por Bell et al., 2004; Wallace et al., 2004; Hilterman and Goverse., 2007), siendo del 41% en Costa Rica (Chacón-Chaverri et al., 2007), en comparación con otras especies, como la tortuga verde

Atlántica *Chelonia mydas* (63.5–86.0%) en Tortuguero (De Haro et al., 2008; Segura and Cajade, 2010), la carey *Eretmochelys imbricata* (78.6%) en las Indias occidentales (Ditmer and Stapleton, 2012) o la tortuga *Caretta caretta* (73.4, 55.7 y 70–80%), reportada en el sur de Carolina (Caldwell, 1959), Florida (Witherington, 1986) y Cabo Verde (Abella et al., 2007), respectivamente.

Tras la eclosión los neonatos emergen hasta la superficie desde el fondo del nido (Fig. 1B), permaneciendo varios días en la cámara del nido: durante este tiempo se absorbe buena parte del vitelo y se produce el estiramiento del caparazón y plastrón (Godfrey et al., 1997). La emergencia se produce principalmente de noche y cuando se detectan las temperaturas más bajas (Patiño-Martinez et al., 2010).

Esta especie se caracteriza como el resto de tortugas marinas, por poseer una determinación sexual dependiente de la temperatura del medio en el cual se incuban sus nidos. Dicha temperatura será determinante en el porcentaje de crías de ambos sexos y por tanto, un factor ambiental de gran importancia para su estrategia reproductiva (Mrosovsky and Yntema, 1980; Davenport, 1997). A lo largo del desarrollo embrionario de los huevos la temperatura entre la tercera y quinta semana o tercera mitad del periodo de incubación determinará la diferenciación gonadal y el sexo de los embriones (Spandora and Spotila, 1985), a este periodo se le conoce como periodo termo-sensible de diferenciación sexual (Wibbels, 2003). El rango de transición de temperatura (TRT) se considera al umbral que incluye una producción mixta de hembras y machos: la temperatura estimada fuera de sus límites produciría un 100% de machos o hembras. El rango estimado para las poblaciones de tortuga laúd es de 29°-30°C (Godfrey et al., 1997; Eckert et al., 2012).

Algunos estudios han demostrado la existencia de un punto térmico de equilibrio denominado temperatura pivotal, que estima la razón de sexos de los embriones dependiendo de una temperatura constante de incubación (Mrosovsky and Yntema, 1980); a esta temperatura la producción de ambos sexos sería equitativa (1:1). Se considera que para esta especie la temperatura pivotal está entre 29.25°- 30.5°C. Siendo las estimaciones más precisas aquellas de 29.43°C de playa Grande en Costa Rica y 29.51°C de Suriname y la Guayana Francesa (Hulin et al., 2009). De tal forma, aquellos embriones que se desarrollen a una temperatura superior a la temperatura pivotal serán hembras y los que se desarrollen a temperaturas inferiores serán machos (Mrosovsky et al., 1984; Hilterman and Goverse et al., 2007). Por otro lado, se ha observado que el periodo de incubación puede servir como indicador de la razón de sexos y está intrínsicamente relacionado con la temperatura de incubación (Godfrey et al., 1997), más que con cualquier otro factor atérmico (Godfrey and Mrosovsky, 2001). En consecuencia, los periodos más largos de incubación implicarán más bajas temperaturas y por tanto, mayor número de machos, y los periodos más cortos, un mayor número de hembras (Mrosovsky et al., 1999). Sin embargo, hay que tener en consideración que los mecanismos fisiológicos que determinan la diferenciación sexual mediante la temperatura podrían cambiar, alterándose la TRT y la temperatura pivotal (Hulin and Guillon, 2007). Además de la temperatura, la precipitación y la humedad relativa de la arena influirán en la razón de sexos y en la mortalidad de los huevos (Houghton et al., 2007; Saba et al., 2012), de tal forma, que las características del micro hábitat del nido tendrán grandes implicaciones en la diferenciación sexual y en el éxito reproductivo de los nidos (Wyneken and Lolavar, 2015).

Conservación y amenazas

La especie *Dermochelys coriacea* se enfrenta a numerosas amenazas tanto ambientales como de origen antropogénico, las cuales van a ser determinantes para que la tendencia demográfica de sus poblaciones incremente o decrezca. Esta especie presenta una baja filopatría natal por determinadas playas de nidificación, lo cual le podría permitir tener una mayor flexibilidad y adaptabilidad frente a cambios ambientales tales como pérdida de playas de nidificación por procesos erosivos, el aumento del nivel del mar (Dickson et al*.,* 2007; Dawson *et al.,* 2009; Hawkes et al., 2009; Fuentes et al., 2010), un incremento de las temperaturas (Santidrián Tomillo et al., 2015) y un aumento en la intensidad de las tormentas (Fuentes and Abbs, 2010; Knutson et al., 2010). Sin embargo, son necesarios más estudios que identifiquen si dicha flexibilidad puede reflejarse en una mayor adaptabilidad ante cambios ambientales extremos. Además de estas amenazas, la contaminación lumínica costera de origen antropogénico se está incrementando en las playas de nidificación, lo que está conllevando importantes efectos en el éxito reproductivo de muchas especies de tortugas marinas (Brei, 2014).

Esta especie suele anidar en la zona media y en menor frecuencia en la intermareal o en la vegetación, lo cual puede reducir el riesgo de que entren raíces en los nidos o que se erosionen por inundación (Chacón, 1999). De tal forma, el lugar seleccionado para la puesta determinará el éxito natural de eclosión. No obstante en los últimos años las playas de nidificación del Caribe de Costa Rica se están enfrentando a una erosión masiva con una asociada pérdida significativa de nidos (Eckert et al., 1999). Dicha erosión reduce el hábitat disponible de nidificación limitándolo a zonas inundables o donde existe una alta dispersión de especies vegetales altamente dañinas para los nidos, como es el caso de *Ipomoea pes-caprae* (Conrad et al., 2011).

El aumento del nivel del mar debido al cambio climático está transformando los ecosistemas costeros, por lo que en un futuro puede convertirse en otra gran amenaza para esta especie (Katsedilis et al., 2014; Rivas et al., 2016b). Dicho aumento estará determinado por el aumento de temperatura y el deshielo de los polos y considerando las predicciones realizadas para las próximas décadas, esta podría ser una gran amenaza a tener en cuenta junto a la feminización de las poblaciones (Kamel and Mrosovsky, 2004; Patino- Martinez et al., 2012; Santidrián Tomillo et al., 2014,15; IPCC, 2013).

Estudios recientes han identificado que ya existe un sesgo en algunas poblaciones hacia la producción de hembras (Chan and Liew, 1995; Binkley et al., 1998; Patino-Martínez et al., 2012; Santidrián Tomillo et al., 2014, 15). El uso de viveros, llevados a cabo por proyectos de conservación en playa, como medida de manejo para la reubicación de nidos, puede también contribuir a dicho sesgo; obteniendo un mayor porcentaje de hembras (Whitmore and Dutton, 1985; Chan and Liew, 1995; Patino-Martínez et al., 2012). No obstante, estudios a largo plazo como el realizado por Santidrián Tomillo et al (2014) en Playa Grande en Costa Rica vislumbran que el porcentaje de hembras producido por viveros puede ser significativamente más bajo que los ubicados *in situ*. Debido a que los nidos reubicados en vivero presentan una mayor mortalidad durante el desarrollo embrionario, liberando menor calor metabólico, lo que produciría un menor número de hembras. Se ha comprobado que las condiciones ambientales de los nidos pueden ser determinantes para el éxito reproductivo, y por tanto, a los programas basados en relocalización de nidos. Por otro lado, aunque se ha considerado que la precipitación puede disminuir la temperatura media de los nidos (Houghton et al., 2007), periodos de precipitación prolongados, la humectación de la arena (Mcgehee, 1990) y los niveles freáticos, van a determinar la mortalidad de las puestas (Kraemer & Bell, 1980), y consecuentemente, los éxitos reproductivos de la especie. De tal modo, considerando las variaciones climáticas previstas por The Fifth Report of the Intergovernmental Panel on Climate Change (IPCC) (2013), los eventos climáticos extremos como el aumento en la intensidad de las tormentas podrían afectar significativamente al éxito reproductivo de esta especie.

Históricamente una de las mayores amenazas ha sido la captura sistemática de hembras en playas de nidificación o el saqueo de sus nidos para el consumo de huevos (Ordoñez et al., 2007; TEWG, 2007). Aunque ha sido penalizado su expolio en varios países como Costa Rica o Panamá, siguen extrayéndose huevos de forma masiva en la mayoría de las poblaciones (Tröeng et al., 2007; Chacón-Chaverri et al., 2007). Asimismo la captura incidental por extracción pesquera tanto artesanal como comercial sigue siendo una de las mayores amenazas a las que se enfrenta esta especie (Tröeng et al., 2004; TEWG, 2007; Alfaro-Sigueto et al., 2007; Seminoff and Shanker, 2008; Doyle et al., 2008).

La amplia dispersión y aumento de las poblaciones humanas, unido a una continuada explotación de los recursos naturales está afectando al equilibrio natural de las costas. Si además, observamos que existe una tendencia hacia el aumento de la contaminación lumínica, la edificación y destrucción de playas naturales, puede que las zonas de nidificación de la tortuga laúd se vean cada vez más afectadas por el desarrollo humano y urbanístico. Uno de los principales factores que puede limitar la nidificación en determinadas zonas costeras o afectar la orientación de los neonatos al mar es la iluminación artificial. Algunos estudios han detectado que esta especie, tanto adultos como neonatos, presentan una alta foto-atracción por la luz artificial (Mrosovsky, 1978; Eckert et al., 2012; Zheleva, 2012). Sin embargo, es necesario un mayor conocimiento sobre el comportamiento de los neonatos frente a amplios rangos de longitudes de onda del espectro visible (Rivas et al., 2016c). Además, otros factores como la deforestación, los troncos arrojados por ríos al mar, o la acumulación de basura en las playas puede dificultar o impedir que los neonatos alcancen la orilla con facilidad (Laurance et al., 2008; Patino-Martínez et al., 2009).

Otra amenaza cada vez más extendida es la presencia de animales domésticos como perros en playas de nidificación. Se ha detectado que pueden ser altamente perjudiciales ya que depredan neonatos y destruyen nidos en los días previos a la emergencia, al igual que los cangrejos fantasmas de la familia Ocypodidae (Tomás, 2004; Marco et al., 2015) o mamíferos como coatíes o mapaches (Leslie et al, 1996). Además, se han descrito en Costa Rica ataques a hembras por jaguares (*Phantera onca)* (Tröeng et al., 2007; Guilder et al., 2015).

Figura 1A. Ejemplar adulto de la especie *Dermochelys coriácea*

Figura 1B. Neonato de la especie *Dermochelys coriacea*

1.2 Justificación y Objetivos

Las poblaciones de tortuga laúd, *Dermochelys coriacea,* del Atlántico Occidental se encuentran catalogadas como Vulnerable (IUCN, 2013). Sus playas de nidificación se concentran en las latitudes tropicales (James et al., 2006), siendo las poblaciones de Costa Rica de las más estudiadas de las últimas décadas (Patiño-Martínez et al., 2008). A pesar de ello, aún hay playas donde existe una falta de conocimiento sobre sus tendencias poblacionales y el rol que juegan dentro de la metapoblación del Atlántico Norte (Rivas et al., 2016a). Se han identificado que las tendencias poblacionales de la región caribeña están estables o en ligero descenso (Tröeng et al., 2004; Chacón-Chaverri et al., 2007). No obstante, en otras poblaciones del Caribe se ha observado un incremento en el número de hembras anidantes (Dutton et al., 2005; Antworth et al., 2006). Todo lo contrario a las poblaciones del océano Índico y Pacífico que han sufrido un descenso muy acusado del 99% en sólo algunas décadas y una tasa de mortalidad anual de hembras adultas del 22% en algunas regiones (Spotila et al., 2000; Reina et al 2002; Tomillo et al., 2007; Chan and Liew, 1996).

Amenazas como alteraciones en la dinámica costera, el posible aumento del nivel de mar y episodios climáticos extremos de precipitación y tormentas debido al cambio climático son factores que están transformando los ecosistemas costeros y en un futuro podrían convertirse en una gran amenaza para esta especie (Fish et al., 2005; Fuentes and Abbs, 2010; Knutson et al., 2010; Fuentes et al., 2011; Santidrián et al., 2015). La erosión de la arena está empujando a las hembras a anidar en zonas más altas de la playas, las cuales suelen estar cubiertas por especies vegetales de duna que influyen negativamente en la mortalidad y éxito reproductivo de la especie (Conrad et al., 2011) y pueden afectar a la supervivencia de los neonatos tras la emergencia. Por lo tanto, estimar el efecto de dichas variables climáticas en el comportamiento de las hembras y su éxito reproductivo será esencial para prever futuros escenarios de cambio climático.

Por otra parte, el aumento de asentamientos en las zonas costeras está aumentando la contaminación lumínica en las costas de todo el mundo (Kamronsky et al., 2012, 2014). Teniendo en cuenta que los neonatos de esta especie presentan una alta foto-atracción por la luz artificial (Mrosovsky, 1968; Eckert et al., 2012) es esencial evaluar cuáles son los posibles efectos de diferentes longitudes de onda del espectro visible en su comportamiento de orientación, así como determinar cuáles son las más adecuadas para ser utilizadas en programas de conservación y manejo en playa.

Con los datos recogidos en esta tesis es posible evidenciar el rol de la playa de Pacuare en la región caribeña, teniendo en cuenta el número de nidos por año que alberga es una de las playas más importantes de la cuarta población más abundante del mundo; siguiendo a las poblaciones de Surinam-Guayana Francesa, Golfo de Guinea, y Trinidad y Tobago respectivamente (Patiño-Martínez et al., 2008). Debido a su alto grado de protección y al continuo registro de datos llevado a cabo en los últimos 20 años desde que se inició el proyecto de conservación, los datos procedentes de esta playa son de gran interés tanto a nivel local como regional. Gracias a ese continuo registro es factible estimar la tendencia demográfica actual de la población, junto a diversos parámetros reproductivos de las hembras nidificantes.

Aunque la población de playa Pacuare se ha mantenido estable por décadas se han identificado una serie de amenazas en los últimos años que podrían tener una gran implicación en la supervivencia de la tortuga laúd. Por lo cual, esta tesis surge para ampliar la información científica sobre aspectos de su biología y ecología y las amenazas a las que se enfrenta, lo que en fin último, contribuya a desarrollar nuevas estrategias de manejo que ayuden a conservar sus poblaciones.

Objetivos

La investigación se ha llevado a cabo en la playa de Pacuare, una playa de nidificación de la especie *Dermochelys coriacea* localizada en la costa caribeña de Costa Rica. El objetivo general de dicha tesis es determinar el impacto de las principales amenazas sobre el éxito reproductivo y comportamiento de *D. coriacea* en esta playa.

Los objetivos específicos que serán desarrollados a lo largo de esta tesis son:

1. Caracterizar la biología reproductiva de la tortuga laúd y la tendencia poblacional de playa Pacuare.
2. Determinar el efecto de la presencia y permanencia de bermas en la playa de nidificación producidas por la erosión de la arena, en el comportamiento de nidificación de las hembras y en su éxito reproductivo.
3. Evaluar el impacto de la presencia de la planta de duna *Ipomea pes-caprae* en el comportamiento de orientación de los neonatos hacia el mar tras la emergencia.
4. Evaluar el impacto de la luz artificial a diferentes longitudes de onda y de la luz natural, en el comportamiento de orientación de los neonatos en su recorrido al mar.

1.3 Diseño de investigación

El diseño de la tesis está estructurado en un número de 6 capítulos. Tanto el primero como el octavo están constituidos por generalidades y conclusiones respectivamente. El segundo capítulo corresponde al estudio de campo realizado en 2008 y el análisis de los datos realizado durante la tesis de máster presentada en 2011. Del capítulo 3 al 6, se presentan los diferentes estudios realizados durante la temporada de nidificación de la tortuga laúd en la playa de Pacuare, entre los meses de marzo y julio de los años 2013-2015.

Los resúmenes de dichos experimentos junto al resto de capítulos son presentados a continuación:

1.4 Resúmenes

Resumen capítulo 2

En este estudio evaluamos la tendencia poblacional y la ecología de la tortuga laúd a lo largo de 19 años (1994 - 2012) de efectiva protección en la Reserva Natural de Pacuare, localizada en la costa caribeña de Costa Rica. La densidad media registrada a lo largo de los años fue de 142 nidos por km^2, lo que supone probablemente la concentración por kilómetro cuadrado más alta de Centroamérica e indica la importancia de esta población dentro de la metapoblación caribeña. Gracias a los esfuerzos de conservación llevados a cabo en Pacuare durante 25 años, se ha reducido significativamente el saqueo de nidos, lo que ha contribuido a mantener una alta producción de neonatos a lo largo de los años. El monitoreo a largo plazo ha permitido obtener parámetros demográficos relevantes como el éxito de nidificación (69.8 ± 7.3 %), tamaño de puesta, el cual está positivamente correlacionado con el tamaño de la hembra, el éxito de eclosión (55.2 ± 6.0 %), el intervalo de remigración (2.5 años) y el rango de crecimiento de hembras remigrantes (0.3 ± 1.0 cm por año). Consecuentemente, los esfuerzos en Pacuare han sido exitosos protegiendo dicha población y permitiendo obtener datos cruciales sobre la biología de la especie. Lo cual manifiesta la importancia de los proyectos de conservación de larga duración en la protección de poblaciones de tortuga laúd.

Resumen capítulo 3

Las poblaciones de *Dermochelys coriacea* han declinado debido a efectos antropogénicos en multiples localizaciones. Sin embargo, se desconoce como esta y otras especies responderán en un futuro a nuevas amenazas como es el cambio climático. La pérdida de zonas adecuadas de nidificación debido al aumento del nivel del mar, el incremento en la frecuencia de las tormentas y las altas mareas podría reducir su éxito reproductivo y consecuentemente, afectar a sus dinámicas poblacionales. En este estudio evaluamos los efectos de los procesos de erosión de arena en el comportamiento de nidificación y el éxito reproductivo de la tortuga laúd de la Reserva Pacuare del Caribe de Costa Rica. Los resultados obtenidos mostraron que la presencia de bermas afectó a la selección de la zona de nidificación incrementando el porcentaje de nidos ubicados en zonas de alto riesgo de inundación (ej. Bajo la línea de marea alta) y disminuyendo el número de intentos de puesta. Sobre un cuarto 24.1% (n = 20) y 18.6 % (n = 19) de las hembras in 2013 and 2014 respectivamente, no superaron la berma independientemente de su altura, y anidaron bajo ella. Además, el porcentaje de nidos ubicados en zonas de alto riesgo de inundación incrementó significativamente ($R^2 = 0.91$) entre el (2008 – 2014). Debido a que el aumento del nivel del mar ha incrementado significativamente en el Caribe entre 1950 y 2010, y las proyecciones prevén un mayor aumento para el siglo XXI, la erosión de las playas puede que llegue a ser una importante amenaza para esta y otras especies costeras amenazadas.

Resumen capítulo 4

Las Tortugas laúd se ven afectadas por un amplio rango de amenazas de origen antropogénico, sin embargo, poco se conoce sobre la respuesta de esta especie ante las amenazas naturales tales como la vegetación de duna, las cuales pueden afectar negativamente a la calidad de los hábitats de nidificación. En este estudio desarrollado en la Reserva Natural Pacuare localizada en la costa caribeña de Costa Rica, evaluamos el potencial impacto de *Ipomoea pes-caprae* en las habilidades de

orientación de los neonatos de tortuga laúd en su recorrido hacia el mar. Para ello, comparamos la velocidad de los neonatos en zonas con y sin *I. pes-caprae*. A su vez, registramos la localización de 1491 nidos los cuales fueron dejados *in situ* y 784 nidos fueron reubicados entre el año 2012 y 2014. La mayoría de los nidos *in situ* fueron localizados en áreas donde la vegetación estaba presente. Se identificó que la vegetación de duna tuvo un efecto negativo en la velocidad de los neonatos, incrementando el tiempo de exposición frente a diversas amenazas como depredadores y/o deshidratación, lo cual podría potencialmente producir un estrés fisiológico en los neonatos, y consecuentemente, incrementar su mortalidad. De tal modo, la presencia de vegetación de duna debe influir negativamente en la idoneidad de los hábitats de nidificación si se incrementan en el futuro los procesos continuos de erosión en estas playas.

Resumen capítulo 5.

Durante las últimas décadas el crecimiento de poblaciones humanas se ha dirigido hacia el aumento de la ocupación de las zonas costeras a lo largo de mundo, incrementando con ello la contaminación lumínica. Por tal motivo, es importante evaluar cómo dicho impacto amenaza la vida silvestre en peligro de extinción. La tortuga laúd (*Dermochelys coriacea*) se enfrenta a una gran variedad de amenazas de origen antropogénico, como es la iluminación artificial en playas de nidificación; sin embargo, poco se conoce sobre sus posibles efectos. En este estudio identificamos los efectos de diferentes longitudes de onda (naranja, rojo, azul, verde, amarillo y luz blanca) en la orientación de los neonatos en condiciones de presencia y ausencia de luz de luna, mediante el análisis de los siguientes parámetros: (i) ángulo medio de orientación, (ii) duración de la trayectoria y (iii) patrón de la trayectoria. La orientación de los neonatos hacia el mar siempre fue mejor bajo las condiciones de control, ausencia de luz. En ausencia de luz de luna los neonatos fueron atraídos hacia la fuente de luz (mis-orientación) para los colores azul, verde, amarillo y blanco. La luz roja y naranja causó menos mis-orientación que el resto de tratamientos y la luz naranja produjo la menor perturbación en la orientación (desorientación). En las noches con luz de luna los neonatos se mis-orientaron únicamente bajo la fuente de luz azul y blanca. La duración de la trayectoria fue baja para los neonatos mis-orientados y alta para los individuos desorientados. En conclusión, los neonatos de tortuga laúd pueden detectar y ser impactados por un amplio rango de longitudes de onda del espectro visible, por lo cual se recomienda evitar la presencia de luces artificiales en playas de nidificación de tortugas marinas. Adicionalmente, aquellas acciones de control y mitigación de luces artificiales deberían ser prioritariamente llevadas a cabo durante noches oscuras con ausencia de luna.

