

# **Factors Affecting Population Dynamics of Eastern Pacific Leatherback Turtles (*Dermochelys coriacea*)**

A Thesis

Submitted to the Faculty

of

Drexel University

by

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in partial fulfillment of the

requirements for the degree

of

Doctor of Philosophy

October 2007

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## **DEDICATION**

To those who stopped taking eggs, those who made a Park, and those who fight for its  
survival.

## ACKNOWLEDGMENTS

First of all, I want to thank the Leatherback Trust and its people in Costa Rica for showing me the real face of conservation. I cannot think of a better place than Las Baulas to learn first hand the struggles of The Fight. I feel privileged to have met and worked closely with Mario Boza, Clara Padilla and Rotney Piedra. Their passion, loyalty, honesty and dedication to conservation are truly inspiring. Rotney has been a friend and colleague over the years and a role model. I am also grateful to Elyzabeth Vélez with whom I shared many professional and personal conversations during my time at Playa Grande. Ely housed me when I had to travel to San José, introduced me to her family and always treated me as a friend. I also learned from the dedication of the special group of Park Rangers: Chico, Adémar, Memo, Carlos Díaz, Alvarito and Bernal, and the cooperation with the local guides: Doña Queta, Zulma, Laura, and Óscar. We all spent many hours together on the beach and I cannot think of better people with whom to share the long hours of waiting. To all of them, I owe a sincere thank you for making me feel part of the team.

I am also indebted to Yanira Vargas and Quique Chacón, their sons Carlos and Eric, Araceli, Danilo and Mosca. Their restaurant is more than a place to eat, and I found a family within its people. I have been lucky to share Playa Grande with all the PIs that have gone through the project while I was there: Walter Bien, Bob George, Paul Sotherland, and especially, Richard Reina. Richard was the person that brought me to Playa Grande, something for which I will always be indebted. He taught me the importance of good field organization and accurate data collection and I learned from his

strong leadership. Lesley Stokes was also inspiring for her dedication and passion and the project could not have had a better field manager than her. I also thank Judy Zabriski for teaching me the importance of education at the local schools. To my friends, colleagues and “brothers”: Eddy Price, Bryan Wallace and Vince Saba, I am proud of having shared so many experiences with them through the years, and having grown and changed together working on the project. I also thank field assistants of all teams I’ve been part of, for sharing good times at Playa Grande, and especially I thank Annette for her help in the field, her constant support since I came to Drexel, and because she really gets what Playa Grande is about. I thank the countless Earthwatch volunteers who reminded me how special working with leatherbacks is. I also thank all the people that helped in the data collection for my project, Patricia Clune, Cassandra Williams, Kim Magrini, Gabi Blanco and especially Jack Suss.

I am again indebted to Bryan for talking me into coming to Drexel and setting up the meeting with Jim, as well as Frank whose advice to me on professional matters has never been wrong. I thank my committee members, Dr. Susan Kilham, Dr. Michael O’Connor and Dr. Harold Avery for all their advice on improvements I have needed to make, and from Hal I have also learned all I know about freshwater turtles.

I will always be grateful to my co-advisor, boss, friend and “godfather” Frank Paladino for taking time to answer my questions in the early days, for being entertaining and for putting his trust in me. I have learned from Frank how to deal with difficult situations, I’ve learned his tricks, and I have learned from him why the project must come first.

I thank my main advisor Jim Spotila for countless things: for admitting me in the program without knowing me very well, for asking for my opinions, for advising and directing my work, for listening, for being supportive, for exposing me to big people in conservation, for making me think as a scientist and for being the mastermind behind the scene. Jim and Frank gave me the opportunity to work and study leatherbacks at the best possible place and I will always be indebted to them.

I also thank all the other students from the Ecology lab that I have met since I came to Drexel especially Gabi, Lucio and Eugenia because their friendship to me is like that I find at home. I also thank Shaya for many hours of practicing talks at the symposium and Kim for the good times at the office. I especially thank Gabi for putting up with me in the last stages of my writing, for keeping me sane and because I can't believe she still talks to me.

Finally, I'm indebted to many people at home that would make this list too long... I thank my other family, the Adánez, for always treating me as one of their own, especially to Esther, for being by my side since we were two, no words needed, and Patricia, because she was the biologist I wanted to become. Thanks to my parents for their support, sisters Ana and Laura for the special bond, Diego and Neil, my great-aunt Dora for taking care of three generations of the family and still counting... and finally to my niece Paula, because two of the most important things in my life started at the same time, my work with sea turtles and Paula.

Earthwatch Institute, The L.D. Betz Chair of Environmental Science at Drexel and The Leatherback Trust provided funding for this research. A special thanks to Thomas Elzey for his interest and support of my project.

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**ABSTRACT**

Factors Affecting Population Dynamics of Eastern Pacific  
Leatherback Turtles (*Dermochelys coriacea*)

Maria del Pilar Santidrián Tomillo

James R. Spotila, Supervisor, Ph.D.

The leatherback turtle (*Dermochelys coriacea*) is critically endangered. The population of leatherbacks that nest at Parque Nacional Marino Las Baulas, in Costa Rica declined by 95% in less than 20 years. Annual mortality rate of adults was higher than expected in a natural population and mortality rates of juveniles could double those of a stable population. Conservation efforts since the Park was established in 1991 resulted in higher production of hatchlings per egg laid. However, the overall hatchling output decreased because of the decreasing number of nesting turtles. Simulations on the effect of egg poaching showed that poaching was the most important cause of population decline at Las Baulas. Heavy poaching resulted in a stepwise decline in number of nesting turtles due to consecutive reductions in each nesting stage. The nesting population declined faster and was extirpated sooner with 90% egg poaching than with 20% adult mortality. However, both protection in the ocean from fishing and on the beach are critical to the survival of the population. Behavior of hatchling leatherback turtles on the walk to the water was driven by predation risk. Hatchling leatherback turtles decreased predation risk emerging in groups and dispersing. Straightness of tracks increased during the process of departure and was lower in areas of higher exposure to light pollution. Nest success of leatherback turtles was driven by environmental variability. High temperatures in the nest reduced its success, and high rainfall and low ambient temperatures resulted in higher production of hatchlings. Predicted emergence

success was related to El Niño Southern Oscillation (ENSO). Leatherback female turtles increased reproductive success over time by increasing number of eggs, number of clutches and arriving earlier in the season, when hatchling production was greater.