Chapter 2. Nesting ecology and population trend of Leatherback Turtles *Dermochelys coriacea* at Pacuare Nature Reserve, Costa Rica

2.1 Abstract

The leatherback turtle (*Dermochelys coriacea*), the only extant species in its family, is currently considered Vulnerable in the North Atlantic Ocean. The protection of relevant nesting beaches and the associated conservation efforts in the Western Atlantic coast of Central America must have contributed positively to the population trends of some of the world's most important rookeries. Here we show the life history, ecology, and population trends of leatherback turtles over 19 years (1994 - 2012) of effective protection in the Pacuare Nature Reserve (PNR), Caribbean Costa Rica. A mean density of 142.0 nests per km, likely the highest in Central America, indicates the importance of this rookery within the Caribbean region. Long-term conservation efforts at PNR have significantly reduced poaching and have contributed to maintaining a high level of hatchling production over the years. Long term monitoring has also permitted the estimation of relevant demographic parameters of the population, such as nesting success (69.8 ± 7.3 %), clutch size which is positively correlated with female size, hatching success (55.2 ± 6.0 %), remigration interval (2.5 years), and growth rate of remigrant females (0.3 ± 1.0 cm per year), which is slightly faster than growth rates reported for Pacific leatherbacks. Overall efforts at PNR were successful at protecting leatherbacks and understanding its life history, and highlight the importance of long-term conservation projects for maintaining endangered leatherback populations.

2.2 Introduction

Leatherback turtles (*Dermochelys coriacea*) were listed in 2000 as Critically Endangered; the species' situation was defined as 'facing an extremely high risk of extinction in the wild in the immediate future' (Sarti-Martínez 2000). Specialists have revised this criteria at the regional level because of opposing population trends in the different ocean basins (Godfrey and Godley 2008; Seminoff and Shanker 2008; Wallace et al. 2013). As a consequence, a recent overview suggested that the majority of the populations in the Atlantic Ocean were stable or increasing, while some subpopulations such as the Northwest Atlantic Ocean have been listed as Vulnerable (TEWG 2007; Girondot et al. 2007; Dutton et al. 2005; Wallace et al. 2013). However, the Pacific populations were experiencing significant declines (Spotila et al. 2000; Reina et al. 2002; Seminoff et al. 2007). These differing trends make it necessary to analyze threats and population responses at the regional level. Wallace et al. (2010) defined Regional Management Units (RMU) as an essential tool in identifying nesting areas while improving inter-regional understanding of sea turtle nesting distribution.

Overall, more information about turtle distributions, and reliable estimates of demographic trends by capture-mark-recapture (CMR) techniques is needed for a better analysis of the status and health of wild populations (Chaloupka and Limpus 2001). Size of leatherback turtles varies among populations (Stewart et al.2007), and Atlantic Costa Rican leatherbacks exhibit greater reproductive output that their eastern Pacific counterparts, due to differences in clutch sizes: 80 - 90 eggs per clutch in the Atlantic and 60 - 65 eggs in the Pacific (Chacón, 1999; Reina et al., 2002; Quiñones et al., 2007; Hilterman and Goverse et al., 2007). Growth rates of adult females after reaching sexual maturity are over 0.2 cm per year in Pacific leatherbacks (Price et al. 2006). It was estimated this species reaches sexual maturity at approximately 5 to 30 years (Zug and Parham 1996; Dutton et al. 2005; Jones et al. 2009) and captive animals mature at approximately 7 to16 years of age (Jones et al. 2011). Remigration intervals are also shorter and more stable in the Atlantic (2 - 3 years) than in the Pacific (~3.7 years), possibly reflecting increased foraging success in the Atlantic (Reina et al. 2002; Dutton et al. 2005; Girondot et al. 2007; Bailey et al. 2012). Additionally, annual mortality rate of adult females was estimated at approximately 11% for the Atlantic population of St. Croix (Dutton et al. 2005) and approximately 22% for the Costa Rican Pacific population (Santidrián Tomillo et al. 2007). Hatching success of leatherback turtles (~50%) is very low compared to other sea turtles (reviewed by Bell et al. 2004; Wallace et al. 2004) such as Atlantic *Chelonia mydas* (63.5 – 86.0 %) in Tortuguero (De Haro et al. 2008; Segura and Cajade 2010), *Eretmochelys imbricata* (78.6%) in the West Indies (Ditmer et al. 2012) or *Caretta caretta* (73.4% and 55.7%), reported in South Carolina (Caldwell, 1959) and Florida (Witherington, 1986), respectively; or even 70 - 80% in Cape Verde (Abella et al. 2007).

Among the main threats identified for this species are poaching, commercial and artisanal fisheries (Santidrián Tomillo et al. 2008; Morreale et al. 1996; Eckert and Sarti 1997; Alfaro-Sigueto et al. 2007; Seminoff et al. 2007), and climate change (Saba et al. 2007, 2012; Reina et al. 2009). However, population responses to threats may differ among ocean basins.

The Caribbean coast of Central America may host the fourth largest nesting population of leatherbacks in the world, after Gabon (West Africa), French Guiana-Suriname and Trinidad &Tobago (Turtle Expert Working Group 2007). Within Caribbean Costa Rica, the most important leatherback rookeries, with long-term monitoring records, are found in Tortuguero, Pacuare Nature Reserve (PNR) and Gandoca beaches (Tröeng et al. 2004; Chacón- Chaverri and Eckert 2007). However, no previous scientific studies have assessed the status of the nesting population at PNR despite the long-term monitoring and conservation program, established in 1994. Because of the nature of the study and the relatively high nesting levels in Caribbean Costa Rica, PNR could be an important contributor to the regional assessments of the species in the Caribbean region.

In this study, we assessed the importance of PNR as a nesting site for leatherback turtles in the Caribbean region by (1) analyzing nesting abundance and trends over 19 years, (2) describing some aspects of their nesting ecology, and (3) identifying main threats to the population and proposing conservation priorities to increase their numbers in the future.

2.3 Methods

Study area

We conducted the study at Pacuare Nature Reserve (PNR) in Caribbean Costa Rica, located 45 km southeast of Tortuguero (Fig.1). The mouth of the Pacuare river is found 1km from the reserve's northern limit (10°13′17″N, 83°16′39″W), and the Mondonguillo lagoon is located at the south end of the Reserve (10°10 ′00″ N, 83°14 ′00″ W). The nesting beach is 5.7 km long. The beaches in this area are high-energy sandy beaches with medium steep slopes. Several beach monitoring projects have been conducted along this coast (Fig.1). However, long-term monitoring programs (longer than ten years) have only been carried out at five of these sites (Table 1).

Nesting surveys

Two stations (North and South) were established at the borders of Pacuare Beach to monitor the total length of the beach. Along the coastline, we placed marker posts to divide the area into 100 m sectors and sub-sectors were positioned every 25 m from south (post 0 - 57). Night patrols have been conducted every nesting season since 1994 (except in 1998) over the total extension of the beach from March 1st to September 30th to accurately monitor all nesting activities and minimize egg poaching.

Each patrolling team monitored the beach in 4-hour watches, starting from each station at 20:00, 22:00 and 00:00. Each turtle encountered was tagged and measured, and clutches found in risk-prone areas were relocated. Turtles were tagged with Monel #49 tags on both rear flippers (National band & Tag Co., Newport, USA). Turtles that had no evidence of tags, scars, holes, or other deformities were considered new recruits to the rookery (Chacón 1999; Tröeng et al. 2004). Since 2001, subcutaneous microchip Passive Integrated Transponder (PIT) tags (less than 5% of annual tagging) have been used, in addition to flipper tags. Morning counts were conducted along the beach, to record every turtle track throughout the nesting season and to camouflage nests by sand flattening to prevent egg poaching and predation by dogs. We estimated the number of nests laid per kilometer to determine nest density by averaging the annual number of nests and dividing it by the length of the beach.

Biometry and nesting ecology

We estimated mean nesting success as the proportion of nesting activities with oviposition in respect to the abandoned attempts.

We measured curved carapace length (CCL) and curved carapace width (CCW) to the nearest mm following Bolten (1999). CCL was measured along the right side of the central ridge. CCW was measured across the widest part of the carapace from the outer most ridges. Before 2000 only the mean values of number of nests, CCL and clutch size were available from annual technical reports (Rodríguez, 1994-1999). Biometric data and clutch size of a sample of remigrant females were also recorded and included in the annual reports. We calculated mean clutch size (number of eggs laid per successful nesting event) for this population over time from 7,131 records. We recorded number of nests observed during female oviposition and without female presence since 2005.

Since 2000, we have marked each nest with sticks and flagging tape and measuring the distances from the nest to the north, south and middle sectorial posts. We monitored nests during incubation and emergence, and excavated them two days after hatching, or 75 days after eggs were laid. We calculated hatching success as the proportion of eggs that produced hatchlings: $H = S/(S+U)$, (where S = number of eggshells, and U = unhatched eggs). Eggshell fragments equal or bigger than 50% of the egg surface were considered as one hatched egg (Miller 1999). The total number of hatchlings hatched at PNR was calculated using the mean number of hatchlings estimated per clutch (hatching success multiplied by number of eggs in a clutch) multiplied by the total number of nests recorded. Research assistant training was conducted every season to use the same methodology.

A variable number of clutches were relocated each season to stable beach zones close to original sites if they were at risk of (1) erosion and inundation and/or (2) poaching.

Remigrant females

Remigrant females were considered as tagged or with evidence of having been tagged previously (presence of holes, scars, and skin deformations). We estimated growth rates and remigration intervals for a subsample of 330 females that were recaptured a minimum of three nesting seasons over the study period and used average CCL (if at least two measurements) for each female encountered in each season. At the end of each season, errors of more than 1 cm among several annual measurements were removed before errors among observers were averaged.

We estimated observed and expected remigration intervals (years passed between consecutive nesting seasons) for every remigrant turtle. These intervals were calculated by dividing the number of years between the first and last oviposition by the number of seasons the turtle had nested. We calculated expected remigration intervals for a sample of 330 turtles by considering 2 years as a minimum remigration interval. We added one nesting event when inter-nesting intervals lasted 4 or more years. To know the inter-annual variation in the number of clutches laid over the years we calculated the coefficient of variation (CV) for this population from the mean and standard deviation (SD) of nests/females per year (CV = SD / mean) (Broderick et al. 2001). Finally, we analyzed the variability in clutch size over time for 197 neophytes recorded at PNR, and for remigrants (n = 330), which laid nests in at least three seasons and twice in a year. We used averages of clutch size when we recorded more than two ovipositions in a season. We analyzed the correlation between CCL and clutch size for this sample of remigrants.

We used XLSTAT.7.5.2 version 2.0 and STATISTICA 7.0 to conduct all statistical analyses. Annual numbers of nesting females (remigrants and neophytes) and correlation between female size and clutch size were analyzed using linear regression. Alpha was set at 0.05. Chi-square tests were used to compare annual fluctuations of nests, nesting success, female size and clutch size, and hatching success over seasons. We used ANOVA to determine clutch size variations between neophytes and remigrants, and observed versus expected remigration intervals.

2.4 Results

Nesting population trend

A total of 14,567 clutches were laid over the 18-year study. The highest nesting density occurred in the months of April and May, followed by March and June (Fig. 2). Due to very low numbers, February and August were excluded from the analysis.

The number of nests increased over the study period (Fig. 3). Overall, there was no significant change in nest numbers over the monitored period (Linear regression, $r^2 = 0.015$, $F_{1,16} = 0.24$, $P = 0.63$, n = 18), but the last year had the greatest number of nests (n = 1206) ever recorded at PNR.

We estimated a mean annual nesting density of 142.0 nests km^{-1} over the duration of the study with the highest annual nesting density (211.6 nests km^{-1}) occurring in 2012. In 2009, the northern sectors (0 - 29) received a total of 380 clutches (126.6 nests per km) while the southern sectors (30 - 60) received a total of 789 clutches (263 nests per km), revealing a trend for higher nesting density in southern sectors compared to northern sectors.

The annual mean (± SD) of nesting females was 342 ± 118, of which 127 ± 77 were neophytes (range 44 - 252) and 215 ± 140 were remigrant turtles (range 32 - 472) (Table 2). Both the annual number of nesting females and the number of remigrant females increased slightly during the study (Linear regressions, $r^2 = 0.40$, $F_{1,17} = 10.75$, $P = 0.005$, n = 18; and $r^2 = 0.83$, $F_{1,17} = 80.9$, $P < 0.001$ respectively).

Over the 18 years of the study, a total of 20,090 nesting activities (nests and false crawls) were recorded at PNR. Since 2005 a mean of 71.2 ± 11.5 % of all nests were recorded during female oviposition every season. The mean (± SD) annual number of nests and abandoned nesting attempts were 809.3 ± 201.6 (range 507 - 1206) and 368.2 ± 184.87 (range 198 - 786) respectively (Table 2). The difference between observed nests and expected nests for the hypothesis of non inter-annual variation was significant (Chi-square test, $X^2 = 587.03$, $P < 0.0001$), reflecting annual fluctuations. Mean (± SD) nesting success at PNR was 69.8 ± 7.3 % (range 54.2 - 79, n = 15) (Table 2, Fig. 3). The percentages of nesting success did not show significant differences over the years (Chi-square test, $X^2 = 10.64$, $P = 0.71$).

Biometry and nesting ecology

The annual CCL mean (± SD) was 152.3 ± 1.28 cm (n = 17 seasons). The smallest turtle size ever recorded in PNR was 138 cm, while the largest one was 178 cm. The annual mean CCW was 111.0 ± 0.9 cm (n = 17 seasons, Table 2). There was not a significant difference in female size among seasons (Chi-square test, $X^2 = 16$, $P = 0.45$). The annual mean clutch size over 10 years was 77.7 ± 2.1 eggs. We did not find significant differences among years in mean clutch size (Chi-square test, $X^2 = 13$, $P = 0.37$).

Mean (± SD) annual hatching success over the study period was 55.2 ± 6.0 % (Table 2) from a total number of 3,927 clutches excavated and on average 47.8 ± 25.5 % of nests (range 13 – 83) were excavated per season. The mean hatching success of nests did not change over time (Chi-square test, $X^2 = 6.47$, $P = 0.77$) (Table 2). Between 2009 and 2012 the mean hatching success was 59.4 ± 25.8 % (range 0 – 100). We estimated that a total of 618,943 hatchlings hatched at PNR over the 18-year study period.

Remigrant females

We estimated that the annual growth rate of nesting females was 0.28 ± 1.0 cm per year (range 0 - 3.1) (n = 330 females). The mean clutch size for the 330 females was 81.3 eggs, with a mean individual variation of 14.5 eggs per clutch (range 1 - 55) for all seasons; this average clutch size was significantly greater than the mean of 74.3 eggs estimated for neophytes (n = 197 turtles) (ANOVA, $F_{(329,196)} = 1.95$, $P < 0.0001$). There was a significant positive relationship between female size and clutch size (Linear regression, $r^2 = 0.12$, F = 37.21, $P < 0.05$, n = 271) (Fig. 4). About 49% of the females (n = 109) showed a variation in clutch size of 0 to 10 eggs difference among clutches over the years, ~25% of the females laid clutches with a variation in number of eggs of 11 to 20 eggs; and13.8% of turtles showed variations in number of eggs of 21 - 30 eggs. For 12% of females, there were differences of more than 30 eggs among clutches laid in different nesting seasons.

Finally, the mean (± SD) remigration interval observed at PNR was 2.5 ± 1.0 years (range 1 - 6, n = 330 turtles) and the mean expected remigration interval was 2.1 ± 0.6 years (range 1 - 9, n = 330 turtles). Remigration interval was not related to female size (ANOVA, $F = 0.33$, $P = 0.56$). The inter-annual variation in the total number of observed clutches in any one season at PNR was low (CV = 0.32).

2.5 Discussion

Nesting trend

PNR is one of the three oldest sea turtle monitoring projects established in Caribbean Costa Rica, following Gandoca - Manzanillo National Wildlife Refuge and Tortuguero National Park (Table 1). Despite conservation efforts along the coast, there are extended sections of unmonitored nesting beaches (Fig. 1), where nest poaching and turtle harvesting are common (Pers. Obs., Tröeng et al. 2004, Chacón-Chaverri et al. 2007).

PNR currently registers the highest density of nesting (142 nests km^{-1}) in Central America; higher than Chiriqui beach (128 nests km^{-1}) which was previously considered the most dense area (Ordoñez et al. 2007), and higher than the 91.6 nests km^{-1} previously estimated for PNR based on aerial surveys (Tröeng et al. 2004). The number of nesting turtles at PNR seems to be increasing, registering a maximum in 2012. Similar trends have been observed in other Atlantic rookeries such as St. Croix (Dutton et al. 2005), French Guiana and Suriname (Girondot et al. 2007), Florida (Stewart et al. 2011), as well as for other sea turtle species in the area (Tröeng et al. 2005; Antworth et al. 2006).

Long-term data is needed in order to correctly interpret inter-annual variations in nesting numbers, the imperfect counting of individuals, and the improvement in surveys over the years (Pfaller et al. 2013).

Over the duration of the project, a high number of neophytes were recruited to the population. The highest number of neophytes (n = 243) was registered in 2001, after which the numbers did not increase any further. In addition, shifting of female leatherback turtles among nesting beaches is common on the Caribbean coast of Costa Rica and we have identified turtles tagged at other projects ranging from northern Costa Rica (Caño Palma, Tortuguero, Fig. 1) to northern Panama (Chiriquí beach). High level of exchange is also suggested by the low nest fidelity occurring at PNR (average 2 - 3 nests per season), compared to that of other populations (mean ~7 nests, Reina et al. 2002).

Biometry and nesting ecology

The size of leatherback turtles was similar to those reported at other nesting sites in the region (reviewed by Thomé et al. 2007). Mean clutch size was similar to those reported for Gandoca and other nesting populations in the Caribbean (Chacón - Chaverri et al. 2007; Patiño-Martinez et al. 2008; Ordoñez et al. 2007), but was slightly lower than in Tortuguero (Leslie et al. 1996). Almost half of the females showed low variability in clutch size among years (range: 0 – 10 eggs among clutches).

Mean hatching success (55.2%) was higher than that reported for Tortuguero (41.5 - 46.5 %; Tröeng et al. 2007), and did not vary significantly among years.

We found a positive correlation between mean carapace length (CCL) and clutch size of remigrant females, similar to other sea turtle species (Hirth 1980), but unlike other leatherback populations (Hirth et al. 1993; Reina et al. 2002). We estimated that growth rate of nesting females was 0.28 ± 1.0 cm per year, faster than the rate reported by Price et al. (2006) in Pacific leatherbacks. With a growth rate of 0.28 cm per year, it would take a turtle that measures 138 cm (the smallest nester) 143 years to reach 178 cm (the largest nester). Thus, it seems reasonable that the variation in female sizes is caused by size variability at the time they reach maturity, rather than a result of growth after the time of first reproduction.

Observed remigration intervals at PNR were 2.5 years, similar to those obtained by Dutton et al. (2005) in St. Croix. Inter-annual variation in nesting numbers was lower than the variations in French Guiana. This low variability probably reflects fairly consistent foraging conditions for leatherbacks across years in the Atlantic (Broderick et al. 2001).

Threats and Conservation implications

There are persistent threats to sea turtles such as fishery by-catch (Georges et al. 2006; Alfaro - Sigueto et al. 2007), egg poaching (Tröeng et al. 2004, 2007; Ordoñez et al. 2007), and tourist impact (Katselidis et al. 2013). We reduced poaching of eggs at PNR over the years due to presence of guards and intense beach patrolling. We registered the lowest number of nests at PNR in 2003, and nesting levels remained low until 2009. Low numbers may have resulted from the high levels of egg poaching that occurred at this site in the past before the early 1990s. Although poaching was reduced to ~1 - 2% per year after protection started, ~10% of clutches were still poached in 2008.

Nesting population levels at PNR show that long-term beach protection may be an effective conservation mechanism. It allows protection of nests from poaching and therefore, it increases beach productivity. Conservation programs in protected areas may effectively preserve marine turtles allowing population recoveries (Revuelta et al. 2012). Beach protection for nearly 20 years at PNR may have had an effect on the Caribbean RMU. Nevertheless, opposite declining trends were reported for Gandoca and Tortuguero in 2004 and 2006 respectively (Chacón –

Chaverri and Eckert 2007; Tröeng et al. 2007). Thus, it is possible that turtles shifted from those locations to PNR due to the low fidelity exhibited in this area. In order to properly assess population trends and status on the Caribbean RMU, it is necessary to exchange information among research projects for a global analysis of this important RMU.

Table 2.1. Sea turtle monitoring locations along the Caribbean Coast of Costa Rica, year when projects started, length of the beach monitored and organizations leading the projects.

Sea turtle monitoring locations	Year	Beach length (km)	Organization
Barra del Colorado Wildlife Refuge - Caño Palma Research Station	2004	5	Canadian Organization forTropical Education and Rainforest Conservation
Tortuguero National Park - S. Francisco	1995	35.6	Sea Turtle Conservancy
La Barra del Río Pacuare	2006	7.1	WIDECAST and La Tortuga Feliz
Pacuare Reserve	1994	5.7	Endangered Wildlife Trust
Las Tortugas Research Station	2000	3	Las Tortugas Research Station
Cahuita National Park-Playa Negra	2000	8.1	WIDECAST/ Asociación ANAI
Manzanillo - Gandoca National Wildlife Refuge	1990	7.7	WIDECAST/ Asociación ANAI

Table 2.2. Summary of biological data recorded from 1994 to 2012. Mean and SD values for 18 years.(FC= False Crawls). Mean values are in bold text; Nd: data not determined *Mean values from 1994 to 1999 were obtained from technical report.

Year	*CCL (cm) (n)	*CCW (cm)	Number of Neophytes	Number of Remigrants	Number of Nests/FC	*Clutch Size	*Hatching Success (%)	*Hatching Success (%)
1994	154 (n = 203)	111.4	252	34	814/443	76.8	Nd	64.7
1995	153.5 (n = 219)	111.5	246	32	747/198	Nd	Nd	79.0
1996	154.1 (n = 201)	111.3	188	45	738/222	Nd	Nd	76.9
1997	Nd	Nd	198	69	1108/419	Nd	Nd	72.5
1999	154.6 (n = 330)	112.6	219	91	781/Nd	Nd	Nd	Nd
2000	152 (n = 370)	110	90	167	814/Nd	74	62	Nd
2001	152 (n = 383)	111	243	185	997/327	78	50 (n = 126)	75.3
2002	153 (n = 613)	111	56	128	848/313	78	52 (n = 110)	73.0
2003	152 (n = 229)	111	68	161	507/287	78	58.3 (n = 120)	63.8
2004	151.9 (n = 238)	110.9	49	226	555/286	77	58.2 (n = 206)	66.0
2005	153.8 (n = 570)	111.7	44	343	706/Nd	81.6	Nd	Nd
2006	151.2 (n = 515)	110	61	213	591/243	75.2	42 (n = 490)	70.9
2007	150.8 (n = 157)	109.3	110	361	678/202	Nd	Nd	77.0
2008	152.1 (n = 425)	110.8	57	235	653/362	76.8	62.1 (n = 354)	64.3
2009	151.2 (n = 801)	110.2	149	451	1171/786	79.1	58.5 (n = 838)	59.8
2010	150.4 (n = 473)	109.5	111	362	899/760	77	57.9 (n = 580)	54.2
2011	151.2 (n = 556)	110.2	63	298	754/218	77.5	55.8 (n = 546)	77.6
2012	151.5 (n = 848)	110.3	80	472	1206/457	81	50.4 (n = 557)	72.6
Mean±SD	**152.3**±1.28 (n = 7,131)	**111.0**±0.86	**126.9**±76.67	**215.2**±140.17	**809.3**±201.6/ **368.2**±184.87	**77.7**±20.6 (n = 4,967)	**55.2**±6.05 (n = 3,927)	**69.8**±7.34

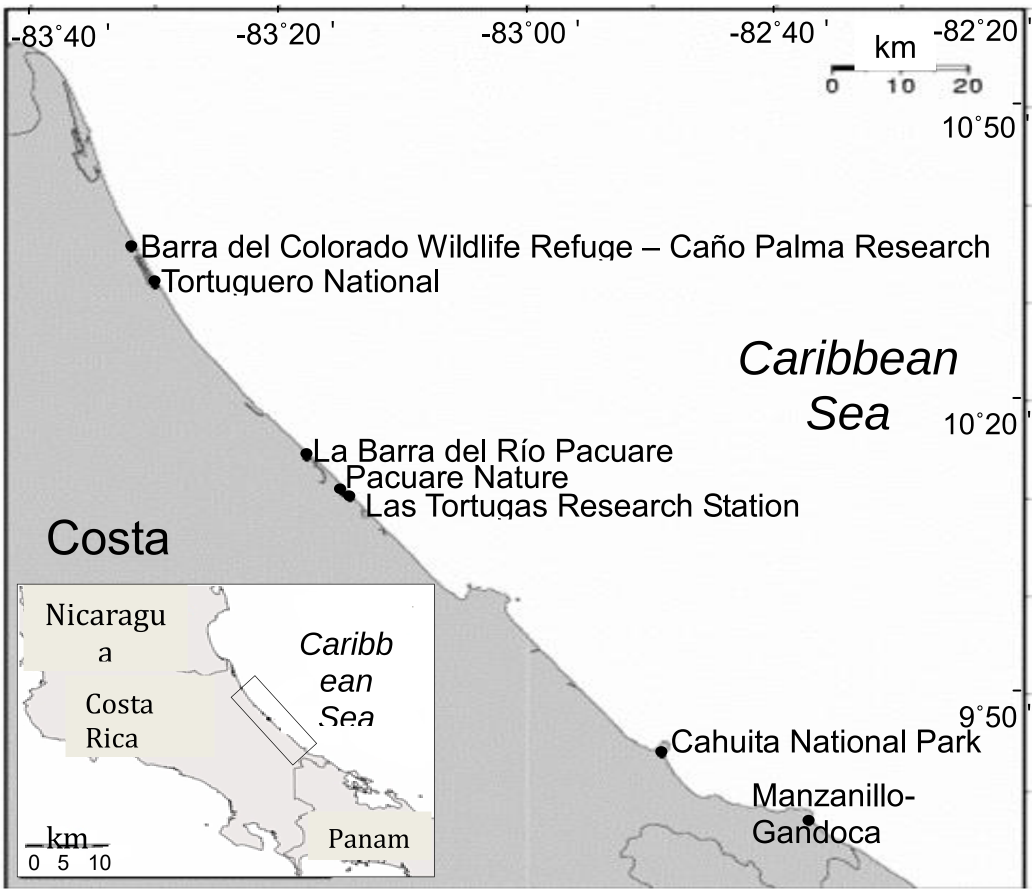


Figure 2.1. Location of PNR in the Caribbean coast of Costa Rica, Central America (inserts), and location of sea turtle monitoring projects along the Caribbean coast of Costa Rica: **1**. Caño Palma Research Station. **2**. Tortuguero National Park - S. Francisco. **3.** La Barra del río Pacuare. **4**. Reserva Pacuare (PNR). **5**. Las Tortugas Research Station. **6**. Cahuita National Park - Playa negra. **7**. Manzanillo - Gandoca National Wildlife Refuge (Punta Mona); and distances (km) between adjacent monitoring projects. Distance a: 7 km, b: 35.6 km, c: 14.8 km, d: 58.2 km, e: 29.8 km.

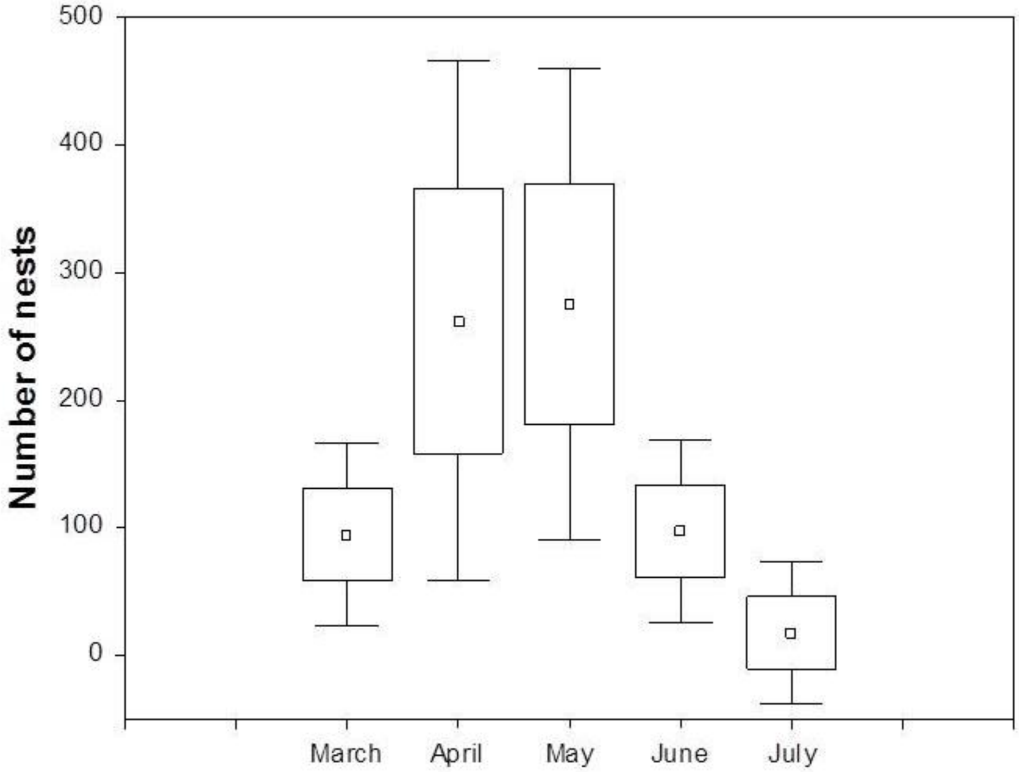


Figure 2.2. Number of leatherback clutches oviposited per month from 1994 to 2012.

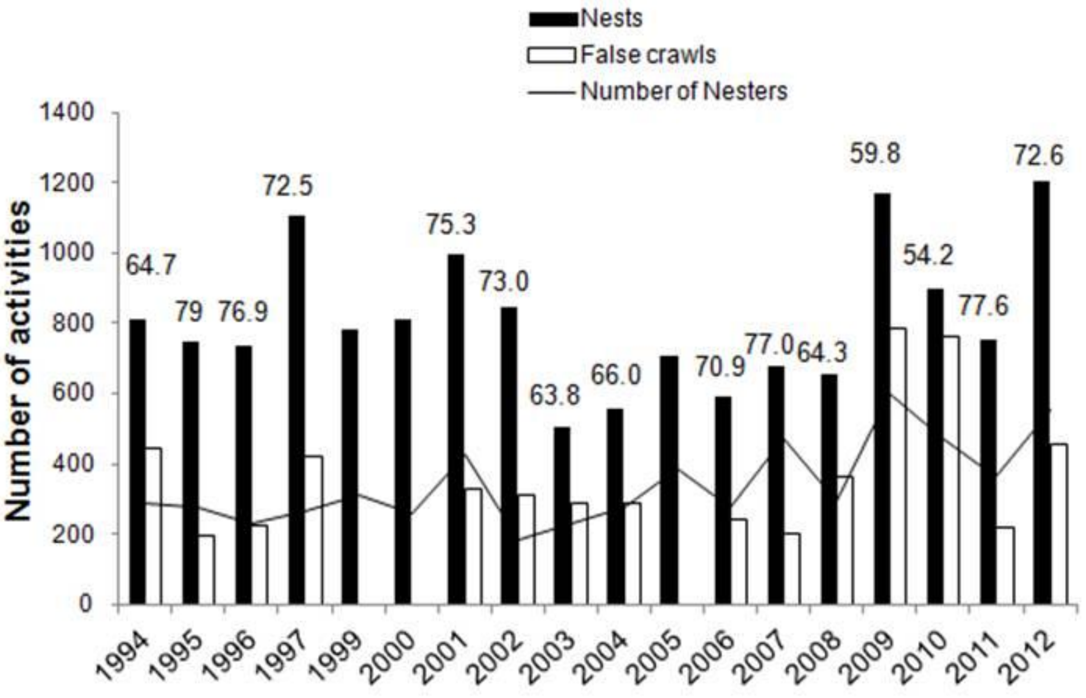


Figure 2.3. Total number of clutches laid, abandoned nesting attempts and percentage of nesting success per year from 1994 to 2012 (1998 is excluded). Solid line shows number of nesting females per year. Nesting success (%) per year above the solid nest columns.

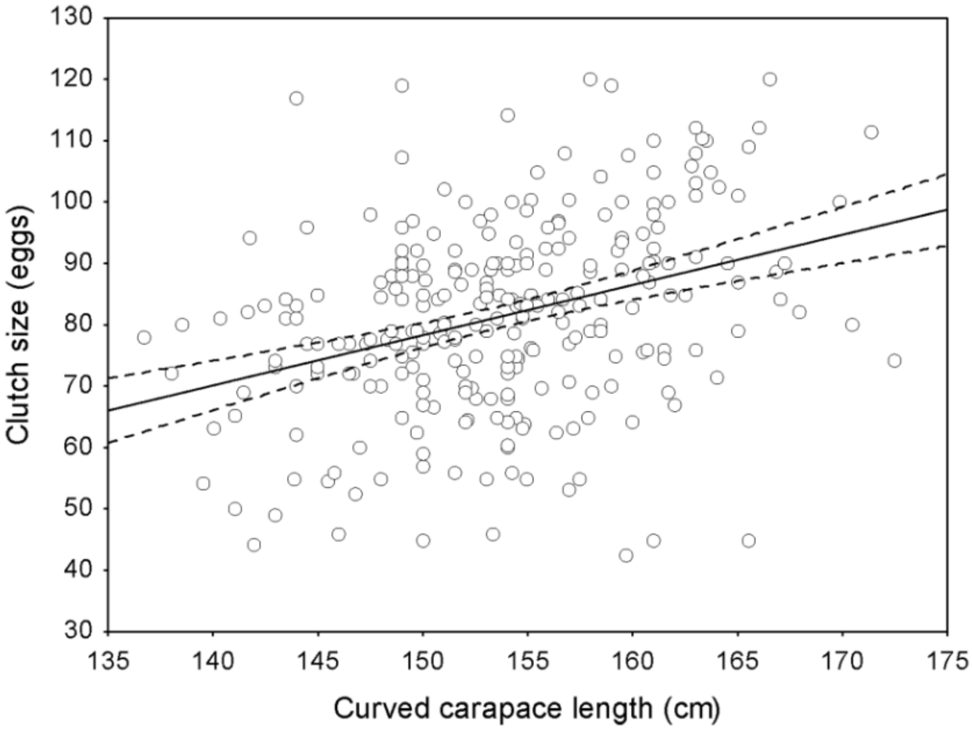


Figure 2.4. Relationship between clutch size and female size (curved carapace length, CCL). Solid line corresponds to loess regression (n = 330 nesting females), outer curves (dashed lines) show approximate pointwise 95% confidence intervals.

Chapter 3. Potential impact of dune scarps caused by beach erosion on the nesting behavior of leatherback turtles

3.1 Abstract

Beaches are constantly being reshaped by storms and high tides; however, increased storm frequency and sea level rise due to climate change could cause the loss of beaches that are vital breeding habitats for sea turtles. Here, we evaluated the effect of erosion/accretion cycles on the nesting behavior (nest site selection related to presence of dune scarps) and nesting success (proportion of nesting activities with oviposition) of leatherback turtles at Pacuare Nature Reserve, in Caribbean Costa Rica. Dune scarps accounted for over 20% of the beach, creating a barrier which prevented turtles from accessing the upper part of the beach where nests would be safe from high tides and the storm line. About a quarter of the turtles, 24.1% (n = 20) in 2013 and 18.6 % (n = 19) in 2014, did not crawl over scarps when they were present, regardless of their height, and laid their eggs below them. Additionally, during the 2008-2014 period, the percentage of nests laid in high-risk areas significantly increased ($R^2 = 0.91$). The end result of the formation of scarps was that nests were laid in areas of being flooded, threatening the survival of those eggs, and therefore to the long-term population survival. Since sea levels have been rising significantly in the Caribbean between 1950 and 2010, and projections show a further increase throughout the 21st century, beach erosion may become an important threat not just for leatherbacks, but for many other endangered coastal species.

3.2 Introduction

Despite a growing interest on the effects of climate change on sea turtle populations, few studies have assessed those produced by certain beach features, such as scarp slopes, that arise as a result of erosion. Coastal dune systems are dynamic and are affected by sand erosion–accretion cycles, which determine coastal orography and affect the quality of sea turtle nesting habitats (Eckert 1987; Mazaris et al. 2009).

One of of beach erosion's consequences is the increased presence of dune scarps (Morton & Sallenger 2003), which are defined as "features with a slope larger than the critical angle of repose of 32° and a minimum height of 0.25 m" (Soulsby 1997; Alegría-Arzaburu et al. 2013). Beach erosion influences the morphological changes that beach scarps undergo and, generally, reduces beach height, width and quality of beaches (Donelly 2007). A scarp's persistence depends on wave overtopping events during high water levels and wave heights during storms (Jackson et al. 2010; Alegría-Arzaburu et al. 2013). Additionally, sea level rise induces long-term erosion on sandy beaches (Bruun 1962; Dickson et al. 2007; Dawson et al. 2009), with the rate of this erosion considered to be about two orders of magnitude greater than the rate of sea level rise (Zhang et al. 2004). Thus, sea level rise may entail a significant loss of sea turtle nesting habitat (Daniels et al. 1993; Fish et al. 2008; Nicholls & Cazenave 2010; Katselidis et al. 2014). This, together with other factors such as the continued increase in storm intensity (Fuentes & Abbs 2010; Knutson et al. 2010), wave energy, height of surge tides (Donelly 2007; Pye & Blott 2008), and astronomical tidal levels considerably affect coastal changes as well as estimates of total sea level increases (Losada et al. 2013; Reguero et al. 2013).

Some studies have shown that different sea turtle species prefer to nest at about 1 m of elevation about sea level, and will move to another section of the beach or to another beach entirely in order to meet this specific requirement (Hays et al. 1995; Boersma 1995; Kolbe & Janzen 2002). Many species prefer to emerge on steeper, instead of shallower beaches (Weishampel et al. 2003; Pfaller et al. 2008; Katselidis et al.2013). In addition, some species preferably nest above the vegetation line in an attempt to avoid storms or the high tide (Horrocks & Scott 1991)

Leatherback sea turtles (*Dermochelys coriacea*) have a circumglobal distribution but nesting sites are concentrated at tropical and subtropical latitudes (James et al. 2006). This species exhibits low fidelity to specific nesting beaches/sites, so a leatherback turtle that nests at Pacuare could later nest anywhere between Tortuguero to Panama (Troeng et al. 2004; Rivas et al. 2015). They tend to nest in the open area between the high tide and the vegetation, although they may occasionally nest below the high tide line (Godfrey & Barreto 1995; Spanier 2010). Because of this proximity to the high tide line when laying their clutches, the species may be more sensitive than others to topographic changes (Whitmore & Dutton 1985; Hays et al. 1995). However, beach parameters such as slopes may determine nest emplacement in other species (Katselidis et al.2013). Nest site selection affects both hatching success and hatchling fitness in sea turtles, and therefore plays a crucial role in maximizing reproductive success (Mrosovsky 1983b; Hays et al. 1995). This is why the loss of suitable nesting habitat, as a product of beach erosion, could be an important disruption in terms of nest site selection (Kamel & Mrosovsky 2004), which could potentially reduce the overall reproductive output of leatherback turtles.

The Caribbean serves as a nesting ground to a large population of leatherback turtles (Chacon 1999; Patino et al. 2008; Rivas et al. 2014). In this region, the species experiences a natural high loss of clutches due to beach erosion and nest inundation (Santidrián Tomillo & Swiggs 2015). Scarps are generally common in tropical regions, but some beaches such as those in the Caribbean are more dynamic than others (Alegría-Arzaburu et al. 2013). For instance, Eckert (1987) estimated that environmental unpredictability could result in 45-60 % annual loss of clutches on some Caribbean beaches. Thus, an increased beach erosion due to climate change may become an important threat to the survival of leatherback turtles in the Caribbean, a region where the natural loss of clutches is already high.

In this study, we analyzed the occurrence of erosion made dune scarps, as well as their effects on the nesting behaviour of leatherback turtles by comparing presence of dune scarps to 1) the number of successful and unsuccessful nesting attempts, 2) nesting success and 3) nest site selection. Studying how sea turtles respond to beach dynamics at present will allow us to understand the effects that future environmental impacts may have on their populations, especially considering the growing influence of climate change.

3.3 Methods

Study site

Our research was conducted at the Pacuare Nature Reserve (PNR), located on the Caribbean coast of Costa Rica. The beach is 5.7 km long and the Reserve's northern and southern limits are at 10°13′17″N, 83°16′39″W and 10°10 ′00″ N, 83°14 ′00″ W respectively. This beach hosts the highest density of leatherback turtle nests in Central America, with a mean density of 142 nests per km, based on over 18 years of data (Rivas et al. 2015). The nesting season extends from the beginning of March until the end of July, with the nesting peak occurring in April and May.

PNR's coastal area is characterized by the presence of dynamic and sandy beaches with slightly steep slopes. The mean tidal range on the Costa Rican Caribbean coast is 0.15 m (Lizano 2006) with a range of 0.40 m at the nearby city of Limón (~40 km from PNR) (IMN, 2014). Daily tide levels can sometimes vary by more than 4 meters (Menendez & Woodworth 2010) and in spring, the tides can engulf the beach completely, sometimes even reaching the vegetation line (Pugh 1996; Losada et al. 2013).

We placed marker posts from south to north along the beach's vegetation line to divide it into equidistant 100 m sectors. Post 0 was situated at the southernmost part of the beach and Post 57 at the northern end. We subdivided each of these sectors by placing markers every 25 m. The width of the beach was then divided into three zones: the intertidal zone (zone A); the higher zone of the beach, above the high tide line (zone B) and the vegetated zone (zone C).

Beach morphodynamics

We observed and monitored the changes in dune scarps throughout the 2013 and 2014 nesting seasons. A scarp was considered as such when its vertical face was higher than 30 cm, and we noted their presence or absence once a week (every Monday at 16:00) in front of each marker post along the beach. We measured the height (h) of each scarp using two sticks located at a 90° angle from the highest point of the crest to the horizontal ground. Additionally, since scarps could be encountered in any of the zones of the beach, we pinpointed their location by measuring the distance from the post to each scarp crest (P-S), and the distance from the bottom of the scarp to the water (S-W) (measured to the previous high tide mark) (Fig. 1A). Due to the fact that scarps could be highly dynamic, we estimated erosion (sand eroded) and accretion (sand deposited) rates and calculated changes in scarp height (cm/day) every two days at 12 of the marker posts, which were chosen depending on where we had observed a previous erosion (13II, 13III, 14, 14I, 14II, 34III, 35, 35I, 35II, 56, 56I, 56II). This estimation was done between April 1st and May 31st 2013

Dune scarp effects on nesting behavior and nesting success

We conducted morning surveys to scan for nesting activities that had occurred during the previous night. In terms of data recording: (1) a nesting attempt was considered when there was a body pit present, indicating the turtle had attempted to nest (a "body pit" was considered as an area of sand that had been disrupted) or (2) an aborted attempt was noted when tracks were present without the presence of body pits. We included instances when females were seen at night and when only the tracks and/or body pits were found at night or in the morning. Nesting success was quantified as the ratio of clutches laid in relation to the total nesting attempts, following Eckert et al. (2012). Additionally, between 2008 and 2014 we calculated the percentage of clutches laid per zone (A, B or C) in order to identify any changes that may have occurred over time in terms of nest-site selection.

In 2013 and 2014, we determined whether a scarp was present or absent for any nesting activity. If a scarp was present we measured the height of the scarp (h), the distance from the scarp (S) to the water (W) (S - W), and distance from the scarp to the nest (S - N) (this distance was measured both when nest were located below and over scarp) (Fig. 1B), after a turtle had nested or aborted. When a scarp was present we classified nesting behaviour into 4 types depending on whether the turtle (1) moved over the scarp and laid eggs (over scarp-laid), (2) moved over the scarp but did not lay eggs (over scarp-aborted), (3) did not move over the scarp and laid eggs below the scarp (below scarp-laid); and (4) did not move over the scarp and aborted the nesting attempt (below scarp-aborted).