In conclusion, the population decline at Las Baulas was mainly caused by egg poaching but is still threatened by high mortality in the ocean. Conservation efforts have been efficient at increasing hatchling production. However, the stochastic nature of nest success and consequently, recruitment rate, may increase the risk of extinction of a population already reduced from past poaching and fisheries.

## CHAPTER 1: General Introduction

Leatherback turtles (*Dermochelys coriacea*) are the only existent species of the family *Dermochelidae*. They are characterized by unique features that distinguish them from other sea turtle species (Pritchard 1997). They have larger body size, dive deeper and longer than any other sea turtle (Hays et al. 2004), their carapace structure is formed by many small bones covered by a thick skin layer (Pritchard 1997), they can maintain body temperature above water temperature, which allows them to distribute to higher latitudes (Paladino et al. 1990) and they exhibit the largest reproductive investment among reptiles (Wallace et al. 2007).

Leatherback turtles are critically endangered worldwide (Hilton-Taylor 2000). However, their status varies among populations. The largest nesting populations are currently in French Guiana, Surinam and Gabon, all located in the Atlantic Ocean. Other large populations are in Andaman and Nicobar Islands, in the Indian Ocean, and Irian Jaya in the Western Pacific (Spotila 2004). Whereas the Atlantic populations seem to be stable or increasing, other populations have collapsed or are declining. For example, the population of leatherback turtles that nested in Terengganu, Malaysia was the largest population in the world until the 1970s-1980s. However, the population collapsed and was extirpated by the mid-1990s (Chan & Liew 1996). Similarly, populations in the Eastern Pacific Ocean have declined rapidly, especially in Mexico, which was also one of the largest leatherback populations in the world (Pritchard 1982, Sarti et al. 2007). One of the best documented declines in number of nesting turtles is that of the leatherback turtles that nest at Parque Nacional Marino Las Baulas (PNMB) in Costa Rica, where the

number of nesting turtles per season was reduced by 95% from the late 1980s to the late 1990s (Spotila et al. 2000).

There is some debate about the factors causing the differential trends in populations of leatherback turtles, and especially between those in the Atlantic and Pacific. Leatherbacks in the Atlantic exhibit higher reproductive output per season than Pacific ones (Boulon et al. 1996, Reina et al. 2002), productivity in the Atlantic is more stable than in the Pacific (Saba 2007), and Atlantic leatherbacks have typically shorter remigration intervals and overall higher production (Wallace et al. 2006). Incidental fishing is assumed to constitute the main threat to leatherback populations worldwide. Fishing efforts in the Atlantic are lower than in the Pacific Ocean. However, catching rates are higher in the Atlantic (Lewison et al. 2004b). The second cause suggested to have affected population declines of leatherbacks worldwide was egg poaching. Heavy poaching of eggs took place in Malaysia during many years, as well as in Mexico and Costa Rica. An additional threat to the survival of populations of leatherback turtles comes from the stochastic nature of some of their reproductive parameters. For example, the prolonged remigration interval under unfavorable conditions (Saba et al. 2007) can ultimately lower the lifetime reproductive output of leatherbacks and, therefore, increase risk of extinction.

The population of leatherback turtles that nest at PNMB was discovered by local inhabitants around the 1950s. However, it was not monitored until the late 1980s. The large number of nesting turtles and the ongoing poaching of eggs, forced the protection of the nesting beaches, and a National Park was established in 1991 (Spotila & Paladino, 2004). Poaching was eradicated shortly after, at the same time that the number of nesting



turtles started to decline (Spotila et al. 1996, Spotila et al. 2000). First population studies showed a low reproductive production, compared to Atlantic leatherbacks with an average of 60-65 eggs per clutch, 7 clutches in a season and average remigration interval of 3.7 years (Steyermark et al. 1996, Reina et al. 2002). Additionally, Saba et al. (2007) recently found the remigration probability between nesting seasons to depend on environmental variability associated with El Niño Southern Oscillation (ENSO). As a result of low productivity (El Niño), the probability of remigration is lower and fewer turtles migrate to nest at PNMB.

The general objective of my thesis is to analyze some of the factors, natural and anthropogenic, that affect population dynamics of leatherbacks at PNMB, especially to highlight the importance of different life stages to the population. In chapter 2, I reassess the population status and analyze the effects of conservation efforts at PNMB in the production of hatchlings and, therefore, in the recruitment to the nesting population. I estimate mortality rates of adults and approximate mortality of juveniles and sub-adults in the ocean. In chapter 3, I simulate the effect of high levels of poaching (90%) on the population and mortality rates of adults due to fishing (20%), to recreate the conditions that pressured the population at PNMB. I compare the effect of different levels of egg poaching on the population, the effect of fishing, the effect of stopping poaching at different times and the effect of relocating eggs under different scenarios. In chapter 4, I describe the process of departure of hatchlings from the beach and its significance to reduce predation risk on the walk to the water. Finally, in chapter 5, I analyze the effects of environmental variability on nest success. Particularly, I look at the effects of incubation temperature, local and global weather on emergence success of leatherback

nests and ultimately, the contribution of nest success to the reproductive success of leatherback turtles. In general, I analyze in this thesis the impact of past and present pressures on the population of leatherback turtles that nest at PNMB, by studying some of the factors that affect their population dynamics and the implications for their survival.

**CHAPTER 2: Reassessment of the leatherback turtle (*Dermochelys coriacea*) population nesting at Parque Nacional Marino Las Baulas, Costa Rica: effects of conservation efforts**

**ABSTRACT**

The number of leatherback turtles (*Dermochelys coriacea*) nesting at Parque Marino Las Baulas declined precipitously in the 15 years that we monitored the population (1988-1989 – 2003-2004). We estimated that the annual survival rate of adults was 0.78 (95% CI: 0.75-0.80) and that mortality rates for juveniles and subadults in the ocean appeared to be double those of a stable population. The proportion of hatchlings produced from eggs laid increased since the Park was established as a result of conservation practices. Since the number of nesting females decreased, the overall production of hatchlings per season declined, but was much greater than would be expected without protection efforts. There were similar numbers of hatchlings leaving the beaches of Las Baulas in 1998-2003 with 68 to 188 nesting females under the current conservation regime as there were in 1988-1989 with 1500 nesting females and no Park. Female leatherback turtles that nest at Las Baulas have a high level of exchange between nesting beaches, thus, protection of both Playa Grande/Ventanas and Playa Langosta is critical for the survival of the population. Despite current protection efforts the population at Las Baulas is still threatened by mortality at sea and development on and behind the nesting beaches.

## INTRODUCTION

The status of leatherback turtle (*Dermochelys coriacea*) populations inferred from nesting ecology studies worldwide has led to the classification of the species as critically endangered (Hilton-Taylor 2000). Longline fisheries have had a great impact on leatherback turtles and are implicated in the decline of their populations (Lewison et al. 2004b). Leatherback nesting numbers on Playa Grande, Costa Rica, declined precipitously in the 1990s. The decline of the population was related to both adult mortality and high levels of poaching in past years (Spotila et al. 1996). However, in spite of the alarming reduction in numbers of nesting females on Playa Grande, the population is still the most important in the Eastern Pacific Ocean (Spotila et al. 2000).

Playa Grande is the primary nesting beach inside Parque Nacional Marino Las Baulas (Steyermark et al. 1996) with two other beaches hosting an important number of turtles. Playa Langosta supported 10 to 15% of the nesting population in the early 1990s (Chaves et al. 1996) and Playa Ventanas also received some nesting. Part of the existing National Park was initially established as the Tamarindo Wildlife Refuge in the late 1980s (including Playa Grande and the estuary of Tamarindo). The protected area was enlarged to include all three nesting beaches and associated estuaries and converted into a National Marine Park by Presidential Decree in 1991 (Spotila and Paladino 2004). The increased protection greatly reduced the poaching of eggs (Steyermark et al. 1996). In 1995 the Park was enlarged again and permanently established by law guaranteeing the protection of all three nesting beaches. Efforts continue to consolidate the Park and protect the beaches and their nesting turtles. For a history of the Park see Spotila and Paladino (2004).

To date, leatherback turtles that nest at different beaches within Las Baulas National Park have been studied independently. Females that nest on Playa Grande and Playa Ventanas have been studied for 15 years. Steyermark et al. (1996) and Reina et al. (2002) described population parameters such as mortality rates, remigration intervals, clutch frequency, clutch sizes, and average female sizes. Meanwhile, Spotila et al. (2000) identified a severe population decline on Playa Grande and Playa Ventanas that threatened the population with extirpation. In a related but independent study Chaves et al. (1996) investigated leatherback nesting at Playa Langosta in 1991-1992 describing female sizes, clutch sizes, and numbers of nesting females. In 1997-1998 E. Vélez and R. Piedra started a project on Playa Langosta that is ongoing to the present. Both Steyermark et al. (1996) and Chaves et al. (1996) found some exchange of nesting leatherbacks between Playa Grande and Playa Langosta. However, saturation tagging and beach patrols were not started until 1997-1998 on Playa Langosta and, therefore, observations of turtles that exchanged nesting beaches were accidental. By combining the data from all three beaches it is now possible to reassess the leatherback nesting population at Las Baulas.

We describe here, for the first time, the nesting population of Parque Nacional Marino Las Baulas as a whole and analyze the use of the nesting beaches within the Park by nesting females within and between seasons. In addition, we evaluate the effects of conservation efforts over the last 15 years on hatchling production and the nesting population of leatherback turtles at Las Baulas.

## METHODS

Parque Nacional Marino Las Baulas is located on the Pacific Coast of Costa Rica in Guanacaste Province. It includes three nesting beaches arranged North to South: Playa Grande (3.6 km), Playa Ventanas (1.0 km) and Playa Langosta (1.3 km). Playa Grande is separated at its south end from Playa Langosta by the Tamarindo Estuary, the town of Tamarindo and the San Francisco Estuary (Fig. 1).

Body pit (depression left by nesting females) counts started on Playas Grande and Ventanas in 1988-1989 and marking of individual female leatherbacks with the use of PIT (passive integrated transponder) tags (Dutton and McDonald, 1994) began in 1993-1994 (Steyermark et al. 1996). In 1997 we began putting PIT tags in both shoulders. From 1997-1998 to 2003-2004 we identified 1246 leatherbacks and never observed the loss of a PIT tag. In a few cases a PIT tag migrated and was not found on the first nesting encounter. In those instances we retagged the turtle, but always detected the missing tag upon the next encounter. Therefore, we determined that there was 100% retention of PIT tags over this time period. We began PIT tagging of females on Playa Langosta in 1997-1998. Tagging methods as well as beach coverage (percentage of all nesting attempts where the female was observed and identified) are described in Steyermark et al. (1996) and Reina et al. (2002). We recorded PIT tag identifications each season at the three nesting beaches. Turtles found on Playa Ventanas were considered together with turtles that nested on Playa Grande. Approximately, 10% of nests laid on Playa Grande and Playa Ventanas, are laid on Ventanas every season. However, individual turtles that nest on Ventanas, usually lay most of their nests on Playa Grande during a season. In addition, we included data collected at Playa Naranjo in 1998-1999 by Drake et al. (2004) and

fortuitous observations of turtles elsewhere to document more distant interchange of leatherbacks between beaches in Costa Rica. Playa Naranjo is located in Santa Rosa National Park, 45 km north of Las Baulas. We recorded nesting histories for each turtle nested at the above beaches and calculated nesting interchange between beaches.