We used a long-term data series (1950-2010) comprising monthly mean sea-level (MSL) records to determine trends in SLR for the Caribbean coast of Costa Rica. We obtained the data series from the Commonwealth Scientific and Industrial Research Organization (SCIRO) (Church et al. 2004). MSL had been estimated as the average surface level (mm), taking into account the seasonal cycle (monthly mean) and the anomalies in time scales from the monthly variations to the long-term changes (Church et al. 2004; Losada et al. 2013). We smoothed the data with a 10-year moving average for easier interpretation.

Statistics

We used STATISTICA v. 7.0 (StatSoft, Inc., Tulsa, USA) to conduct all statistical analyses. MSL trend and location of nests were analyzed using a linear regression and the Kruskal-Wallis test. Alpha was set at 0.01. We used; χ^2 tests to compare the number of activities and nesting success recorded in the presence and absence of scarps; and Kruskal-Wallis and ANOVA tests were used to compare differences between scarp height and mean distances between nests and scarps.

3.4 Results

Beach morphodynamics

Scarps were commonly found and were present at on average (±SD) 31.0 ± 12.2 % and 19.9 ± 8.7 % of the 232 beach posts, in 2013 and 2014 respectively. There was not a significant difference in the percentage between both years (Chi-square test: $\chi^2 = 1.62$, $p = 0.203$). Scarps were relatively stable and mean scarp persistence was of 50.8 days (Table 1). The mean distance from the vegetation line to the scarp (P-S) varied significantly between marker posts along the beach, showing no trend within ($R^2 = 0$) (ANOVA, $F_{(6,246)} = 16.41$, $p < 0.01$, 2013; ANOVA, $F_{(6,205)} = 2.88$, $p = 0.01$, 2014) and between years (ANOVA, $F_{(1,471)} = 15.38$, $p < 0.0001$) (Table 1; Fig. 2A). The mean change in scarp height, recorded every two days, was 6.7 cm/day and it significantly varied between the 12 selected markers (Kruskal- Wallis test, $H = 24.43$, $df = 11$, $p = 0.01$) (Table 1; Fig. 2B).

Dune scarp effects on nesting behaviour and nesting success

The percentage of clutches that were laid between 2008 and 2014 significantly increased in areas which presented a high risk of flooding (zone A) (Linear Regression, $R^2 = 0.91$, $p = 0.001$), significantly declined in the open beach area (zone B) (Linear Regression, $R^2 = 0.90$, $p = 0.001$) and did not change in the vegetated area (zone C) (Linear Regression, $R^2 = 0.26$, $p = 0.24$) (Fig. 3).

In 2013, females emergence occurred less frequently in areas that had scarps (Chi-square test, $\chi^2 = 33.81$, $p < 0.001$). In total, 15.7 % of nesting attempts (n = 515) and 20.9 % of nests (n = 327) were recorded in areas with scarps. Both the number of nesting attempts and the number of nests per kilometer were lower in areas with scarps in comparison to those without scarps (Chi-square test, $\chi^2 = 8.69$, $p = 0.003$) (Table 2). On the contrary, nesting success was greater in areas where scarps were present, although the difference between these areas was not significant (Chi-square test, $\chi^2 = 3.53$, $p = 0.060$) (Table 2).

In 2014, females also emerged from the sea less frequently in areas that did have scarps (Chi-square test, $\chi^2 = 20.0$, $p < 0.001$). In total, 11.9 % (n = 837) of nesting attempts and 13.6% (n = 537) of nests occurred in areas with scarps. Again, the number of nesting attempts and the number of nests per kilometer were lower in areas with scarps than without scarps (Chi-square test, $\chi^2 = 8.69$, $p = 0.003$). The difference in nesting success in the presence and in the absence of scarps was not significant (Chi-square test, $\chi^2 = 0.81$, $p = 0.369$) (Table 2).

When looking at the activities in areas with scarps, 39.8 % and 36.3 % (in 2013 and 2014 respectively) of turtles that encountered scarps did not move over them. In terms of the nesting success, it was found to be 55.7 % for those who remained below the scarp and 88.7 % for those who moved over it (Table 3). Females aborted nesting attempts more frequently when they were below, rather than over a scarp (Chi-square test, $\chi^2 = 26.11$, $p < 0.001$). In 2013 a 6.1 %, and in 2014 a 3.5 % of nests laid on the entirety of the beach were located below scarps.

Scarp height influenced nesting behaviour. There were significant differences between the mean scarp height next to nests placed above and below the scarp in 2013 (ANOVA, $F_{1,57} = 5.09$, $p = 0.03$), but these differences were not significant in 2014 (ANOVA, 2014 $F_{1,100} = 0.02$; $p = 0.89$) (Table 3, Fig. 4A). Similarly, there were significant differences in scarp height next to areas where females laid and aborted the nest in 2013 (ANOVA: $F_{1,81} = 14.55$; $p = 0.0003$), but not in 2014 (ANOVA: $F_{1,100} = 0.9p = 0.33$) (Fig. 4B). In 2013, females aborted nesting attempts with a greater frequency when the scarp was higher. Considering only the cases when females did not move over the scarp, there were no differences in scarp height between clutches laid and aborted (ANOVA, $F_{1,50} = 1.88$, $p = 0.18$) (Table 3, Fig. 4C).

The mean distance between the scarp and the water (S - W) for females that remained below the scarp and aborted nesting was lower than those that laid clutches (Table 3) (ANOVA, $F = 0.58$, $p = 0.01$). The distance between the scarp and the water (S - W), including only instances when turtles laid eggs, was significantly different in areas where eggs were laid below and over the scarps (ANOVA, $F_{1, 98} = 29.7$; $p < 0.01$) (Table 3). In total, 44.8% and 60.3 % of nesting females in 2013 and 2014 respectively laid their clutches in areas with high risk of flooding ($S - W \leq 5$ m). More than 50% of these females laid their clutches within a distance of 2 m below or over the scarp (Fig. 5A).

The presence of scarps did not influence the percentage of nests laid in zone A compared to those in other zones in 2013 (Chi-square test, $\chi^2 = 0.96$, $p = 0.33$). However, in 2014 there were significantly more nests in zone A when scarps were present than in absence of them (Chi-square test: $\chi^2 = 21.41$, $p < 0.01$) (Table 4).

In terms of the turtles that laid eggs, the distance between the scarp and the nest (S - N) was significantly lower when turtles had not moved over the scarp (0.71 ± 1.35 m) than when turtles did do so (4.64 ± 4.25) (ANOVA, $F_{(1, 90)} = 34.01$, $p < 0.01$) (Fig. 5B). In conclusion, 80.0% ($n = 16$) of clutches in 2013 and 89.5% ($n = 17$) of clutches in 2014 were laid within a distance of less than 2 m (S - N) to the scarp (Table 5).

3.5 Discussion

Dune scarp effects on nesting behavior and nesting success

Dune scarps are observed year-round at PNR (Per. obs.), but their presence and frequency was never recorded until we began conducting this study. In 2013 and 2014, scarps covered more than 20-30% of the whole beach; scarps were recorded by noting their presence every 25 m. A scarp was usually present on average for over two months. Taking into account the fact that the percentage of clutches that are laid in areas with a high risk of flooding has significantly increased over time, we believe that erosion-accretion cycles should be monitored regularly on nesting beaches so that we can characterize both site-specific beach dynamics and changes overtime in order to determine the potential effects on sea turtle populations.

Our results show that the presence of dune scarps significantly influenced the nesting behaviour of leatherback turtles by (1) reducing the number of activities in areas where scarps were present, compared to the rest of the beach. It also resulted in (2) a high percentage of females that did not move over scarps and therefore (3) resulted in their clutches being laid below the high tide line. Nests located in these lower areas are more likely to become inundated by tidal action; eggs are more prone to being washed out (Eckert 1987; Caut et al., 2010; Patiño et al. 2014), and there is a higher mortality rate due to the fall in sand temperature (Houghton et al. 2007). Therefore, nest emplacement influences the environment in which clutches develop, decreasing hatchling production (Mrosovsky 1983; Pfaller et al. 2008). Taking into consideration that nest site selection patterns seem to be affected by a variety of environmental factors (Wood & Borndal 2000), it seems highly likely that in the future they will be disrupted by these ever-changing processes of erosion.

The effects of climate change may ultimately result in the shifting of nesting sites, as it is possible that turtles will adapt to these increasing levels of erosion by simply moving away to other beaches, if they can find any that are undeveloped and with the suitable conditions. In fact, the leatherback sea turtle's nesting range may already be shifting to higher latitudes (McMahon et al. 2006). However, if high erosion is present along the Caribbean coast it will make it more difficult for leatherback turtles to find new places to nest. Consequently, climate change poses new challenges on multiple fronts that sea turtles would need to respond to.

Effects of SLR on nesting habitats

Recent studies have identified sea-level rise and/or increased storm frequency as factors that affect those endangered species whose nesting success depends on the stability of their coastal habitats (Fish et al. 2005, 2008; Fuentes et al. 2010, 2011; Katsedilis et al. 2014) . Sandy beaches would be especially prone to the increased levels of erosion (Brown et al. 2013) resulting from storms and tidal level changes (Webster et al. 2005; Pye & Blott 2008).

While global mean SLR is projected to rise, projections might differ substantially among regions (Suzuki & Ishii 2011; Slangen et al. 2012). The sea level on the Caribbean side of Costa Rica increased between 1950 and 2010 (linear regression, $R^2 = 0.83$, $p < 0.001$) (Fig. 6). On average, the sea level rose 0.2 cm per year in that timeframe. If the same trend continues, sea levels could rise by another 20 cm by the end of the 21st century compared to current levels. However, the Intergovernmental Panel on Climate Change's (IPCC) projections recently predicted a further rise of between 0.40 and 0.63 m for the end of the 21st century, with the most pessimistic scenario predicting these values to range from 0.52 to 0.98 m (IPCC 2013). If these scenarios become a reality in the near future we may observe dramatic effects on sea turtle nesting grounds.

Conservation implications

Suitable nesting habitats are decreasing due to anthropogenic and environmental factors (Fish et al. 2008; Mazaris et al. 2009). To mitigate nest loss, sea turtle monitoring projects along this coastline have implemented conservation measures where doomed clutches are relocated to alternative safer locations (Mrosovsky 1983; Mrosovsky 2006; Rivas et al. 2015). These clutches are taken to hatcheries or to optimal beach locations. This technique, however, could potentially reduce hatching success and alter sex ratios (Spanier, 2010; Sieg et al. 2011; Patiño et al. 2012; Santidrián Tomillo et al. 2012, 2014). Thus, these strategies should be used with caution. Firstly, we suggest conducting an assessment of the quality of the nesting habitat (Mazaris et al. 2009; Torio & Chmura 2013) to develop and prioritize conservation plans (Schlacher et al. 2007). Likewise, long–term studies should be conducted in order to identify whether this species, and other sea turtle species, exhibit phenotypic plasticity in terms of their nesting behaviour or if, on the contrary, their risk of extinction is exacerbated due to climate change.

Table 3.1. Mean (± SD) and range of scarp persistence (days) recorded once a week during a period of 85 days in 2013; scarp height (m) in both years and distance (P-S) (m) shown by year; and scarp height (cm/day) recorded every two days at 12 posts in 2013.

	Scarp persistence (days)	Scarp height (m)	Distance (P-S) (m)		Scarp height (cm/day)
			2013	2014	
Mean±SD	50.8 ± 20.3	0.7 ± 0.4	9.6 ± 3.2	12.2 ± 9.5	6.7 ± 7.4
Range	20.0 – 85.0	0.4 – 1.1	0 – 30	0 – 41.3	0 – 37.5

Table 3.2. Percentage and number of nesting attempts as number of nest attempts (considered when clutches were laid or when body pit present) and aborted attempts in the presence and absence of scarps in 2013 and 2014; number of nesting attempts and nest attempts per km; and percentage of nesting success (%) in the presence and absence of scarps for the same years.

	Nesting attempts % (N)/per km			Nest attempts % (N)/per km			Aborted attempts %(N)			Nesting success (%)	
	2013	2014	Total	2013	2014	Total	2013	2014	Total	2013	2014
Scarps	15.7 (81)/45.1	11.9 (100)/86.6	181	20.9 (68)/37.8	13.6 (73)/63.2	141	6.9(13)	9.0(27)	40	84.0	73.0
No scarps	84.3 (434)/108.4	88.1 (737)/158.6	1171	79.1 (259)/64.7	86.4 (464)/99.9	723	93.1 (175)	91.0 (273)	448	59.7	63.0

Table 3.3. Type of nesting behaviour in relation to scarp height (m) and the distance (m) from scarp to the water (S – W). Mean (± SD), minimum and maximum height and S- W distances . Percentages (%) and numbers (N) for each activity at distances S - W ≤ 5 are also shown.

	Mean height (m)		Min height (m)		Max height (m)		%(N)		S-W (m)		Min S - W (m)		Max S - W (m)		% (N) (S-W≤ 5)	
	2013	2014	2013	2014	2013	2014	2013	2014	2013	2014	2013	2014	2013	2014	2013	2014
Below scarp -aborted	0.6 ± 0.3	0.5 ± 0.1	0.3	0.3	1.3	0.8	15.76(13)	17.6(18)	2.1±4.8	1.4±3.1	0	0	15	11.3	90.0(9)	94.4(17)
Below scarp -laid	0.5 ± 0.1	0.4 ± 0.2	0.3	0.3	0.7	0.8	24.1(20)	18.6(19)	6.6±5.8	8.6±6.5	0	0	19.1	20.7	38.9(7)	31.6(6)
Over scarp -laid	0.4 ± 0.1	0.4 ± 0.1	0.1	0.2	0.9	1	57.8(48)	52.9(54)	7.2±6.6	3.7±5.1	0	0	19.8	20.5	47.5(19)	70.4(38)
Over scarp -aborted	0.8 ± 0.2	0.5 ± 0.1	0.7	0	0.9	0.9	2.4(2)	10.8(11)	4.5±0.2	2.7±5.1	4.3	0	4.6	14.1	100(2)	81.8(9)

Table 3.4. Percentage of nests (%) laid per zone.

	Zone A (%)		Zone B (%)		Zone C (%)	
	2013	2014	2013	2014	2013	2014
Scarps	32.8	34.2	67.2	65.8	0	0
No scarps	26.2	13.0	73.3	86.8	0.5	0.2

Table 3.5. Percentage of nests (%) and number of nests (in brackets) classified by their distance (m) to the dune scarps (S – N). Distances were grouped into 2 meter group. Results are shown by year.

	0 – 2 m		2 – 4 m		4 – 6 m		6 – 8 m		8 – 10 m		> 10 m	
	2013	2014	2013	2014	2013	2014	2013	2014	2013	2014	2013	2014
Below scarp	80 (16)	89.5 (17)	20 (4)	5.3 (1)	0	0	0	5.3 (1)	0	0	0	0
Over scarp	16.7 (4)	26.5 (13)	54.2 (13)	14.3 (7)	29.2 (7)	20.4 (10)	0	11.3 (6)	0	1.9 (1)	0	20.7 (11)

A

B

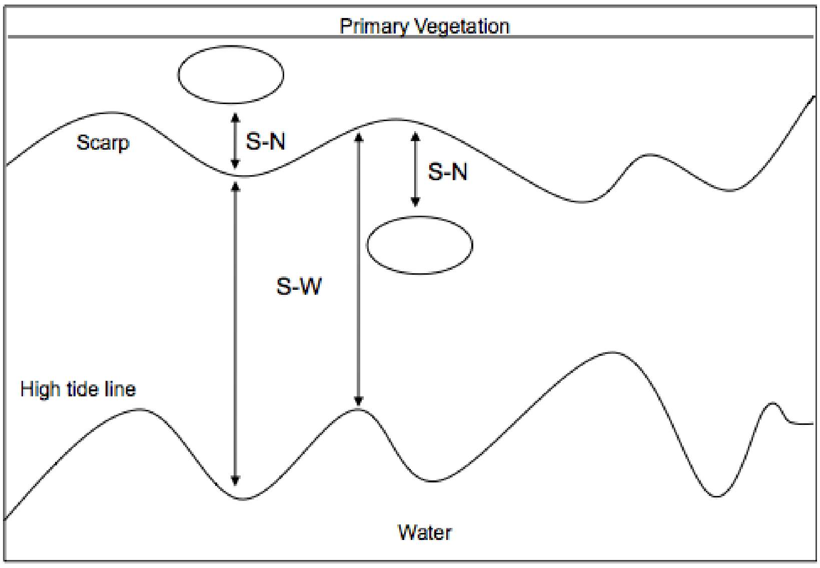
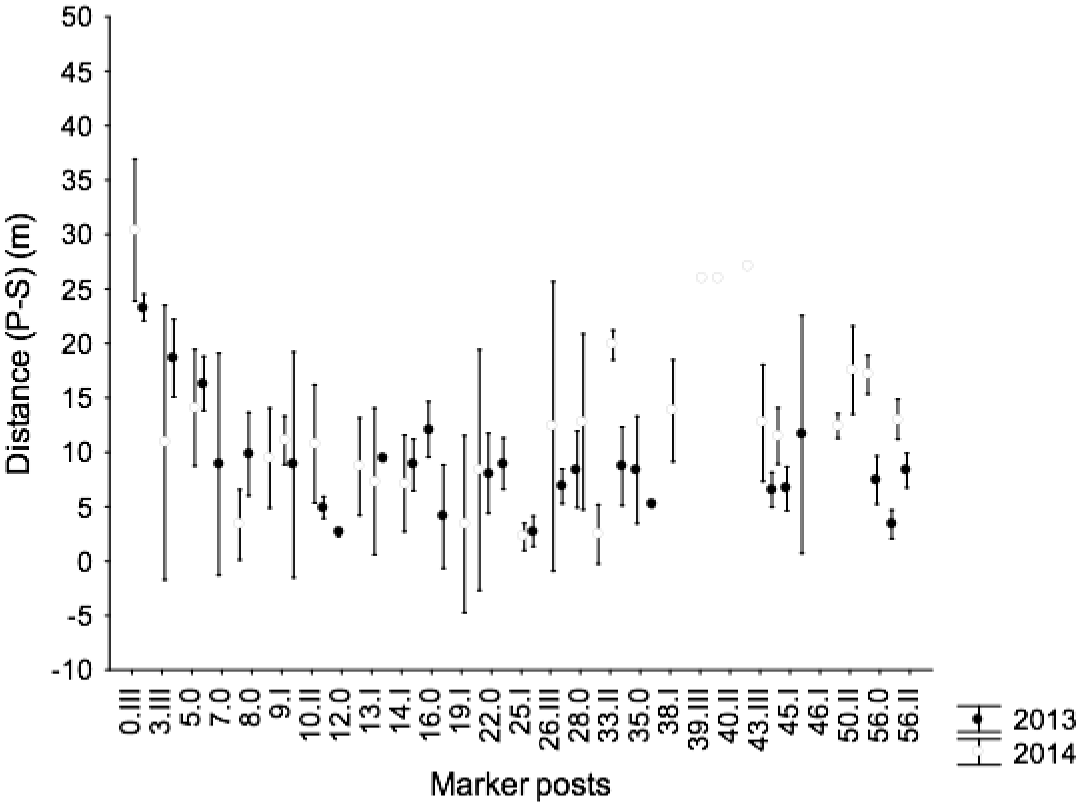


Figure 3.1. (A) The non scarped section of the beach and the scarped section with measurements taken to characterize beach morphodynamics: h - scarp height, P-S - distance from fixed posts located in the vegetation to the scarp, S-W - distance from scarp to the water. (B) when nesting females encountered scarps. S-N - distance from scarp to the nest, S-W - distance from scarp to the water.

A


Distance (P-S) (m)
50
45
40
35
30
25
20
15
10
5
0
-5
-10
0.III
3.III
5.0
7.0
8.0
9.I
10.II
12.0
13.I
14.I
16.0
19.I
22.0
25.I
26.III
28.0
33.II
35.0
38.I
39.III
40.II
43.III
45.I
46.I
50.II
56.0
56.II
Marker posts
2013
2014

B

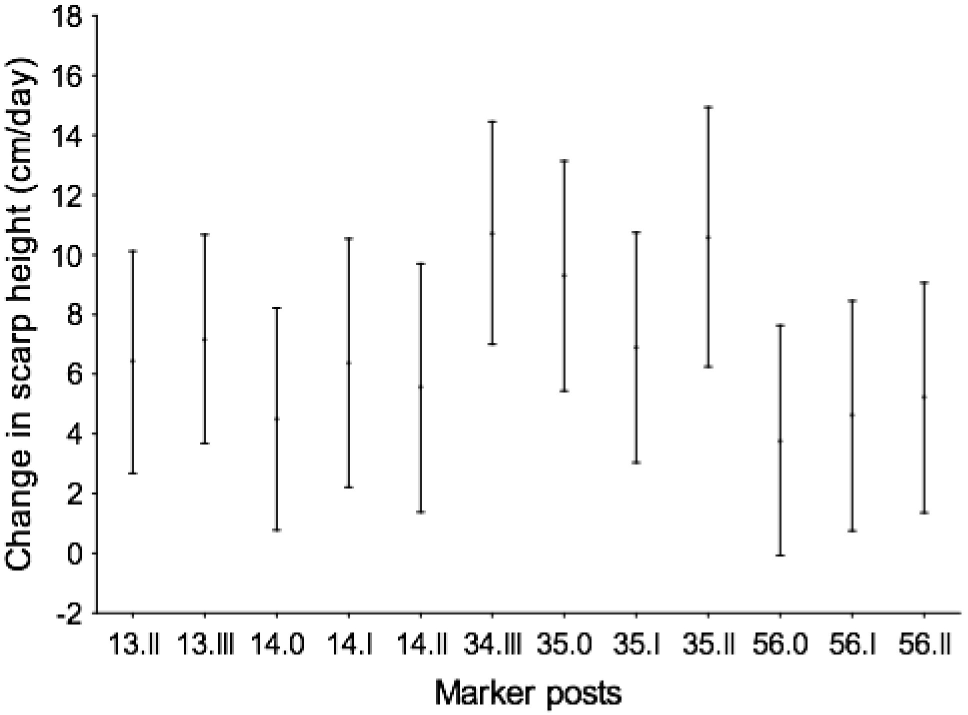


Figure 3.2. (A) The average distance from each post to the scarp (P-S) (m) for every marker post located along the beach. Points represent the mean (± SD) distance along the season. (B) Mean beach erosion/accretion rates (vertical movement cm/day) for 12 marker posts located along the beach.