We estimated the number of nesting females at Las Baulas per season by adding the number of turtles uniquely marked as individuals with PIT tags identified on Playa Grande and Playa Ventanas to the number of turtles identified on Langosta from 1997-1998 to 2003-2004. To account for turtles that may nest outside the main nesting season (October through February), we added the correction used by Reina et al. (2002) based on body pit counts recorded during two full years. On average, 7% of body pits were found between the 1st of March and the 31st of September. Our estimation of number of female turtles from 1988-1989 to 1992-1993 was based on body pit counts (Reina et al. 2002). We previously determined that the average percentage of turtles that nested only on Playa Langosta within a nesting season, for those years for which we had data, was 10% of the total number of turtles at the Park. We added 10% to the estimation of annual number of turtles from 1988-1989 to 1996-1997 to account for turtles that may have nested only on Playa Langosta.

For each season we calculated the number of turtles identified, the number and percentage of turtles that remigrated in later seasons, the remigration interval for the next time we saw each turtle and the number and percentage of turtles that we never saw again. We calculated the average remigration interval for the population by first averaging the remigration intervals per individual and then by calculating the average remigration interval for the population across all seasons.

We were confident that any turtle that was unmarked from 2000-2001 to subsequent seasons was a new recruit to the population because that was seven years after we began saturation PIT tagging and only 1% of remigrant turtles had remigration intervals longer than seven years. It was likely that unmarked turtles within the 1999-2000 season were also new recruits because only 2 to 4.6% of turtles had remigration intervals longer than six years. However, caution must be applied to this conclusion because 25% of the turtles that remigrated from the 1993-1994 season did so after seven years. Therefore, several turtles from the 1992-1993 season, before we began PIT tagging, could have been returning for the first time in 1999-2000.

We used a Cormack-Jolly-Seber (CJS) model to estimate apparent annual survival rates using the program MARK v 4.0. The CJS model estimates apparent survival rates and recapture probabilities. Since leatherback turtles do not nest every year, the recapture probability depends (1) on the probability of capturing a turtle when she is in the area and (2) on the nesting probability. Beach coverage is an average 90% at Las Baulas and the Estimated Clutch Frequency (ECF) is 7 clutches. Thus, the probability of missing a turtle every time she nests in a season is  $0.10^7$ . Thus, since we see every turtle during the nesting season, the probability of capture is 1 and the recapture probability equals the nesting probability. We considered the nesting probability to be a quadratic function of the years since last nesting. This was the best model that fit the data with the lowest Akaike Information Criterion (AIC). Eleven seasons were included in this analysis: 1993-1994 to 2003-2004.

We estimated hatchling production per season in the Park from the total number of eggs laid on the beach and egg survival. We considered levels of poaching to be 90%



until 1990-1991 (Steyermark et al. 1996; Spotila & Paladino 2004), 50% in 1990-1991, 25% in 1991-1992 and 1992-1993 and 0-2% from 1993-1994 to present-season. We assumed that each female laid an average of 65 eggs per clutch, 7 clutches per season (Reina et al. 2002) and had a hatching success of 50% (Bell et al. 2003). We estimated that 10% of the clutches were lost due to tidal inundation (Nordmoe et al. 2004) before 1998-1999, mainly at the north and south ends of the beach. From 1998-1999 we moved clutches that were in danger of being inundated to a beach hatchery. Early in the season when high tides covered most of the beach, occasionally reaching the vegetation, we moved all the clutches to the hatchery. Later in the season, when the tides were lower we relocated clutches to a safer area on the beach or to the hatchery depending on height of tides, number of turtles nesting on the beach at once and space available in the hatchery. We counted all hatchlings that emerged in the hatchery and released them into the ocean at various points along the beach, varying the location from day to day.

## RESULTS

*Population analysis.* —From 1993-1994 to 2003-2004 we PIT tagged 1719 leatherbacks at Las Baulas. Only 448 have returned to nest again. Average remigration interval for leatherbacks in the population was  $3.7 \pm 1.4$  years. The most common remigration interval duration for females coincided with the large La Niña event that began in mid 1998 and affected the 1999-2000 and especially the 2000-2001 nesting seasons (when a large number of turtles nested, Table 1). Percentage of turtles identified in a given season that were not seen again was between 60% and 79% for the seasons for which enough years (6) had passed (before 1997-1998) for most of the turtles to come

back to nest (Table 1). The CJS model indicated that the apparent annual survival rate was 0.78 (95% CI: 0.75-0.80). The annual nesting population decreased precipitously from 1504 in 1988-1989 to an average of 188 from 2000-2001 to 2003-2004 (Fig. 2).

*Effects of conservation efforts.* — There were 343 new leatherbacks that nested from 2000-2001 to 2003-2004, comprising 49.5% of all the females in those four seasons (Fig. 3). There were another 127 unmarked turtles that nested in 1999-2000. Most of those turtles were probably new recruits as well. However, due to the long remigration interval (seven years) of 25% of the remigrant turtles from 1993-1994 we cannot be sure that all of the unmarked turtles in 1999-2000 were nesting for the first time. We reviewed our data sheets to attempt to clarify the status of those turtles. We placed flipper tags on all leatherbacks in 1992-1993 and even though those tags were probably lost within a few years, turtles that had been flipper tagged usually are missing a piece of tissue from their rear flipper where the tag sloughed out. That disfigurement, called a tag scar, is easily recognized and recorded when a turtle is encountered. Of the 127 unmarked turtles in 1999-2000 only seven had tag scars. Therefore, up to 120 of those turtles were probably new nesters. Thus, between 343 and 463 new leatherbacks nested at Las Baulas between 1999-2000 and 2003-2004.