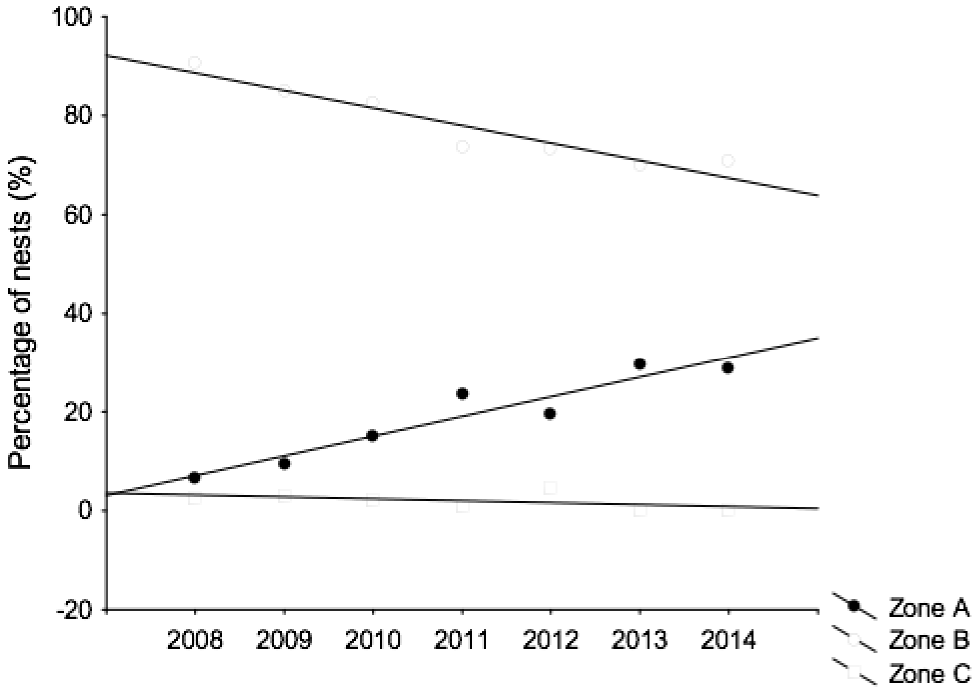
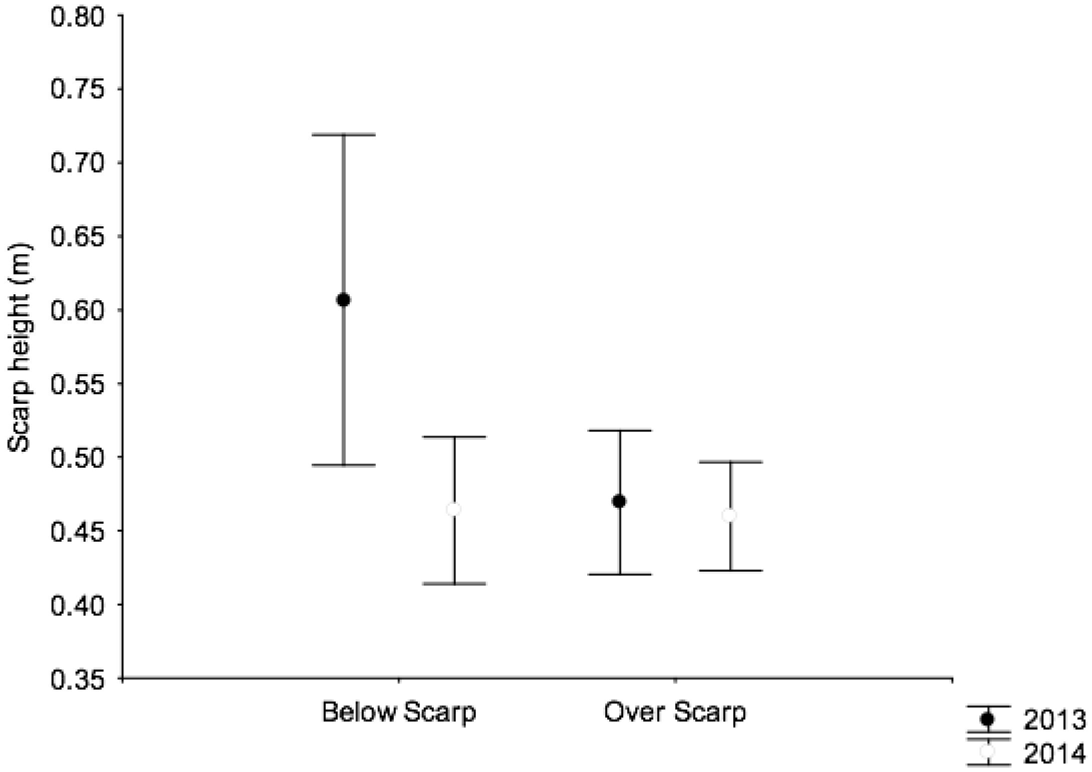


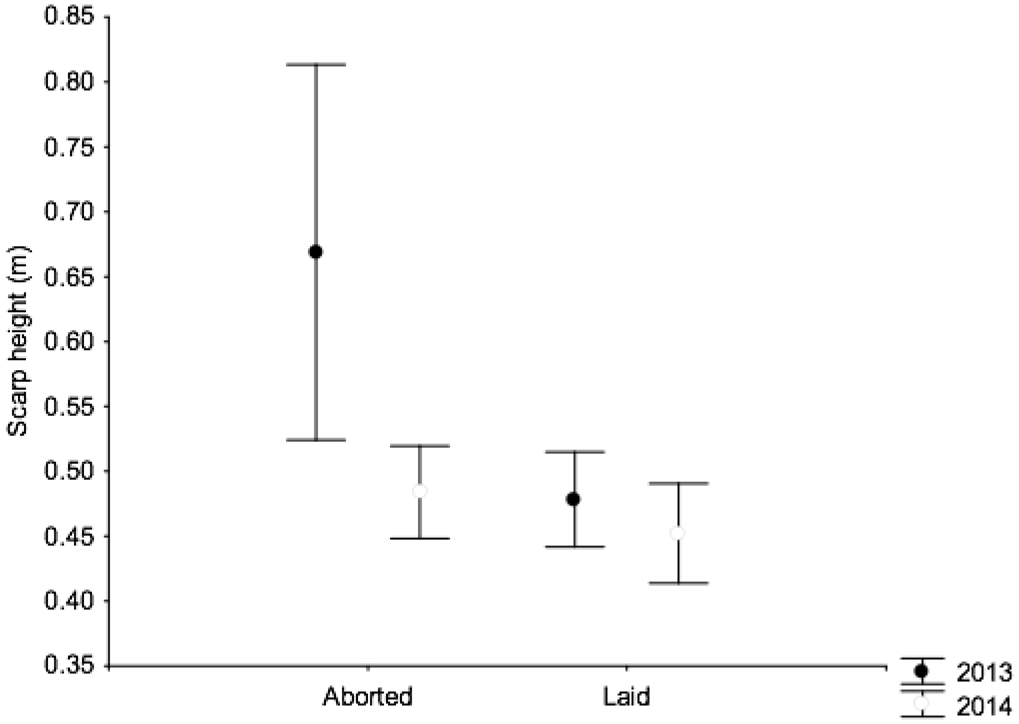
Figure 3.3. Percentage of nests (%) laid per zone (A, B, C) from 2008 to 2014 at PNR. The beach width was divided into three zones: the intertidal zone (zone A); high beach zone above the high tide line (zone B) and in the vegetation (zone C).

A



0.80
0.75
0.70
0.65
0.60
0.55
0.50
0.45
0.40
0.35
Scarp height (m)
Below Scarp
Over Scarp
2013
2014

B


Scarp height (m)
0.85
0.80
0.75
0.70
0.65
0.60
0.55
0.50
0.45
0.40
0.35
Aborted
Laid
2013
2014

C

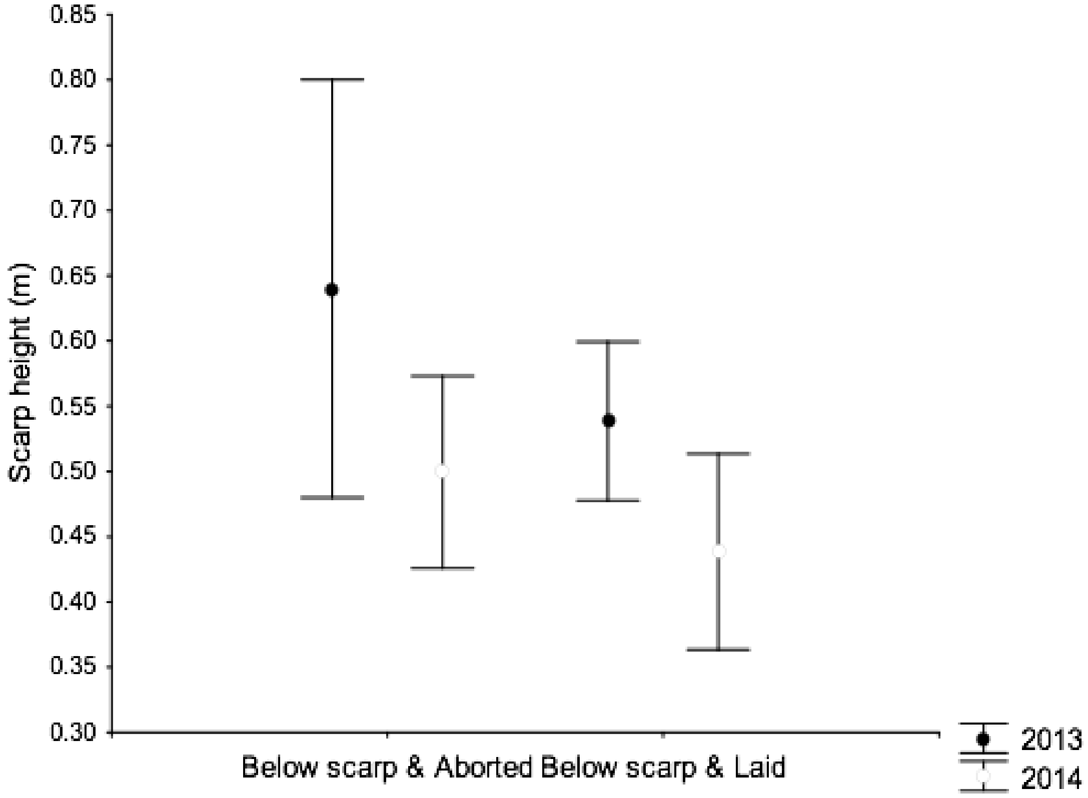
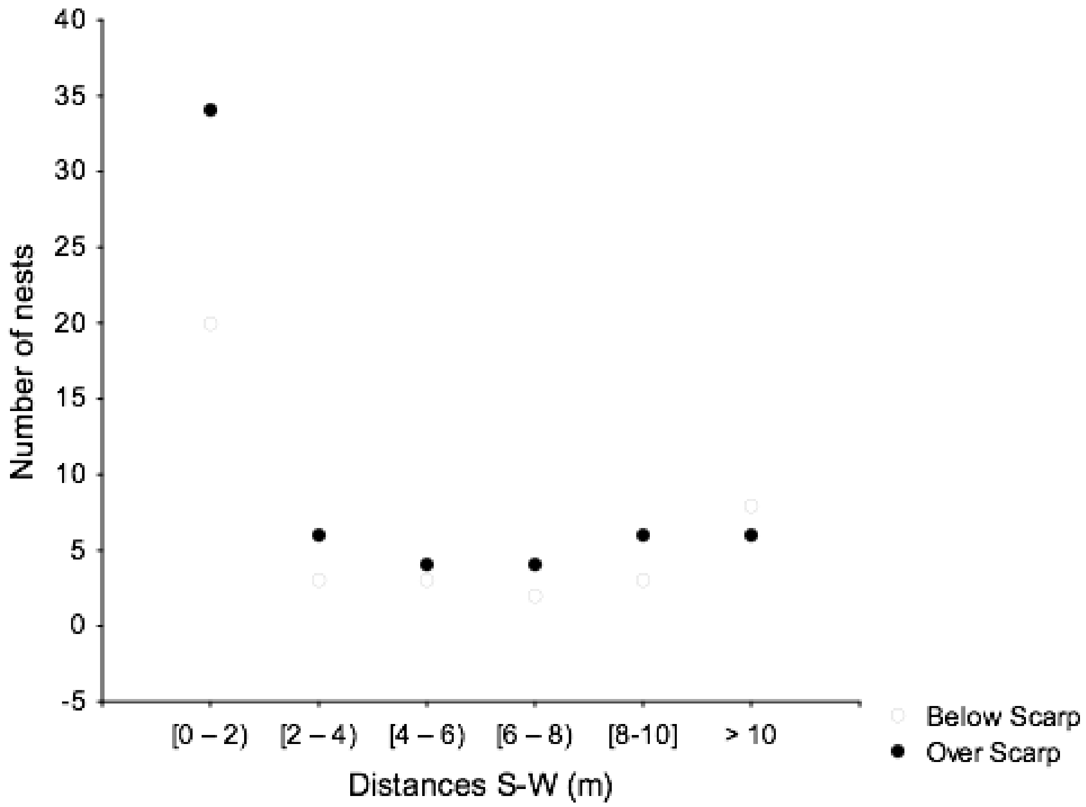


Figure 3.4. (A) Mean scarp height (m) in instances when clutches were laid over or below the scarp. (B) Mean scarp height (m) with respect to clutches that were either laid or aborted (including nests below and over scarps) and (C) Mean scarp height (m) of clutches laid versus nests aborted below the scarp in 2013 and 2014.

A


Number of nests
40
35
30
25
20
15
10
5
0
-5
[0 – 2)
[2 – 4)
[4 – 6)
[6 – 8)
[8-10]
> 10
Distances S-W (m)
○ Below Scarp
● Over Scarp

B

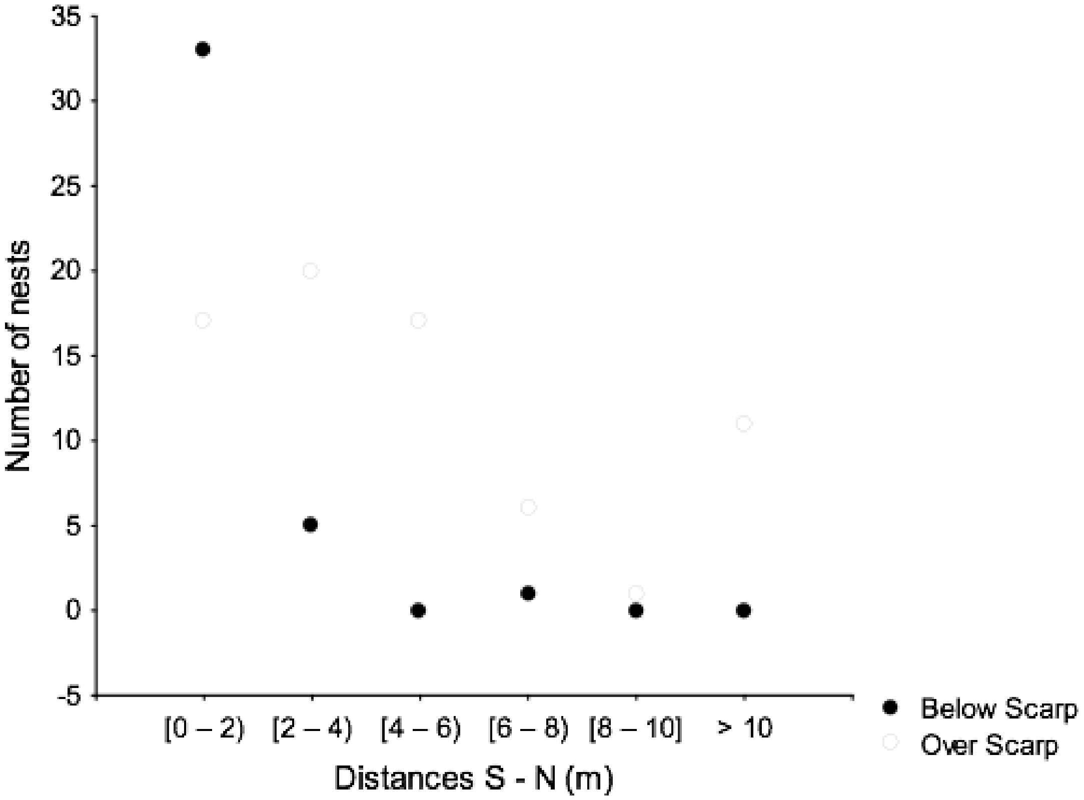


Figure 3.5. (A) Scarp distances from the water (S-W) for clutches laid over the scarp versus below by nesting females. **(**B) Distances from scarp to the nest (S-N) of clutches laid over and below the scarp.

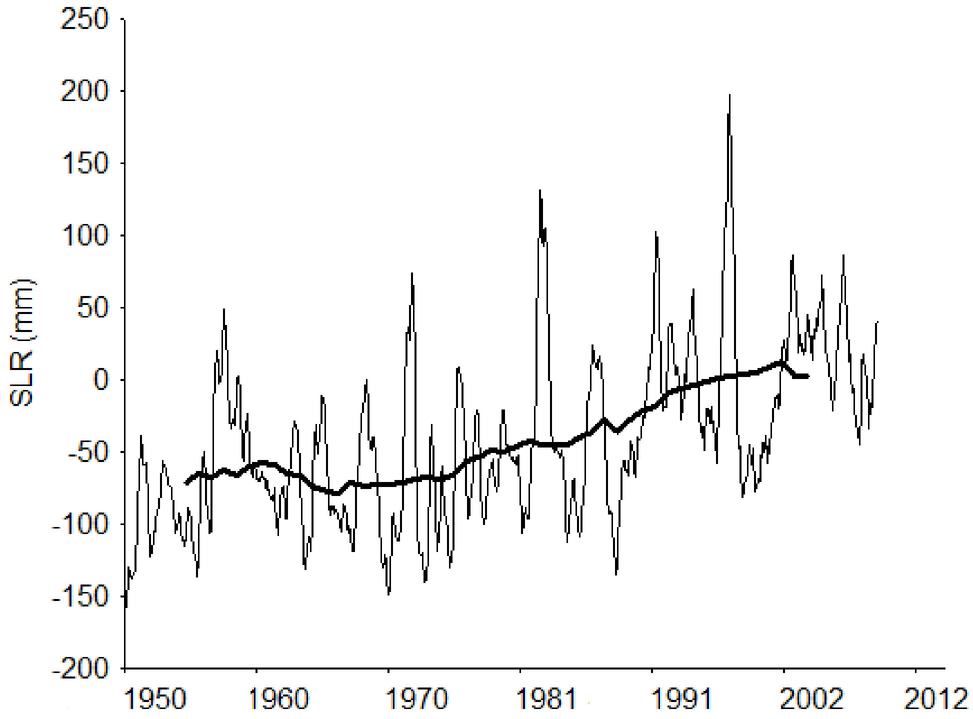


Figure 3.6. Mean monthly sea-level (MSL) trend (mm) in the Caribbean region from 1950 to 2010. Data was smoothed with a 10-year moving average.

Chapter 4. The effect of dune vegetation on leatherback hatchlings sea-finding ability

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4.1 Abstract

Leatherback turtles, *Dermochelys coriacea,* are affected by a range of anthropogenic stressors throughout their range. However, little is known about the species' responses to natural threats such as dune vegetation, which can have a negative effect on the quality of nesting habitats. In this study we assessed the potential impact of *Ipomoea pes-caprae* on the sea-finding abilities of leatherback hatchlings at the Pacuare Nature Reserve on the Caribbean coast of Costa Rica. To analyse their effects on hatchling behaviour we measured and compared the speed at which hatchlings managed to reach the water at open beach locations and vegetated locations. We recorded nest locations of 1,491 nests, which were left *in situ,* and 784 that were relocated between 2012 to 2014. The majority of *in situ* nests were located in areas where the vegetation was denser than in open beach. We found that dune vegetation had a negative effect on hatchling speed, which led to an increased exposure time to predators and dehydration and could potentially entail extreme physiological stress affecting hatchling mortality. Thus, the presence of vegetation might negatively influence the suitability of nesting habitats if beach erosion processes increase on nesting grounds in the future.

4.2 Introduction

Dune morning glory, *Ipomoea pes-caprae,* is a coastal sand dune plant with a pantropical distribution, that is common in the Caribbean (Castillo and Moreno-Casasola 1996; Mendoza-González et al. 2013). It is characterised by its fast growing vines, which spread superficially over sandy beaches, and deep roots that can penetrate up to several meters in all directions including vertically downwards. In this species growth is controlled by erosion-accretion cycles on dynamic beaches (Devall 1992; Devall and Thien 2005) and it can sometimes cover the entire width of eroded beaches (Per. obs. Fig 1A). Dune vegetation is usually considered to be a natural way of controlling erosion by preventing the loss of nesting habitat through the stabilization of the beaches where it is present (Feagin et al. 2005; Hannan et al. 2006). However, a recent study suggests that certain spreading species, such as *Ipomoea pes-caprae,* can negatively affect sea turtle hatchling production and reduce suitable nesting habitat (Conrad et al. 2011).

Leatherback turtles, *Dermochelys coriacae*, nest at tropical latitudes (James et al. 2006) where dune plants such as *I. pes-caprae* are common (Devall 1992). This species mostly nests in the middle or open areas of the beach (Mrosovsky 1983), which are free of plants, and depends on high quality nesting habitats. However, due to the erosion of beaches, suitable nesting sites, which are free of vegetation, have been reduced and vegetated areas have frequently been selected for the relocation of nests (Rivas et al. in press). After emergence, hatchlings from these nests need to cross areas colonised by *I. pes-caprae* in order to reach the sea. Vegetation may entangle hatchlings and therefore reduce their sea-finding capabilities (Godfrey and Barreto 1995). Hence the presence of spreading dune vegetation at nesting beaches could be an important factor to take into account when considering the reproductive success of sea turtles. Sea turtle nesting beaches are threatened by environmental impacts caused by climate change such as beach erosion and sea-level rise (Eckert, 1987; McMahon et al. 2006; Schlacher et al. 2007; Wallace and Saba 2009; Patiño-Martinez et al. 2014; Pike et al. 2015). However, little is known about how abiotic changes could affect nesting beaches decreasing suitable habitat in coastal areas and increasing the presence of dune vegetation. *In situ* and relocated nests are mainly located at sites where *I. pes-caprae* is present and our hypothesis was that this dune vegetation might disrupt the hatchling sea-finding ability, increasing the time of exposure on the beach and decreasing the hatchling's speed.

4.3 Methods

We conducted this study at Pacuare Nature Reserve (PNR) in 2014, which is located at (10°13′17″N, 83°16′39″W) and (10°10 ′00″ N, 83°14 ′00″ W) and hosts an important leatherback nesting site on the Caribbean coast of Costa Rica (Rivas et al. 2015). The experiment consisted in measuring hatchling speed in areas where *I. pes-caprae* was abundant compared to their speed in areas of open beach, in order to assess the effect of this plant species on leatherback turtle hatchling's sea-finding ability. To record nests location we placed marker posts amongst the vegetation every 100 m to divide the beach (5.7 km-long) into 100 m-wide sections. Post 0 was placed at the southern most part of the beach and post 57 was placed at the northern end. During 2013, 2014 and 2015 the width of the beach was classified in three zones: the intertidal zone (zone A); the higher part of the beach, above the high tide line (zone B); and the area nearest to the vegetation (zone C) (Fig 1A). Nests were either left *in situ* or relocated when there was a high risk of predation, sand erosion, vegetation growth, etc. The location of each nest was recorded. A sample of 8 nests was relocated to a hatchery near an area with natural vegetation. In 2014 the stretch of sand (containing areas with and without vegetation) chosen in which to conduct the experiment was in sector 4 at the South station of PNR, the area closest to primary vegetation (nearest the hardwood trees boundary). The exact location selected for the experiment was a stretch of the beach where *Ipomoea pes-caprae* covered more than 70% of the beach surface. After hatchling emergence, a sample of 10 hatchlings from each of the 8 hatchery nests were released onto the area where dune plants were present, which covered 10 m of the width of the beach. Hatchlings were therefore placed at a distance of 20 m from the sea to standardise the distance travelled to the sea (Fig 1A). The time each hatchling took to cross the 10 m-wide section of vegetation was recorded to determine speed (m/s) within a maximum interval time of 30 minutes after which it was considered that hatchlings could not cross the vegetation section (Fig 1B). Another sample of 10 hatchlings from each of the same 8 hatchery nests was used as an experimental control. These were released onto an area 20 m from the shore; equidistant to where the other hatchlings were placed, but with all vegetation removed (open beach) (Fig 2). All hatchlings were released into the sea following the experimentation.

4.4 Results

Due to erosion processes the number of relocated and *in situ* nests in zone B and C was greater than in zone A (Table 1). The mean percentage of relocated nests over the years was 52.8 ± 9.44 (mean ± SD) and 88.9 ± 6.5 for *in situ* nests (Fig. 3). Hatchlings took significantly more time to cross the vegetated areas (15.05 ± 6.16 min) than they did to cross open beach (4.14 ± 2.23 min) (t test, t = 12.01, df = 102; $p < 0.0001$) (Fig. 4). There was also a significant time difference between nests and between experiments (two-way ANOVA, $F_{7,131} = 23.36$; $p < 0.0001$). In addition, there were time differences between hatchlings from different nests in crossing the vegetated (ANOVA, $F_{7,79} = 39.39$; $p < 0.0001$) (Table 2a) and open beach (ANOVA, $F_{7,79} = 3.97$; $p < 0.001$) (Table 2b) stretches. The Bonferroni post-hoc analysis showed significant differences among nests in vegetated areas ($p < 0.001$) but not between nest 1 and 3, 2 and 5, 4 and 6, 4 and 7 and 6 and 7. In open beach areas there were only differences between nest 6 and 8 ($p < 0.01$). A total of 28 hatchlings did not cross the vegetation before 30 minutes (35 ± 35.46%; range = 0 – 100, n =80). This percentage of hatchlings that took more than 30 min to crawl across the 10 m width of vegetation was significantly greater than on open beach (0%) (Chi-square test, $\chi^2 = 6.0$, $p < 0.01$). The mean hatchling speed in vegetation was 1.32 ± 0.59 m/s (range = 0.57 – 2.71, n = 52), whereas for open beach it was 4.63 ± 1.69 m/s (range = 1.08 – 8.05, n = 80). Hatchlings placed on open beach were significantly faster than on areas with dune vegetation (t test, t= - 13.57, df = 130; $p < 0.0001$) (Fig. 5).

4.5 Discussion

This study shows that the majority of nests at PNR are located where *I. pes-caprae* is abundant and that this factor may influence leatherback post-emergence survival. Hatchling speed was negatively affected by dune vegetation and was significantly different among nests. The additional time hatchlings spend reaching the sea when emerging amongst dune vegetation has a significant extra energetic cost that could influence their survival during the first swimming hours (Patiño et al. 2015). Furthermore, a significant proportion of hatchlings from vegetated areas did not reach the sea compared with those that had to crawl over open beach. Consequently, this experiment shows that the spreading dune vegetation that is becoming more abundant on nesting beaches might play an important role on leatherback post-emergence survival (Conrad et al. 2011) as well as on hatchling production.

Future climatic scenarios predict important environmental changes, which will affect coastal ecosystems due to sea-level rise (IPCC 2013; Losada et al. 2013; Mendoza-Gonzalez et al. 2013) and storm frequency (Knutson et al. 2010; Fuentes et al. 2011). Sandy beaches could be prone to these environmental changes that would cause beach erosion, which reduces nesting habitat availability. Consequently, beach erosion could push nesting females to lay eggs at sites in or closer to vegetation or at flooding sites (Rivas et al. in process). Furthermore, the presence of dune vegetation also reduces open beach availability. Thus, the increase of spreading dune vegetation on nesting beaches could also be an important threat to bear in mind.

Conservation measures undertaken by sea turtle monitoring projects are focusing on the relocation of doomed clutches to higher ground locations where, in turn, dune vegetation negatively affects the gene pool and hatching success (Mrosovsky 2006; Conrad et al. 2011). Our results suggest that low hatchling speed in vegetation could entail an increase in hatchling mortality due to longer exposure times to dehydration as well as to predators, such as crabs and birds (Barton and Roth 2008; Santidrián Tomillo et al. 2010). Therefore we would suggest that nest relocation techniques should take into consideration the effects of dune vegetation on hatchlings in addition to the environmental conditions of each habitat (Wallace et al. 2004; Garret et al. 2010). For instance, before relocating nests randomly, an assessment should be carried out to identify high quality relocation sites and/or vegetation should be removed before hatchling emergence. In effect, beach conservation management must be reinforced to ensure positive outcomes from conservation strategies on sea turtle nesting habitats and the maximum viability possible.

Table 4.1. Number of In situ and relocated nests in zones B and C and the total number of nests on the beach in 2012, 2013 and 2014.

	2012		2013		2014	
	Nests in B+C	Total	Nests in B+C	Total	Nests in B+C	Total
Relocated	171	399	113	210	108	175
In situ	787	879	206	251	343	361

Table 4.2. Time (in minutes) that hatchlings took to cross the dune vegetation after emergence. The maximum time interval was 30 minutes to cross the 10 meters (a) with dune vegetation *Ipomoea pres-caprae* and (b) in open sand. The table also includes the mean time with its standard deviation, as well as the maximum and minimum times that hatchlings took, and N = the proportion of hatchlings that crossed the vegetation within 30 min/hatchlings that did not cross the vegetation within 30 minutes.

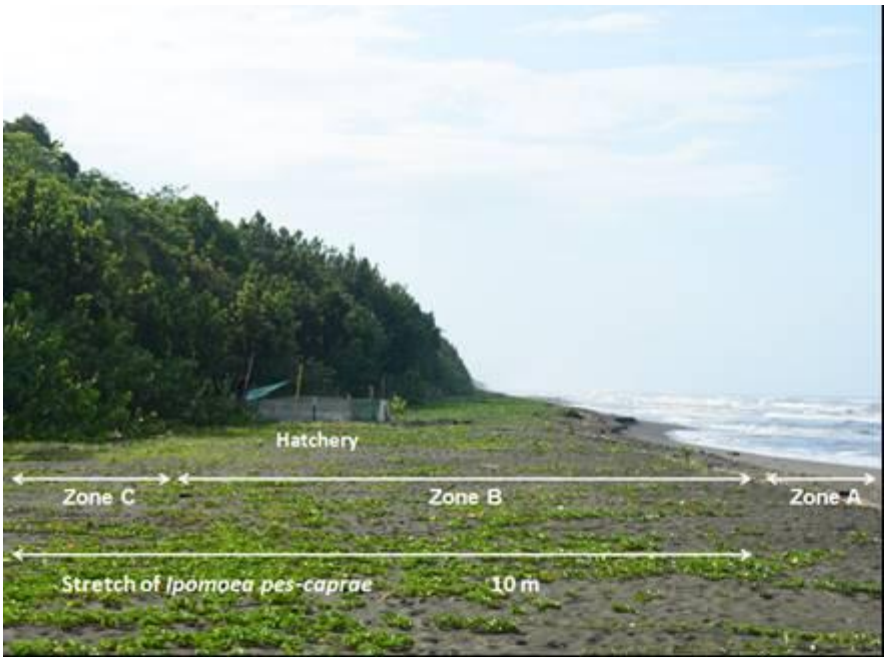
(a)

Nest	Mean ± SD	Min.	Max.	N (Yes /No)
1	16.93±4.59	10.59	26.17	9/1
2	8.37±2.32	6.16	14.00	10/0
3	15.27±3.56	12.03	21.22	8/2
4	0	0	0	0/10
5	10.38±3.61	7.5	19.10	10/0
6	20.01±2.87	16.53	23.25	7/3
7	24.53±4.64	18.35	29.39	4/6
8	20.55±3.94	17.15	26.24	4/6

(b)

Nest	Mean±SD	Min.	Max.	N (Yes /No)
1	4.46±0.97	2.54	5.25	10/0
2	3.16±0.95	2.07	5.07	10/0
3	3.53±1.33	2.31	6.15	10/0
4	5.55±4.24	2.47	15.39	10/0
5	3.47±0.87	2.34	4.47	10/0
6	6.39±2.35	3.55	10.39	10/0
7	4.88±1.70	3.03	7.37	10/0
8	2.90±0.61	2.45	4.26	10/0

A


Hatchery
Zone C
Zone B
Zone A
Stretch of *Ipomoea pes-caprae*
10 m

B

Figure 4.1. A. The site used for the experiment at the Pacuare beach. A. The stretch of *Ipomoea pes-caprae* and the hatchery location with zones A, B and C are marked on the image. B. A leatherback hatchling becoming entangled in *I. pes-caprae*.

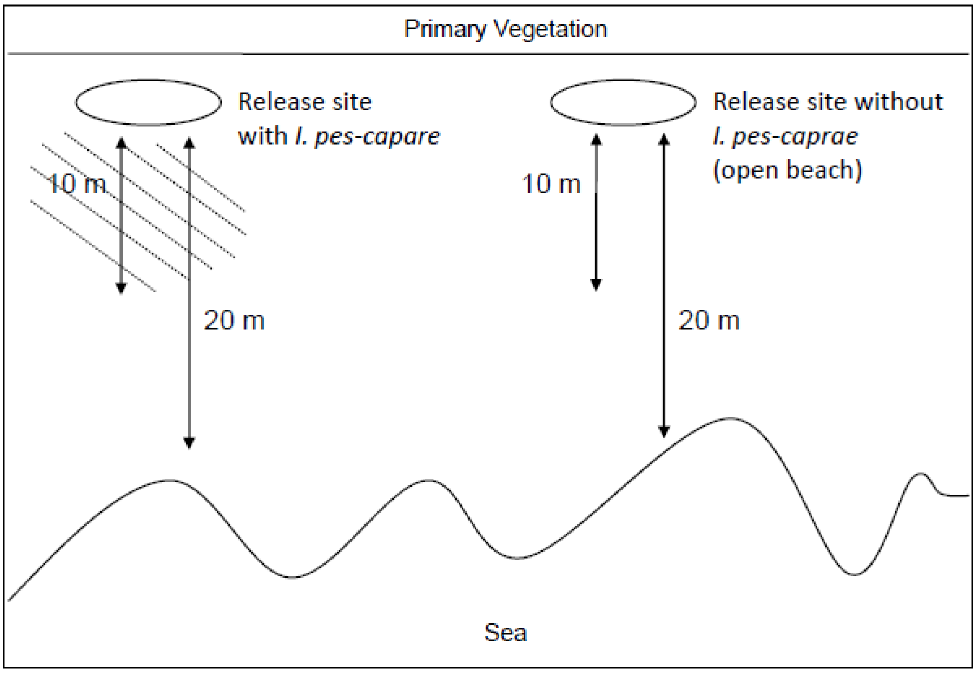


Figure 4.2. A sketch of the site where the study was conducted. Two locations were selected in close proximity with the hatchery in an area where *I.pes-caprae* covered more than 70% of the whole sand surface. *I pes-caprae* was removed from an adjacent area so that the space could be used as a control site (open beach). Hatchlings were released just seaward of the primary vegetation line and a total of 20 m from the sea. They needed to cross 10 m of vegetation and 10m of open sand to get the water.

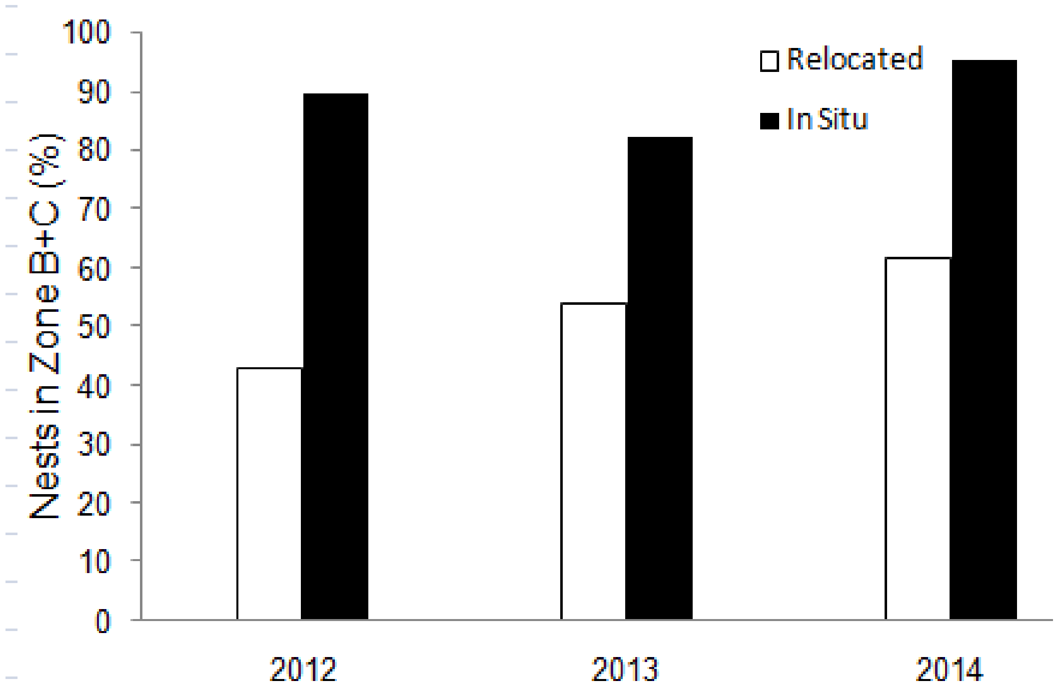


Figure 4.3. Percentage of relocated and in situ nests (%) located in zone C in 2012, 2013 and 2014.

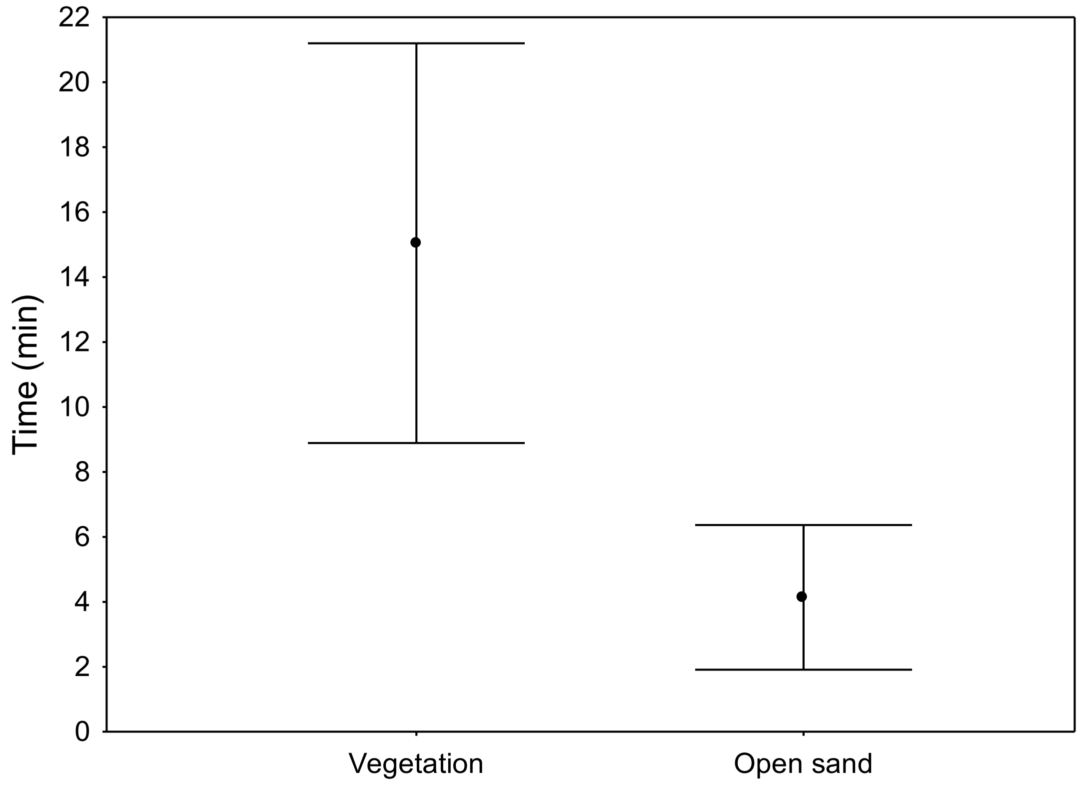


Figure 4.4. Time (min) that hatchlings took to cross the vegetated area in comparison with that on open beach. The middle point is the mean, and the whiskers indicate the Standard Error.

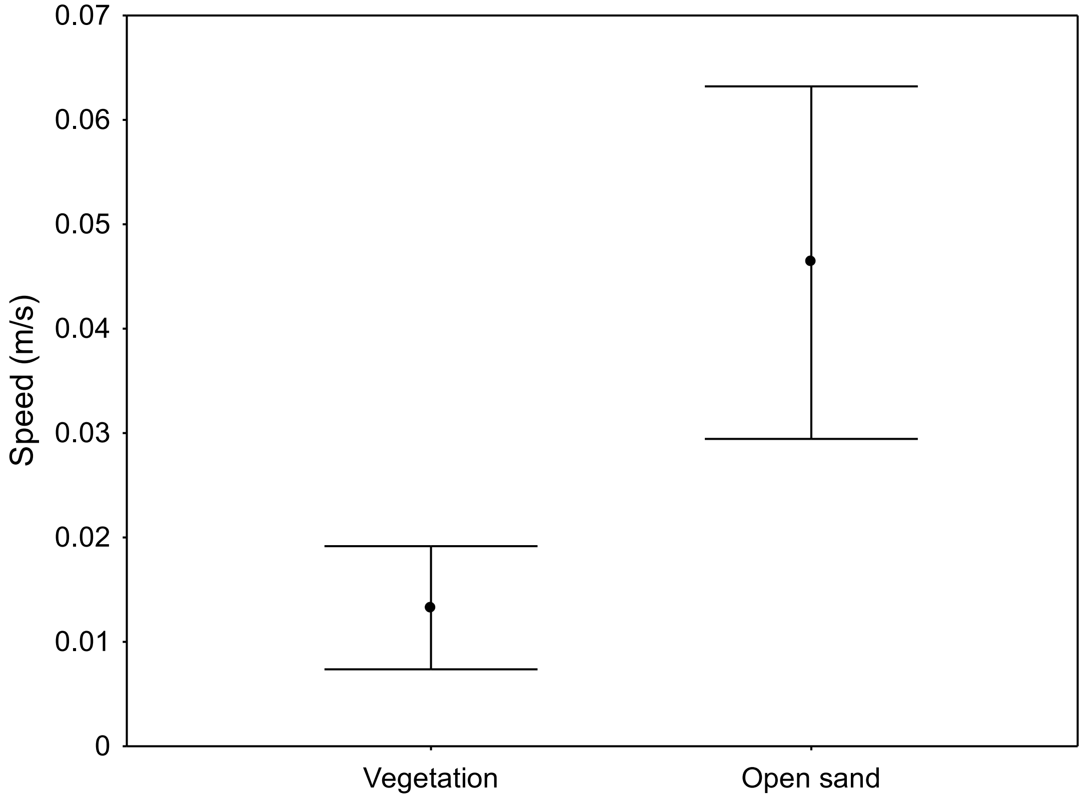


Figure 4.5. Hatchling speed (m/s) in dune vegetation and in open beach. The middle point is the mean and the whiskers indicate the Standard Error.

Chapter 5. Leatherback hatchling sea-finding in response to artificial lighting: interaction between wavelength and moonlight.