Hatchling production increased substantially since the Park was created. There were 30,788 and 30,180 hatchlings produced on the beach in 1988-1989 and 1989-1990 respectively, when the number of nesting females was the highest. The maximum of 153,547 hatchlings were produced on the beach in 1992-1993, despite a decline in number of turtles from 1504 to 1000 (Fig. 4). The lowest hatchling production was 15,374 in 2002-2003 due to the lowest number of nesting turtles that season. However,

that hatchling production was approximately half the number of hatchlings produced in 1988-1989 while number of nesting females was 95% lower. In addition, there were a similar number of hatchlings coming off the beaches of Las Baulas in 1998-2003 with 68 to 188 nesting females under the current conservation regime as there were in 1988-1989 with 1500 nesting females and no Park. In 1999 and 2000 the 246 and 417 nesting females produced two to three times as many hatchlings as were produced in 1988 and 1989. Beach protection and establishment of a hatchery helped to offset the effect of the decline in numbers of nesting females. Since the Park was established in 1991 there were 994,451 hatchlings produced, of which 20,951 were produced in the hatchery (Table 2).

*Beach Exchange.* —We identified 1252 individual leatherback turtles at Las Baulas from 1997-1998 to 2003-2004. Most of the turtles,  $71\% \pm 3.0$  (SE) nested only on Playa Grande/Ventanas within a given season,  $10\% \pm 1.9$  nested only on Playa Langosta, and  $18\% \pm 2.4$  exchanged beaches at least once in a season (Table 3). In 1998-1999, 6 turtles nested only at Playa Naranjo, 1 turtle nested at Playa Naranjo and Playa Langosta and 1 turtle from Playa Grande/Ventanas nested later at Ostional on her departure from Costa Rica.

Exchange rates between beaches in different seasons were high. Of 209 turtles that nested in two seasons, 136 nested both seasons on Playa Grande/Ventanas, 13 turtles nested only on Playa Langosta and 60 turtles exchanged beaches between seasons or within a season (Table 4). Of 22 turtles that nested in three seasons, 13 nested on Playa Grande all three times, none nested exclusively on Playa Langosta each season and 9 turtles exchanged nesting beaches between seasons. Only 1 turtle nested four seasons and it nested exclusively on Playa Grande/Ventanas all four times. In the past we analyzed

the population by counting only the turtles that nested on Playa Grande and Ventanas. Therefore, we did not account for the females that nested only at Playa Langosta during a given year. In doing so, we missed 9 % of turtles that nested only one season, 15% of turtles that nested two seasons and 9% of turtles that nested three seasons because they nested exclusively at Playa Langosta during at least one of the seasons (Table 5). This underestimated both the population size and the survival rate of the turtles.

## **DISCUSSION**

Parque Nacional Marino Las Baulas comprises two major nesting beaches: Playa Grande (including Playa Ventanas) and Playa Langosta that are both used by a large number of individual nesting leatherbacks. Leatherback turtles that nest at Las Baulas show a high fidelity to a single beach, but movements between Playa Langosta and Playa Grande are not uncommon. On average, 72% of leatherbacks nest only on Playa Grande/Ventanas, 10% nest only on Playa Langosta and 18% nest on both beaches in a given year. In other years leatherbacks may shift to nest primarily on a different beach. Furthermore, 82% of the turtles that nested at Langosta within two seasons nested also at Playa Grande/Ventanas and 100% of the turtles that nested at Langosta within three seasons occasionally nested also at Playa Grande/Ventanas.

There are three hypotheses that evaluate this behavior. Tucker & Frazer (1991) hypothesize that a leatherback population contains two components. Most of the population is faithful to one beach or a small area. Another segment of the population shows less site fidelity and nests on beaches over a larger area. For example leatherbacks at St. Croix also nest at Culebra and on other beaches in the region (Eckert et al. 1989).

Based on aerial surveys and personal communications from other Leatherback projects on the Pacific side of Costa Rica, we know that 85-90% of the leatherbacks that nest on the Pacific side of Costa Rica, do so at PNMB. Furthermore, most of the turtles that have been seen at other locations have no tags from PNMB. Thus, it appears that Las Baulas leatherbacks are, in general, faithful to the beaches of the Park and seldom wander to more distant beaches. Therefore, this hypothesis does not explain nesting of leatherbacks in this population.

Nordmoe et al. (2004) suggest that a proximity hypothesis would better explain nesting distribution than a fidelity hypothesis. The authors conclude that leatherbacks simply nest close to the site of their previous nest as opposed to being faithful to a particular location on the beach. However, this study was conducted on nest locations only on Playa Grande, whereas the scope of our analysis revealed that there is considerable shifting of nesting by leatherbacks between the beaches of the Park, more than expected by chance ( $> 5\%$ ). Therefore, the proximity hypothesis cannot address nesting distribution among beaches within the Park.

Nearly 90% of leatherbacks at Las Baulas nest at Playa Grande. Of these individuals, 71% nest only on Playa Grande/Ventanas and 18% nest on both Playa Grande/Ventanas and Playa Langosta. Therefore, a third hypothesis seems to be appropriate, that environmental conditions may influence selection of nesting beaches within Las Baulas Park. Thus, Playa Grande may be the principal nesting beach for leatherbacks within the Park because of unique aspects of its location and physical characteristics. It is the largest beach and may provide the best physical conditions for approaching the beach from the sea. Playa Grande may also provide nesting conditions,

such as sand characteristics, beach slope, or tidal dynamics that are more suitable for leatherback nests and embryonic development. In order to effectively evaluate this hypothesis, properties of the beach and near-shore physical structure and dynamics require further investigation.