5.1Abstract

Over the last decades, growing human populations have led to the rising occupation of coastal areas over the globe causing light pollution. For this reason, it is important to assess how this impact threatens endangered wildlife. Leatherback turtles (*Dermochelys coriacea*) face many threats of anthropogenic origin including light pollution on nesting beaches. However, little is known about the specific effects. In this study we studied the effect of different light wavelengths (orange, red, blue, green, yellow and white lights) on hatchling orientation under the presence and absence of moonlight by analyzing: (i) the mean angle of orientation, (ii) crawling duration, and (iii) track patterns. Hatchling orientation towards the sea was always better under controlled conditions. In the absence of moonlight, leatherback hatchlings were phototaxically attracted to the experimental focus of light (misoriented) for the colours blue, green, yellow and white lights. Orange and red lights caused a lower misorientation than other colors, and orange lights produced the lowest disrupted orientation (disorientation). On nights when moonlight was present, hatchlings were misorientated under blue and white artificial lights. Crawling duration was low for misoriented hatchlings and high for the disoriented individuals. Our conclusion to this is that hatchlings can detect and be impacted by a wide range of the light spectrum and we recommend avoiding the presence of artificial lights on nesting beaches. Additionally, actions to control and mitigate artificial lighting are especially important during dark nights when moonlight is absent.

5.2 Introduction

Sea turtles nest on sandy beach ecosystems. These habitats are severely threatened by global climate change and anthropogenic effects (Schlacher et al. 2007). Light pollution associated with coastal development is one of the important anthropogenic alterations that can reduce the reproductive success of sea turtles (Verheijen, 1985; Witherington, 1996). Artificial illumination on nesting beaches alters both the nest site selection by females, hatchling behaviour and also has a direct impact on hatchling survival (Witherington, 1996; Kamrowski et al., 2012). After emergence, sea turtle hatchlings crawl rapidly from the nest towards the sea to avoid predation (Salmon and Wyneken, 1987; Santidrián Tomillo et al., 2010). Sea-finding seems to be mainly visual as sea turtle hatchlings are proven to be attracted to the brightest area within their field of vision and is also related to the brightness and lower elevation of the sea. Moreover, sea-finding abilities can also be affected by the presence of dark silhouettes that are cast by dunes and other objects (Mrosovsky, 1970; Salmon et al., 1992, Bartol et al., 2003; Tuxbury and Salmon, 2005; Limpus and Kamrowski, 2013) that continue to be important even after they enter the aquatic environment (Bartol et al., 2003). However, a hatchling's ability to detect these natural cues is reduced in the presence of artificial lights (Lorne and Salmon, 2007). As a result, beach lighting disrupts the orientation of hatchlings, which will eventually lead to exhaustion, dehydration, entanglement in dune vegetation, and/or an increase of the risk of predation (Salmon, 2003; Zheleva, 2012).

The effects of artificial light on hatchling disorientation (when they crawl in circuitous paths and are not able to find a cue) and misorientation (when they direct themselves to the artificial source) have been previously documented (McFarlane, 1963; Philibosian, 1976; Verheijen, 1985; Salmon and Witherington, 1995). However, the effect on the behaviour of the turtles varies among species and depends on the light's characteristics such as its intensity, wavelength, polarization and periodicity (Witherington, 1985).

Previous field experiments conducted on loggerhead (*Caretta caretta)* and green turtles (*Chelonia mydas*) show that both short and long light wavelengths at any intensity influence hatchling orientation. The effect of artificial lighting on hatchling orientation was reduced in the presence of moonlight and its effects on hatchlings varied depending on the characteristics of the luminaries (Witherington and Bjorndal, 1991a; Witherington, 1991; Witherington and Martin, 1996; Witherington and Salmon, 2005). There are differences in the behavioral response between species (Witherington and Bjorndal, 1991b). Green turtles show phototactic spectral sensibility (phototaxis or light attraction) for the wavelength of the visible light region 440-700 nm, and show signs of slight ultraviolet discrimination (Levenson et al., 2004). Loggerhead turtles show positive phototaxis (misorientation) for blue (450 nm), green (500 nm) and yellow (580 nm) colors (Young et al., 2012). Likewise, olive ridley (*Lepidochelys olivacea*) (Karnad et al., 2009), hawksbill (*Eretmochelys imbricata*) (Eckert and Horrocks, 2002) and flatback turtles (*Natator depressus*) (Pendoley, 2005; Fritsches, 2012) show preferential orientation towards low wavelengths.

The disorientation of hatchling leatherback turtles (*Dermochelys coriacea*) as a consequence of light pollution has been documented in Gabon. This important nesting site was highly contaminated by light pollution and hatchlings showed a higher attraction to artificial lights than to silhouettes (Bourgeois et al., 2009). Although leatherback turtles respond to a wide range of light wavelengths and are capable of color vision (Horch et al., 2008), no experimental studies have analyzed the effect of the presence of artificial lights of different wavelengths (colors) on the sea-finding behaviour of hatchlings under natural conditions. This type of studies is important not only because of the increasing number of artificial lights on beaches, but also because of the use of lights by tourists and observers on the nesting beaches. Given the increasing pressure of coastal development on nesting beaches and the critical situation of some leatherback populations, it is important to assess the impacts of artificial lighting on hatchling behaviour and therefore on the overall reproductive success of the species. Consequently, the aim of this study was to characterize the effects of both artificial lights (different wavelengths) and natural lights (the presence or absence of moonlight) on hatchling behaviour. Studying the impact of light sources on leatherback turtles provides the basis for understanding the effects of this growing environmental threat. This information is essential to characterize the threat and prioritise responses and mitigation strategies in sea turtle conservation efforts (Hamann et al., 2010; Wallace et al., 2011).

5.3 Methods

Study site

The study was conducted at Pacuare beach, located in the Pacuare Nature Reserve (PNR) (10°10 ′00″ N, 83°14 ′00″ W), an important leatherback nesting beach on the Caribbean coast of Costa Rica (Rivas et al., 2014). The experiment was done during the leatherback hatchling season (May through August) in 2013. Between March and May, 39 clutches laid by nesting turtles were relocated to a protected fenced hatchery. These clutches were laid on the first kilometer of the beach and were relocated due to the high risk of inundation in this area. After hatchlings emerged from the nest, seven hatchlings were randomly taken to run the experiments. Experiments with lights were conducted during the night (between 18:00h and 02:00h), immediately after hatchlings emerged from the nest. Each hatchling was immediately released from the experimental area located close to the hatchery after the experiment was completed.

Natural beach light

Experiments with light in the turtle’s natural beach conditions (in the presence and absence of moonlight) were conducted in June and July 2013. Before conducting each experiment, the level of natural sky light was measured on the beach with a portable photometer, the Sky Quality Meter (SQM) by Unihedron. This photometer measures average luminance from a relatively wide solid angle (1.5 steradian; the Half Width Half Maximum (HWHM) of the angular sensitivity is ~42°) and measurements are displayed in astronomical units of magnitude per square arcsec (mag/arcsec^2). The SQM is temperature calibrated and gives the luminance with the precision of 0.1 mag/ arcsec^2, which is equivalent to 10 percent in linear (cd/m^2) units. Sky brightness was converted to the standard luminance scale (SL) (cd/m^2) using the formula $(SL) = 10.8 \times 10^4 \times 110^{(-0.4*[mag/arcsec2])}$ (www.darkskiesawareness.org/sqm-zlpa.php) (increasing luminance values correspond to lower brightness levels). Measurements were taken by pointing the device at the horizon on the seaside at 1.0 meter above the sand, always from the same place and before each experiment was conducted. Light readings were recorded during the absence of moonlight (during the new moon, before moonrise or after moonset, and/or with total cloud cover) and presence of moonlight (any lunar phase). Considering the fact that cloud coverage amplifies sky luminance (Kyba et al., 2011), cloudy nights were defined as with or without moonlight depending on luminance recordings: absence of moonlight (more than 500 µcd/m^2) and presence of moonlight (until 500 µcd/m^2).

The anthropogenic lights from the town of Limón are visible from Pacuare (~45 km) and therefore the mean angle of Limon from the emplacement of release was recorded (angle between Limon and hatchling releasing emplacement, Fig. 1) to assess the effect of these lights on the sea-finding orientation of hatchlings.

Experiments with artificial light

The experiments were conducted ten meters away from the hatchery and ten meters away from the highest tide line. A 2-meter radius circle was drawn in the sand around the point of release. The light source was located 5 meters away from the center of the circle in the direction opposite to the sea and the light was focused towards the center of the circle (Fig. 1). The light source was fixed to a stick at 1.0 meter above the surface of the sand. Seven treatments were used, one being a control in dark conditions and six using colours of the visible spectrum: orange, red, blue, green, yellow, and white. Conventional LED headlamps were used as artificial light sources (28 - 35 lumens), as they are frequently used by conservationists on sea turtle nesting beaches (Nichia, PETZL and Nebo brands). Polycarbonate filters were used for the yellow light. Seven hatchlings from each nest were randomly assigned to one light treatment. Hatchlings were placed in the center of the circle and were allowed to crawl by themselves. Information was collected on the following parameters under two natural light conditions (presence or absence of moonlight):

(1) Orientation. Previous methodology described by Salmon and Witherington (1995) and Salmon (2003) was followed. The point where hatchlings crossed the circle perimeter was considered to define the angle of orientation. The source of light was at 270°tand the ocean at 90°n(Fig. 1).

(2) Crawling duration. The time that it took the hatchling to move from the light emplacement to leave the circle was recorded. The maximum time allowed was four minutes. After four minutes we considered the test as a “no exit”oresult.

(3) Track pattern. Two types of track patterns were defined based on the hatchling’s movements: “S” when the hatchling left the circle following a straight path regardless of the direction and “W”hwhen the hatchling left a wavy track or moved in circles.

Due to the fact that hatchlings can react to artificial lights by a) becoming disoriented (they crawl in circuitous paths and are not able to find a cue to orient themselves) or b) misoriented (they direct themselves to the artificial source; Salmon and Witherington, 1995), hatchling orientation was further classified into four groups depending on the exit point from the circle: group 1 (45° to 135°), group 2 (315° – 45°), group 3 (135° – 225°) and group 4 (225° – 315°) (Fig. 1). This classification allowed us to assess the relationship between crawling duration and disorientation/misorientation.

Statistical analysis

Multiple regression analyses and nonparametric tests were used to analyze the effects of natural beach luminance on hatchling orientation. Circular statistics were also used to determine the mean angle of orientation (a) and r-vector (r) as a measure of angular dispersion with a range of 0-1 (Zar, 1999; Lorne and Salmon, 2007). For these tests, we used Oriana version 4. Rayleigh tests were used to assess differences in hatchling orientation among light experiments and a General Linear Model was used to analyze the effects of lunar phases, color treatments, track patterns and orientation groups on crawling duration. Bonferroni Post-hoc tests were used to determine differences among groups for the significant variables, F – tests to assess differences in hatchling orientation by color treatments in presence or absence of moonlight and χ^2 – tests to test for differences between track patterns. We used Statistica Release 10 program (Stata Corp 2007) and SPSS v. 20.0 (IBM Corp 2011) to conduct statistical analyses.

5.4 Results

Hatchling orientation

There were significant differences in natural luminance between nights in which moonlight was present and absent (Mann-Whitney test, $Z = 1.96$, $p = 0.006$). The mean luminance values were 4899.5 µcd/m^2 and 443.9 µcd/m^2 in moonless and moonlit nights respectively. Light pollution from the city of Limón was also detected at Pacuare beach located at a mean angle of 30°, with respect to the 360 degrees of the diagram (Fig 1). Luminances of light treatments used were:

control (16.47 µcd/m^2), orange (8.77 µcd/m^2), red (8.45 µcd/m^2), blue (8.15 µcd/m^2), green (7.54 µcd/m^2), yellow (6.82 µcd/m^2), and white (6.18 µcd/m^2).

In the absence of moonlight, significant differences were found in hatchling orientation for most light treatments (Watson-Williams F-test, $F = 45.25, p < 0.0001$). In general terms, hatchlings in control, orange and red experiments were predominantly capable of moving towards the sea. However, hatchlings exposed to blue, green, yellow and white lights were predominantly misoriented and moved towards the experimental source of light (Fig. 2A). Although some hatchlings exposed to orange and red lights were eventually able to move towards the sea, they showed high levels of disorientation predominantly moving in the direction of the sea and the town of Limon (Table 1, Fig. 2A). On moonlit nights, hatchlings under control, orange, red, green and yellow lights were capable of finding the sea while hatchlings exposed to blue and white lights were misoriented (Fig. 2B).

There were significant differences in the mean vector of hatchling orientation between the control and each of the light treatments during moonless nights (Watson-Williams f-tests, $F = 45.2, p < 0.001$) (Table 2). On the contrary, there were only significant differences between the mean vectors of the control and blue, and control and white treatments during moonlit nights (Table 2). Rayleigh tests showed that the mean direction and the mean vector length of hatchling orientation were significantly different among all light treatments in the absence of the moonlight. With moonlight present, there were significant differences among light treatments with the exception of blue (Rayleigh test, $Z = 2.8, p = 0.054$) and white lights ($Z = 0.42, p = 0.66$) (Table 3).

Crawling duration and track pattern

The general linear model showed a significant effect of track shape on crawling duration ($F_{1,262} = 47.1, p < 0.001$), interactions between track shape and orientation group ($F_{1,262} = 5.2 , P = 0.006$) and between color treatments and track shape ($F_{1,262} = 2.3$, $P = 0.03$). The Bonferroni post-hoc analysis showed significant differences in crawling duration between groups 1 (towards the sea) and 2, and between groups 2 and 4 (towards the light treatment) ($p < 0.001$ for both). Hatchlings in groups 1 and 4 (oriented and misoriented, respectively) were the fastest at leaving the circle (mean ± SD duration: 1.33 ± 0.18 min and 1.40 ± 0.18 min respectively), compared with hatchlings in groups 2 (1.83± 0.19 min) and 3 (1.77 ± 0.34 min). The post-hoc analyses also showed significant differences in crawling duration among treatments with red and yellow lights ($p < 0.01$), and among treatments with red and white lights ($p = 0.005$). The shortest mean crawling duration occurred under yellow light (mean = 1.14 min, n = 36). Under this treatment, hatchlings were mainly misoriented.

The longest mean crawling duration occurred under red light (mean = 1.83 min, n = 41). Under the red light and without the presence of moonlight, 22% of hatchlings (n = 41) were disoriented and unable to leave the circle, or took more than 4 minutes to acquire the capacity to leave the circle. On the other hand, all hatchlings under the orange light were able to leave the circle. In this case, the percentage of hatchlings that were within orientation group 2 were 41.4% and 46.5% for red and orange lights respectively (Table 1).

On moonless nights, the frequency of track patterns was affected by light treatment ($X^2 = 51.51$; gl = 6; $p < 0.0001$, n = 234) (Fig. 3). Red and orange lights resulted in the highest number of hatchlings moving in a wavy zig-zag pattern. The frequency of wavy crawls was significantly higher under the red light (70.3%) than under the orange light (35%) ($X^2 = 9.58$; gl = 1; $p = 0.002$; n = 87). However, in the presence of moonlight, there was not a significant influence of the light treatment on track pattern although results were close to being significant ($X^2 = 12.11$; gl = 6; $p = 0.06$; n= 96).

5.5 Discussion

Hatchling orientation and interactions with natural beach lighting

Color light treatments had a negative effect on hatchling orientation but the overall effect depended on the presence or absence of moonlight. Absence of moonlight resulted in misorientation under blue, green, yellow and white light, and disorientation under orange and red lights; hatchling disorientation was greater under the red than under the orange light. Crawling duration was low for hatchlings that were oriented or misoriented, and high when hatchlings were disoriented.

Our results confirm that leatherback hatchlings are less sensitive to long wavelengths (~700 nm) near red than to shorter wavelengths such as short deep blue (~380 nm). Although some hatchlings still found the ocean on moonless nights under red and orange treatments, orientation was impaired as shown by the long crawl durations. Studies that used electroretinography confirmed that both loggerhead and leatherback turtles can see from wavelengths near to UV, showing a maximum sensitivity or phototaxis at 500 - 580 nm (blue –green) and a second peak at 380 nm near UV (Witherington and Bjorndal, 1991; Constantino and Salmon, 2003; Levenson et al., 2004; Horch et al., 2008). Most studies on the spectral sensitivity of sea turtles have been conducted on loggerhead and green turtles in the laboratory. Although the capacity for color vision in leatherback turtles had also been previously described, there was little information on ranges of discrimination and behavioral responses to different wavelengths in natural conditions. Leatherback hatchling spectral sensibility seems to be similar to that of loggerhead hatchlings (Witherington and Bjorndal, 1991; Levenson et al., 2004; Horch et al., 2008) and other sea turtle species (Eckert and Horrocks, 2002; Pendoley, 2005; Karnad et al., 2009; Fritsches, 2012). However, behavioral responses to the same wavelengths can differ among populations of a single species. For example, loggerhead hatchlings show an orientation aversion to yellow light in the US (Witherington and Bjorndal, 1991a,b), but not in Australia (Fritsches, 2012). Therefore, light sensitivity could also differ among hatchlings from different populations in other sea turtle species.

Although leatherback turtle hatchlings are less sensitive to the longest wavelengths of the human visual spectrum (Horch et al., 2008), hatchling orientation was still affected by red light stimuli during sea-finding orientation, increasing crawling times and increasing the frequency of circling movements in comparison to the control. Additionally, there was less-frequent circling and a higher percentage of hatchlings left the circle under the orange light than under the red light experiment (Fig. 3A). Orientation circles are more commonly displayed while crawling to the ocean in leatherback hatchlings than in other species (Mrosovsky and Shettleworth, 1975). We found that the frequency of circling was also affected by the colour of the light source and among hatchlings that were capable of orienting, frequency of circling was the lowest under control, followed by orange and then by the red treatment. The orange light source emitted the lowest luminance value among colors tested. Hatchling disorientation under the red light could also result from higher brightness of this source in comparison to the orange one.

Previous studies have shown that variances in the natural beach light due to solar and lunar positions significantly influence hatchling orientation. Seaward orientation depends on phototaxic reactions to light and visual assessments of the brightness of the horizon (Mrosovsky, 1972; Witherington, 1992; Limpus and Kamrowski, 2013). The shape and/or elevation of natural cues (i.e. high silhouettes) and the slope of dunes and vegetation can provide additional cues on hatchling orientation towards the sea (Mrosovsky, 1972; Salmon et al., 1992). Interactions between natural cues and artificial lighting such as the presence of high silhouettes and moonlight can also affect the orientation of hatchling sea turtles (Tuxbury and Salmon, 2005). Our results show that there is an interaction between the moonlight's presence/absence and the effects that artificial lighting has on hatchling behaviour. On moonless nights, all light treatments had a negative effect on hatchling orientation, which was stronger in the treatments that resulted in misorientation (blue, green, yellow and white lights) than in those causing disorientation (orange and red lights). Some hatchlings could still find the direction of the water under orange and red light treatments. With moonlight, misorientation was only observed among hatchlings exposed to blue and white lights. Overall, our results confirmed those by Salmon and Witherington (1995), who suggested that natural beach light plays an important role on the effects of artificial lighting in the sea-finding mechanisms used by hatchlings. Finally, it must be noted that the small headlamps that are frequently used by conservationists and tourists on the beach were used as light sources in this study. Therefore, it could be plausible that exposure to more intense lights, such as those of buildings, can likely cause a stronger effect on hatchlings.

Conservation and management implications

Artificial lighting constitutes an important anthropogenic impact that has been threatening sea turtle populations on their nesting beaches around the world for decades (Carr and Ogren, 1960; McFarlane, 1963; Kamrowsky et al., 2012). In the Caribbean region, artificial lightning can reduce reproductive success in sea turtle populations, and accelerate their extinction, which can be associated with economic impacts (Brei et al., 2014). Therefore, keeping nesting beaches in dark conditions is the best and most highly recommended management strategy. On the nesting beaches, red lights are sometimes used for beach monitoring because white light was proved to produce phototaxis and disrupted orientation (Carr and Ogren, 1960; Mrosovsky and Shettleworth, 1975; Mrosovsky and Carr, 1967). In this study, the orange light yielded better results than those of the red treatment, but the most suitable conditions for hatchling orientation were under the control treatment where no artificial lights were applied. As mentioned above, coastal artificial lighting or photo-pollution is a grave threat to sea turtles especially as anthropogenic settlements are increasing along coastal areas around the globe and are determined by economic activity (Bourgeois et al., 2007; Gallaway et al., 2010; Kamrowski et al., 2014). These impacts disrupt behavioral responses in many organisms and affect their reproductive success (Kyba et al., 2011; Kamrowski et al., 2012; Brei et al., 2014). If this increasing trend of artificial lighting continues, future coastal biodiversity may be compromised (Brei et al., 2014). There was an influence of light pollution from the town of Limón on hatchling orientation at Pacuare, even though the town was relatively far from the beach (~45 km). There were more disoriented hatchlings in orientation group 2 (Limón would be located at 30° between groups 1 and 2) than in orientation group 3 (away from Limón) that had very few hatchlings. The presence and location of towns should be considered in management plans since lights from nearby towns can also affect the orientation of sea turtle hatchlings. The use of orange/red lights in unprotected areas of influence (i.e. on roads or nearby towns that are visible from the beach) is recommended when darkness is not possible. However, management strategies on the nesting beaches should prioritize dark conditions over any type of light.

In addition to the management efforts that focus on the control of light sources at many sites, other measures such as the restoration or reinforcement of natural cues could also improve the sea-finding of hatchling sea turtles (Witherington et al., 1992; Tuxbury and Salmon, 2005; Bourgeois et al., 2009). Keeping the beaches dark is essential. However, unprotected beaches often suffer the effects of lights. In these cases, we also recommend the use and reinforcement of natural vegetation fences to minimize the effects of light emissions from nearby coastal settlements on unprotected nesting beaches.

Table 5.1. Number and percentage of leatherback hatchlings that did not leave the circle or took longer than four minutes ("no exit"), left the circle in orientation group 1 (45° to 135°), group 2 (315° – 45°), group 3 (135° – 225°) or group 4 (225° – 315°) under each light treatment in absence of moonlight (see Fig. 1 for a diagram of location groups).

Treatments	no exit		Group 1		Group 2		Group 3		Group 4	
	N	(%)	N	(%)	n	(%)	N	(%)	N	(%)
Control	2	5.9	22	64.7	10	29.4	0	0	0	0
Yellow	0	0	1	4.2	4	16.6	0	0	19	79.2
Red	9	22	9	22	17	41.4	2	4.9	4	9.7
Orange	0	0	14	32.6	20	46.5	1	2.3	8	18.6
Green	2	5.7	4	11.4	3	8.6	0	0	26	74.3
Blue	0	0	4	11.1	1	2.8	0	0	31	86.1
White	0	0	2	5.3	0	0	1	2.6	35	92.1

Table 5.2. Summary of statistical results from the Watson-Williams F- tests. The Multi-sample test used comparisons of the mean vector of hatchling orientation between every light color and the control in absence or presence of moonlight. *Mean vector for the experimental group.

Variables	N		F		P		Df	df2		Mean*	
	Absence	presence	absence	presence	absence	presence	abs/pres	absence	presence	absence	presence
Control & Yellow	(32 & 24)	(17 & 10)	139.8	0.18	<0.001	0.67	1	54	25	22.03	73.52
Control & Red	(32 & 31)	(17 & 10)	10.71	0.04	0.002	0.84	1	61	25	46.01	72.03
Control & Orange	(32 & 43)	(17 & 10)	20.04	0.34	<0.001	0.56	1	73	24	37.08	67.23
Control & Green	(32 & 33)	(17 & 10)	156.4	0.31	< 0.001	0.58	1	63	25	06.55	74.42
Control & Blue	(32 & 36)	(17 & 10)	200.0	33.02	< 0.001	< 0.001	1	66	25	354.7	52.81
Control & White	(32 & 38)	(17 & 10)	324.2	11.08	<0.001	0.003	1	68	25	330.9	71.48

Table 5.3. Summary of results from the Rayleigh (Z) tests that discriminated whether hatchlings orientated on the beach randomly or showed attraction or rejection to specific stimulus of light source. Tests were conducted in presence or absence of moonlight.

Color Source	Control		Yellow		Red		Orange		Green		Blue		White	
	absence	presence	absence	Presence	Absence	presence	absence	presence	absence	presence	absence	presence	absence	presence
Rayleigh (Z)	24.23	10.12	13.03	6.19	8.91	8.49	10.84	2.89	16.47	5.19	19.23	2.84	26.76	0.42
Rayleigh (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	<0.001	0.05	<0.001	0.003	<0.001	0.054	<0.001	0.666

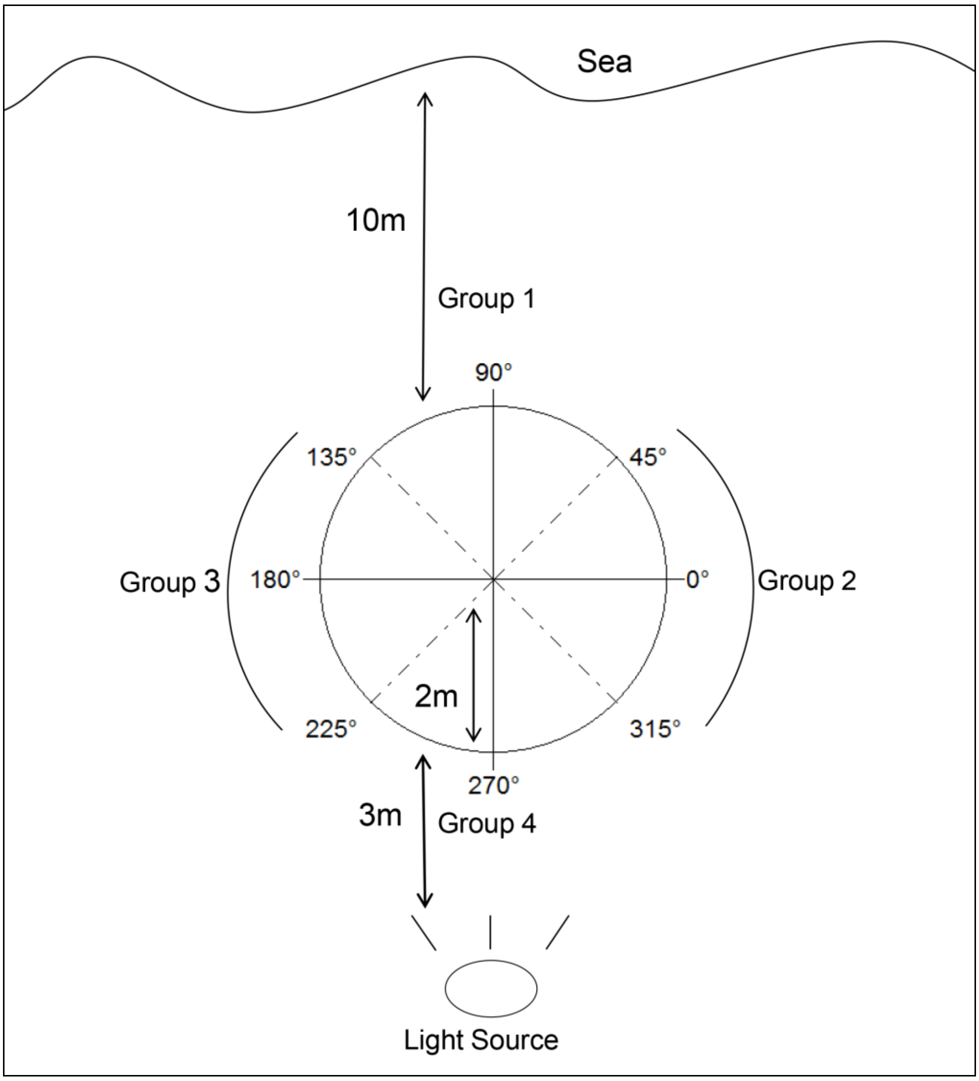
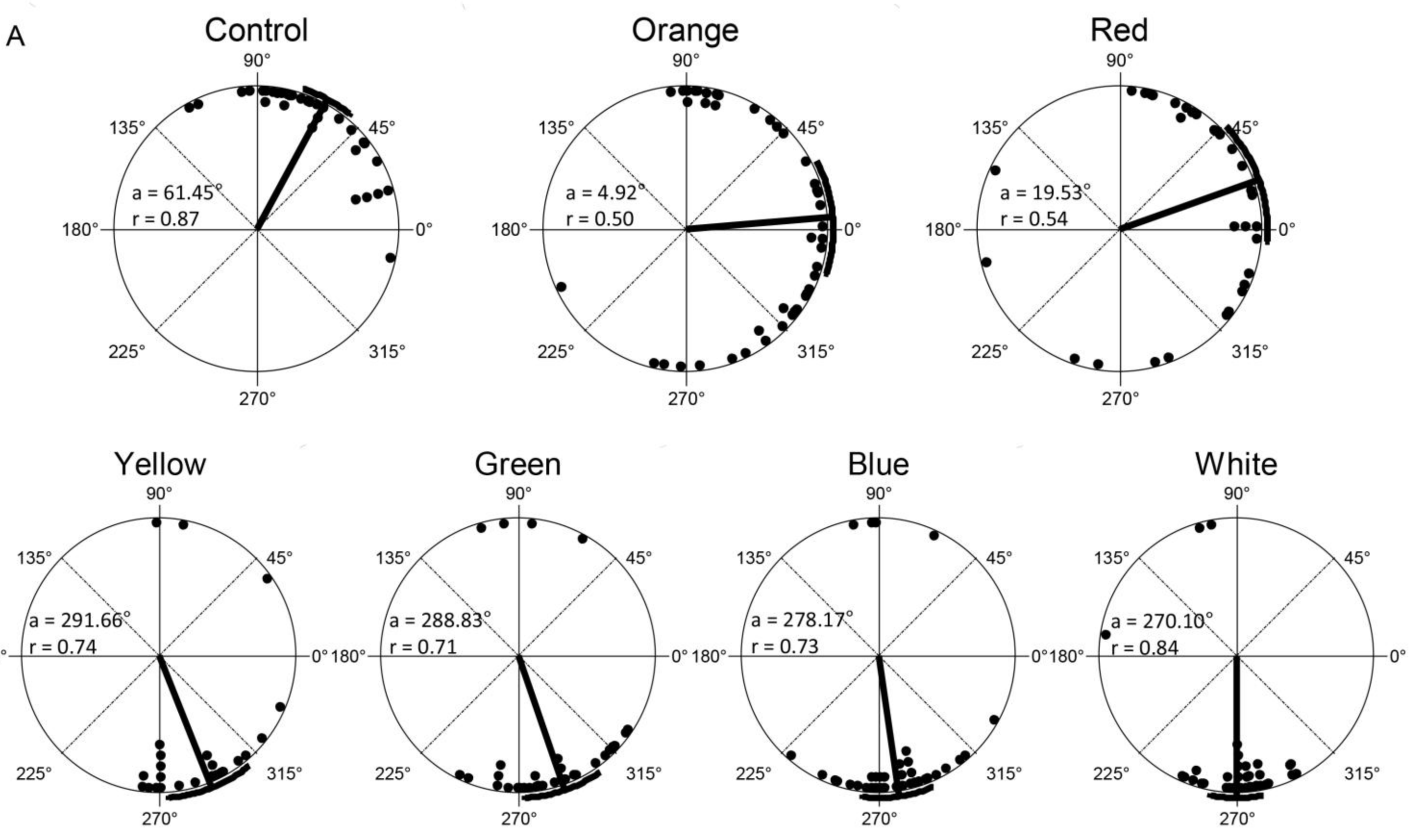


Figure 5.1. Diagram of the experiment conducted on leatherback turtle hatchlings to test their orientation under different light treatments at Pacuare, Costa Rica. The light was fixed to a stick 1 meter above the sand directed toward the sea and perpendicular to the beach. A 2-meter radius circle was drawn in the sand 5 meters away from the visual stimulus. Light source was directed to the center of the circle. Hatchlings were classified based on the point of exit from the circle in orientation group 1 (45° to 135°), group 2 (315° (345°), group 3 (135° , 225°) or group 4 (225° o315°).


A
Control
90°
135°
45°
a = 61.45°
r = 0.87
180°
0°
225°
315°
270°
Orange
90°
135°
45°
a = 4.92°
r = 0.50
180°
0°
225°
315°
270°
Red
90°
135°
45°
a = 19.53°
r = 0.54
180°
0°
225°
315°
270°
Yellow
90°
135°
45°
a = 291.66°
r = 0.74
180°
0°
225°
315°
270°
Green
90°
135°
45°
a = 288.83°
r = 0.71
180°
0°
225°
315°
270°
Blue
90°
135°
45°
a = 278.17°
r = 0.73
180°
0°
225°
315°
270°
White
90°
135°
45°
a = 270.10°
r = 0.84
180°
0°
225°
315°
270°

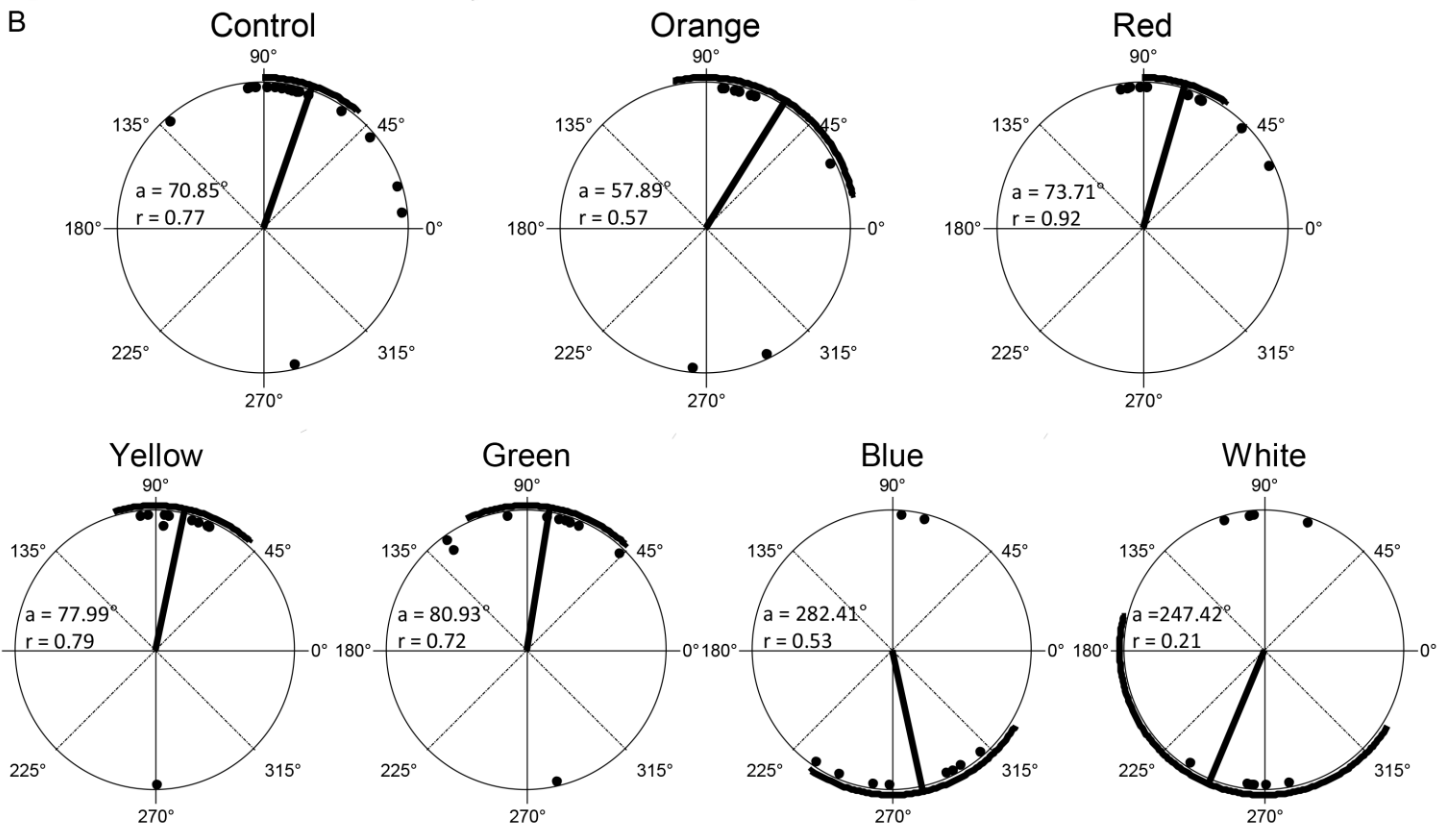


Figure 5.2. Mean angle of orientation of hatchling leatherback turtles in response to light treatments in (A) absence of moonlight and (B) presence of moonlight. Black points represent hatchling position at leaving the circle. Black lines are mean vector and the outer circular black line represents circular variance.

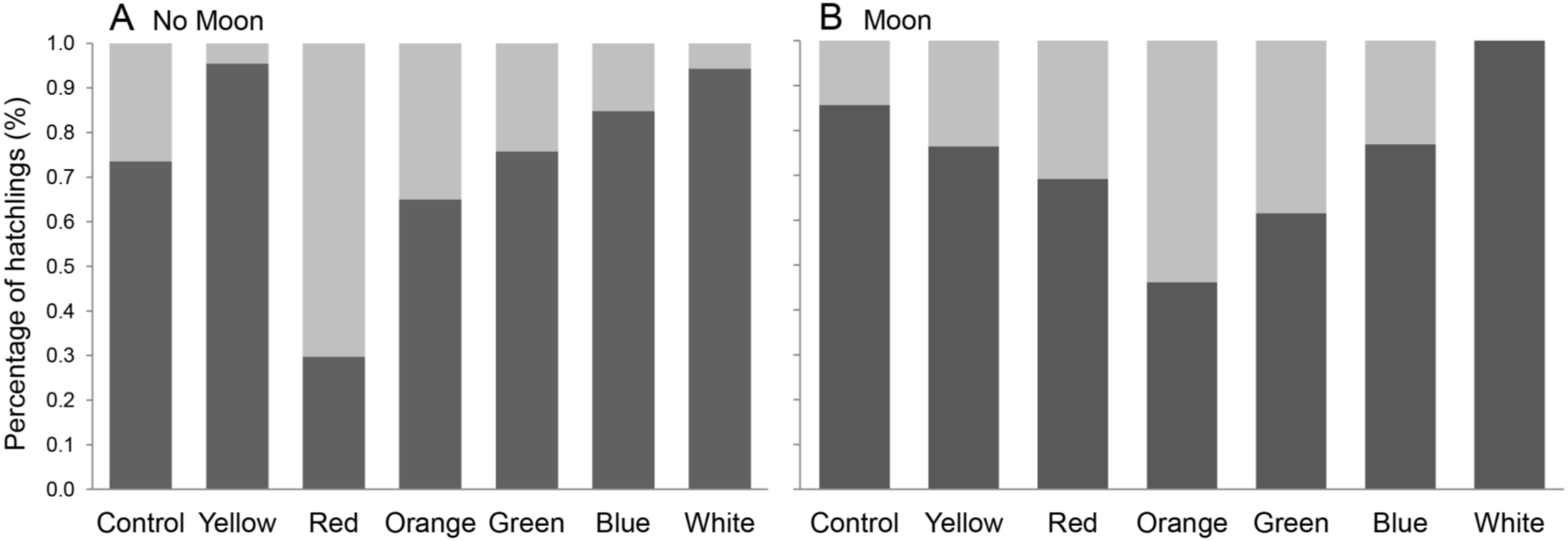


Figure 5.3. Percentage of hatchlings in each treatment that were classified as leaving straight tracks (in grey), or wavy tracks (in light grey) after leaving the circle (A) in absence of moonlight or (B) in presence of moonlight. Only hatchlings that succeeded in leaving the circle during treatments were included.

Capítulo 6. Conclusiones generales

1 La tendencia poblacional de la playa de la Reserva Natural Pacuare se mantiene estable o se incrementa ligeramente gracias a programas de conservación a largo plazo, además, dicha playa alberga la mayor densidad de nidos por km^2 de Costa Rica: lo que hace que sea la playa más importante de este país y probablemente una de las de mayor densidad de nidos de Centroamérica.

2 El monitoreo a largo plazo llevado a cabo durante 18 años ha permitido obtener importantes parámetros biológicos sobre la especie. De entro ellos, es destacable mencionar que: A) el rango de crecimiento anual tras el primer episodio reproductivo es muy bajo (0.3 cm/año), B) a mayor tamaño de hembras mayor es el tamaño de las puestas.

3 La erosión de la arena y la formación de bermas en las playas de nidificación debido a procesos derivados del cambio climático afectan el comportamiento de las hembras al nidificar, incrementando el número de nidos abortados y la localización de un número significativo de puestas en zonas inundables o potencialmente inundables.

4 La presencia de especies de vegetación de duna como *Ipomoea pes-caprae* incrementa el tiempo de exposición de los neonatos en su recorrido al

mar, disminuyendo su velocidad media y afectando su habilidad de orientación hacia el mar.

5 El número de nidos tanto *in situ* como reubicados localizados en zonas cercanas a la vegetación secundaria, donde existe una mayor exposición a especies vegetales de duna, ha incrementado a lo largo de los últimos años.

6 Los neonatos de tortuga laúd presentan foto-atracción para todo el rango de longitudes de onda del espectro de luz visible, con una menor atracción en condiciones con luz de luna. Los colores que menos foto-atrae a los neonatos son el rojo y naranja, siendo el naranja la que menos les desorienta en su recorrido al mar.

7 Si tenemos en cuenta las amenazas abióticas inmediatas derivadas del cambio climático a las que se enfrentan las playas de nidificación, como son: la erosión por el aumento del nivel del mar y la frecuencia en las tormentas; y si además consideramos, los modelos climáticos predictivos que prevén en las próximas décadas un aumento significativo de la temperatura global y de episodios de precipitación (IPCC, 2013), estudios como los desarrollados a largo de esta tesis son esenciales para comprender mejor las amenazas a las que se enfrenta esta especie. Por lo cual, se proponen las siguientes recomendaciones que contribuyan a programas de manejo y conservación.

1. Programas continuos de monitoreo a largo plazo contribuyen a mantener tendencias poblacionales estables y obtener datos biológicos esenciales para obtener información científica esencial sobre la biología de la especie.
2. La ausencia de diferencias significativas en los porcentajes de eclosión entre nidos relocalizados e *in situ*, hace que los programas basados en reubicación sigan siendo de gran importancia para la supervivencia de poblaciones con alto riesgo de pérdida de hábitat: ya sea por factores bióticos como abióticos.
3. Las medidas de reubicación de nidos como estrategias de manejo frente a pérdida de hábitat deberían priorizar el uso de zonas estables similares a las zonas originales de puesta, con localización dispersa a lo largo de la playa de nidificación. Recomendamos que siempre que sea posible se dejen el mayor número de nidos *in situ*.
4. Evaluaciones previas sobre las características del micro hábitat son indispensables para identificar zonas óptimas para la reubicación de los nidos en las playa de nidificación y así, evitar el efecto de factores bióticos como: la presencia de vegetación o abióticos como: sesgos en la razón de sexos, la erosión, aumento del nivel del mar, la precipitación y/o altos niveles de freático.

5. Estudios a largo plazo sobre la dinámica erosiva de la playa puede permitir elaborar un perfil orográfico que permita identificar zonas con mayores procesos erosivos que otras y zonas óptimas de reubicación para evitar mortalidad de nidos por inundación o erosión.

6. Recomendamos evitar el uso de fuentes de luz en playas de nidificación, ya que elimina los efectos de desorientación en los neonatos o atracción hacia las fuentes de luz; la luz naranja de baja intensidad debería ser usada cuando sea indispensable. Además, se debería restringir el uso de luces a noches con alta luminosidad natural.

Futuras líneas de investigación

1. Es esencial obtener información científica de datos biotérmicos en nidos *in situ* y reubicados y estimar cuál es la sex ratio actual en el mayor número posible de playas de nidificación de la tortuga laúd tanto a nivel local como regional para comprender mejor la biología reproductiva de esta especie, y determinar cuáles son las previsiones productivas para dichas poblaciones en un futuro.

2. Es fundamental identificar estrategias que permitan proponer medidas más activas de mitigación para el manejo en playa de las poblaciones de tortuga

laúd (Hawkes et al., 2009), mediante el uso de técnicas *ex situ* como son el uso de viveros y de incubadoras con temperaturas de incubación controladas.

3. Si el sesgo observado hacia hembras es general, en la mayoría de playas de nidificación, no solo a nivel local, se podría estar generando un mono sexuado que podría colapsar las poblaciones en el futuro. Estimar sex ratios en el mayor número de playas aportaría información esencial para identificar zonas prioritarias de producción de machos.

4. Estudiar los mecanismos desarrollados por las hembras nidificantes en la selección de zonas de puesta e identificar patrones individuales de nidificación puede permitir establecer medidas de manejo más eficientes para programas de reubicación de nidos.

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