Because of the mixing of leatherbacks between Playas Grande/Ventanas and Langosta, analyzing the nesting population at the two beaches independently leads to errors and an underestimate of the population size and nesting dynamics of the population. This also leads to an incorrect estimation of remigration intervals if we consider exclusively turtles that nest at either beach. The data presented here emphasize the importance of all beaches in the National Park and the necessity of coordinated protection within the Park to ensure the survival of the population.

Nesting cohorts of leatherbacks at Las Baulas showed variable remigration intervals across seasons. The most common remigration intervals for most cohorts coincided with the higher than average nesting season in which 417 turtles nested (2000-2001). The second most common remigration interval coincided with the 1999-2000 season when 246 turtles nested. These years were both “La Niña” years of increased productivity in the Pacific Ocean. Remigration intervals in some species of sea turtles have been related to El Niño Southern Oscillation (ENSO) (Limpus & Nicholls 1988; Solow et al. 2002; Hays 2000), and some studies have suggested that Las Baulas leatherbacks were also affected by this phenomenon (Steyermark et al. 1996; Wallace et al. 2006). However, additional analyses are required to elucidate this relationship.

Adult annual mortality rates calculated with the CJS model (22%) were slightly lower than the 25% previously estimated by Reina et al. (2002). This revised estimate

was due to the inclusion of four more years of data that documented additional remigrant females. For example, Reina et al. (2002) included the years from 1993-1994 to 1999-2000, whereas the present analysis included data from 2000-2001 when a large number of turtles nested after the occurrence of a La Niña, as well as integrated data from Playa Langosta. While this revised estimate is more accurate, a 22% annual mortality rate is still unsustainable for the population and double the 11% recently estimated for the leatherback turtles that nest at Sandy Point, St Croix (Dutton et al. 2005). Demographic modeling (Spotila et al. 1996) indicates that this rate will lead to extinction of the population.

This population faces a dire situation as indicated by the annual mortality rates and a shrinking temporal buffer to avoid extinction (Fig. 2). Conservation on the beach has significantly increased the production of hatchlings and poaching has been reduced from 90% to less than 1% since 1990. Since the Park was declared Park rangers, local guides and researchers have been protecting natural nests on the beach to prevent poaching. Equally, nests threatened by tidal inundation are moved to a hatchery or relocated to a safer area on the beach, thus increasing by 10% the production of hatchlings on the beach. Increasing production of hatchlings will eventually result in a higher proportion of neophyte nesters and enhanced recruitment. Currently, 49.5% of the turtles are new nesters, which probably reflects the increasing protection on the beach in past seasons. At St. Croix 51.5% of leatherbacks were new nesters after several years of conservation efforts (McDonald & Dutton 1996).

On the other hand, fewer clutches were laid since 1988-1989 as the number of nesting females decreased apparently due to high levels of adult mortality. Survival of

late life history stages in a population is critical to the growth of turtle populations (Crowder et al. 1994). Congdon et al. (1993, 1994) reported that slow growing and late maturing species such as turtles cannot sustain increased levels of adult mortality due to human harvesting. Crowder et al. (1994) and Crouse and Frazer (1995) concluded that sea turtles, in general, are severely limited in their ability to respond to current levels of mortality. Spotila et al. (1996) reported that simulations indicated that increases in adult mortality as low as 1% caused a slow decline in an otherwise stable leatherback population and an increase in adult mortality of 5% caused a rapid decline in such a population. Thus, incidental capture of adults and sub-adults in the oceans by fishing activities could still lead to a population decline regardless of the conservation efforts on the beach (Crouse et al. 1987; Heppell et al. 1996; Heppell & Crowder 1998). However, the simulations by Spotila et al. (1996) indicated that increased production of hatchlings could, under some circumstances, compensate for an incidental adult mortality of up to 5%.

To understand to what extent beach protection could offset incidental fisheries mortality, we made a first approximation of recruitment for the Las Baulas population. We made the following assumptions based on our previous studies, data in this paper and other studies. A leatherback at Las Baulas lays 65 eggs per clutch, 7 clutches a season, and nests every 3.7 years (Spotila et al. 1996; Steyermark et al. 1996; Reina et al. 2002; this study). If she has a reproductive life of 20 years (Hughes 1996; Spotila et al. 1996) and 10% of the clutches are lost due to tidal inundation she would produce 2,215 eggs during her lifetime. Due to protection on the beach poaching dropped from about 90% in 1988 to near zero by 1993-1994. Considering a hatching success of 50% (Bell et al.



2003), 1,108 hatchlings would be produced to replace herself and a male if the population was stable and the sex ratios were 1:1. Thus, 554 hatchlings would be needed to produce an adult turtle without human-induced mortality at any level. Thus, we can assume that production of 550 hatchlings should result in one female returning to nest 9 to 11 years later (Zug & Parham 1996; Dutton et al. 2005). We recorded 343 new turtles in four seasons from 2000-2001 to 2003-2004. If we total the hatchlings produced on the beach during four consecutive seasons and assume an average age at maturity of 9 years then the 439,885 hatchlings produced from 1991-1992 to 1994-1995 should have resulted in 794 new turtles recruited during 2000-2001 to 2003-2004. If age at maturity was 10 years, we would expect 719 new turtles and if age at maturity was 11 years we would expect 702 new nesters. The actual number of new recruits was less than half these quantities, which suggests that mortality rates in the ocean before maturation are double the levels of those of a stable population. Although age to maturity might be longer and more variable among females than the assumptions used here, the timing of the observed increase in the St. Croix leatherback nesting population suggested that recruitment of neophytes occurred approximately 10-12 yr after significant conservation efforts to enhance hatchling production began (Dutton et al. 2005). Given these several assumptions, this first approximation of the expected recruitment to the nesting population is lower than expected despite conservation efforts on the beach. These conclusions place further emphasis on increased consideration of fishing impacts on the Pacific leatherback population.

Beach protection has proven effective elsewhere to maintain leatherback populations in the Atlantic and Indian Oceans. At St. Croix 30% of nests were in danger

of tidal inundation, erosion or being poached and were relocated to safer areas from 1982 to 1996. This population showed an exponential growth since 1991-1992, nine years after the beach protection was intensified, as a consequence of the increased hatchling production on the beach (Boulon et al. 1996; Dutton et al. 2003). Equally, the nesting population of Tongaland, KwaZulu-Natal in South Africa was protected after the area was declared a Marine Reserve. Consequently, the annual nesting population increased from 18 to over a 100 females per nesting season within 10 years (Hughes 1996). The leatherback populations that nest at St Croix and South Africa are examples of successful conservation efforts on nesting beaches. The St. Croix population, however, has lower mortality rates in the ocean as adults than Pacific leatherbacks that nest at Las Baulas (Lewiston et al. 2004a). Beach protection is insufficient as a sole measure to ensure the survival of the Las Baulas nesting population. Our study suggests that only a combination of beach protection and a reduction of mortality rates to the critical life history stages in the ocean can prevent the extirpation of this population.

**Table 1.** Number of leatherback turtles that nested each year and time in years until they first remigrated to nest again. Individuals are included in the count of nesting turtles every season that they nested. Numbers in bold correspond to the 2000-2001 season.

Season	Nesting turtles (N)	Number of turtles remigrating at different intervals to next season									Nested again		Not seen again	
		1 year	2 years	3 years	4 years	5 years	6 years	7 years	8 years	9 years	N	%	N	%
1993-1994	150	0	2	6	6	5	5	<b>8</b>	0	0	32	21	118	79
1994-1995	438	1	27	50	11	34	<b>23</b>	4	0	3	153	35	285	65
1995-1996	324	0	4	10	33	<b>34</b>	1	0	4	-	86	27	238	73
1996-1997	116	0	0	7	<b>27</b>	5	1	0	-	-	40	34	76	66
1997-1998	215	0	20	<b>52</b>	6	5	2	-	-	-	85	40	130	60
1998-1999	118	0	<b>21</b>	7	5	9	-	-	-	-	42	36	76	64
1999-2000	226	<b>1</b>	23	14	23	-	-	-	-	-	61	27	165	73
2000-2001	383	1	6	53	-	-	-	-	-	-	60	16	323	84
2001-2002	74	0	8	-	-	-	-	-	-	-	8	11	66	89
2002-2003	62	0	-	-	-	-	-	-	-	-	0	0	62	100
2003-2004	174	-	-	-	-	-	-	-	-	-	0	0	174	100

**Table 2.** Number of hatchlings produced in the hatchery on Playa Grande at Las Baulas Park from 1998-1999 to 2003-2004.

Season	Hatchlings produced in the hatchery
1998-1999	5768
1999-2000	1983
2000-2001	4515
2001-2002	3859
2002-2003	3029
2003-2004	1797

**Table 3.** Number and percentage of leatherback turtles, *Dermochelys coriacea* that nested only at Playa Grande, only at Playa Langosta, at both Playa Grande and Playa Langosta, or at Playa Grande, Playa Langosta and other locations during each nesting season from 1997-1998 to 2003-2004.

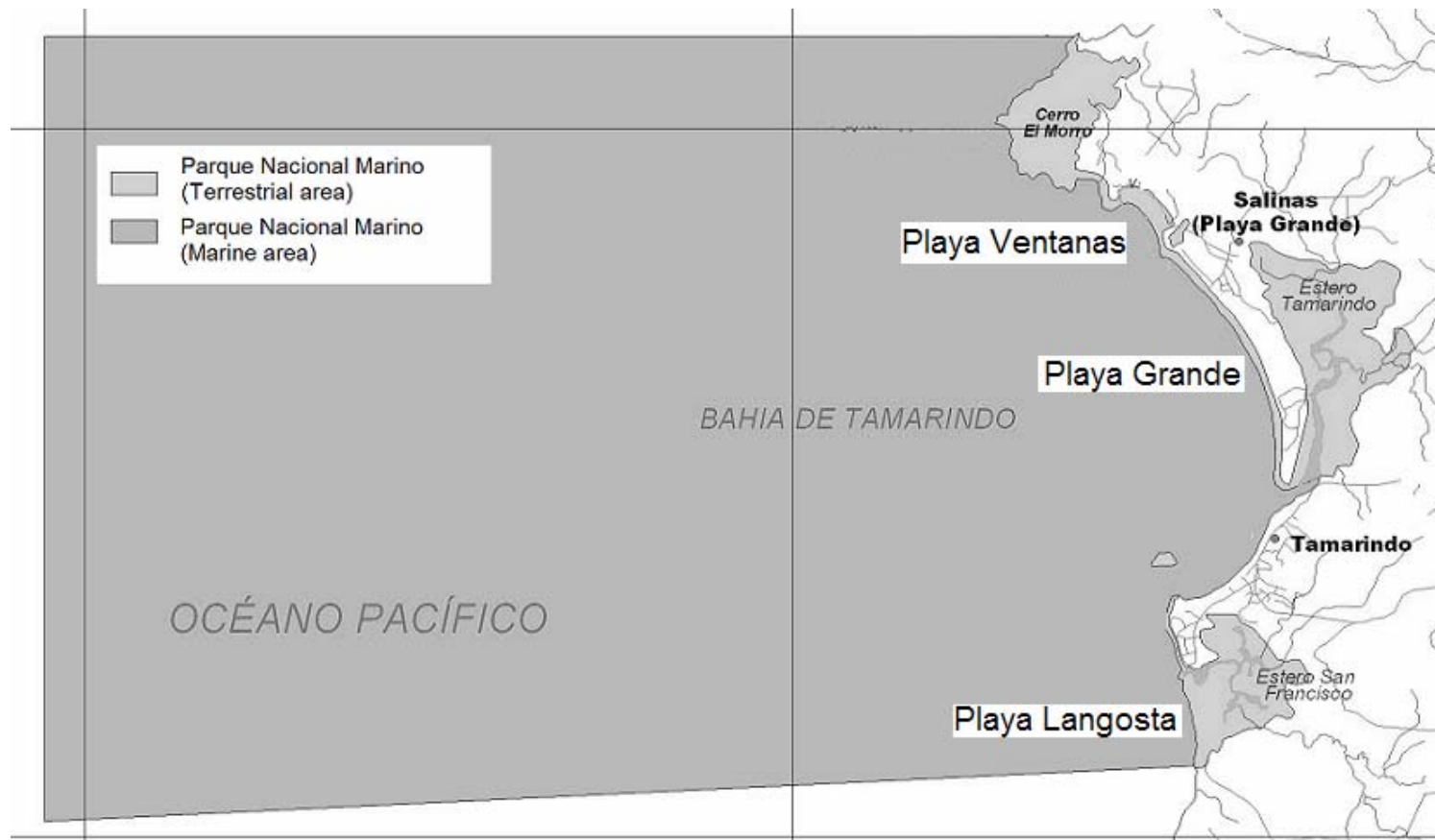
Season	Playa Grande		Playa Langosta		Both		Total Playa Grande	Other	Total
	(N)	%	(N)	%	(N)	%	(N)	(N)	(N)
1997-1998	122	57	37	17	56	26	178		215
1998-1999	95	81	4	3	11	9	106	2	112
1999-2000	169	75	22	10	35	15	204		226
2000-2001	282	74	20	5	81	21	363		383
2001-2002	52	70	11	15	11	15	63		74
2002-2003	41	66	5	8	16	26	57		62
2003-2004	132	76	15	9	27	16	159		174
X		71		10		18			

**Table 4.** Nesting beach at which leatherback turtles nested each season (Playa Grande (G), Playa Langosta (L) or both Playa Grande and Playa Langosta (B)) for turtles that nested 1, 2, 3 or 4 seasons.

Number of seasons nested	Nesting beach	Number of turtles (N)
1	G	535
1	B	152
1	L	67
2	GG	136
2	BB	17
2	LL	13
2	GB	7
2	BG	18
2	GL	1
2	LG	4
2	BL	6
2	LB	7
3	GGG	13
3	GGB	1
3	GBG	1
3	GBB	1
3	BGG	3
3	BBG	1
3	BLL	1
3	BBL	1
4	GGGG	1

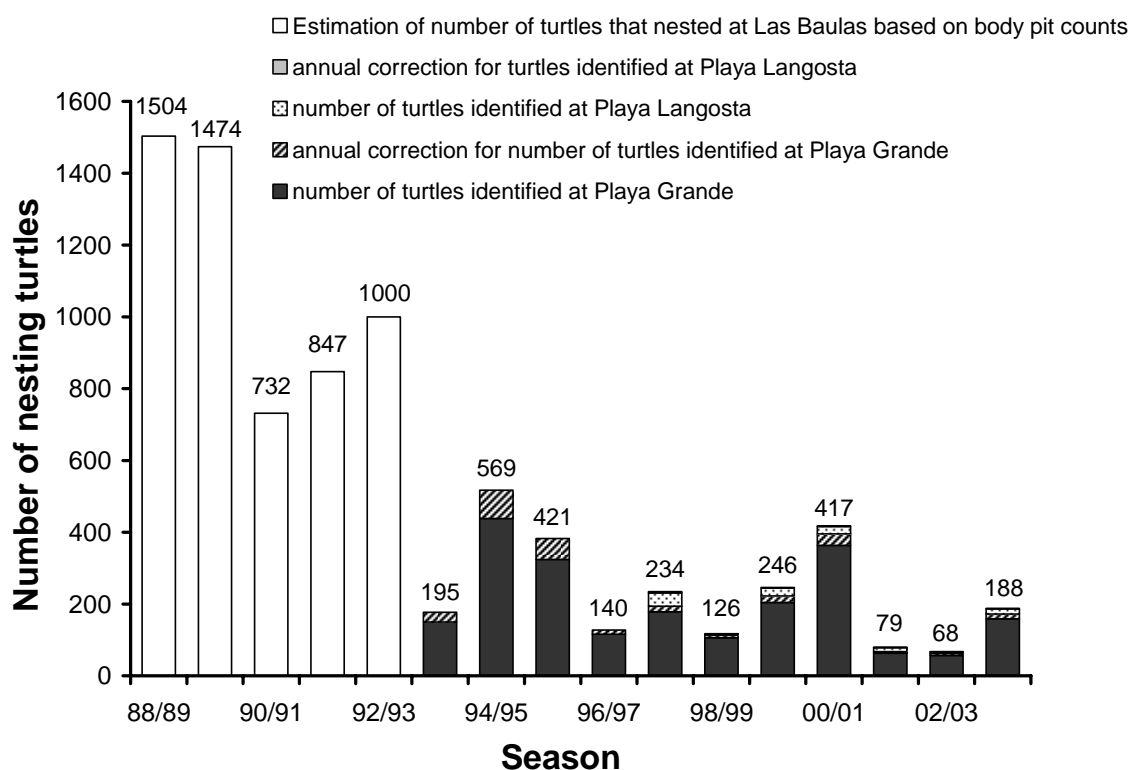
**Table 5.** Number of leatherback turtles that nested always at the same beach (Playa Grande or Playa Langosta) or at different beaches between seasons, and number of turtles that would have been missed at least one season without information from Playa Langosta.

Number of seasons nested (N)	Number turtles (N)	Nested at the same beach each season		Nested at different beaches		Turtles that would have been missed	
		(N)	%	(N)	%	(N)	%
1	754					67	9
2	209	149	71	60	29	31	15
3	22	13	59	9	41	2	9
4	1	1	100	0	0	0	0

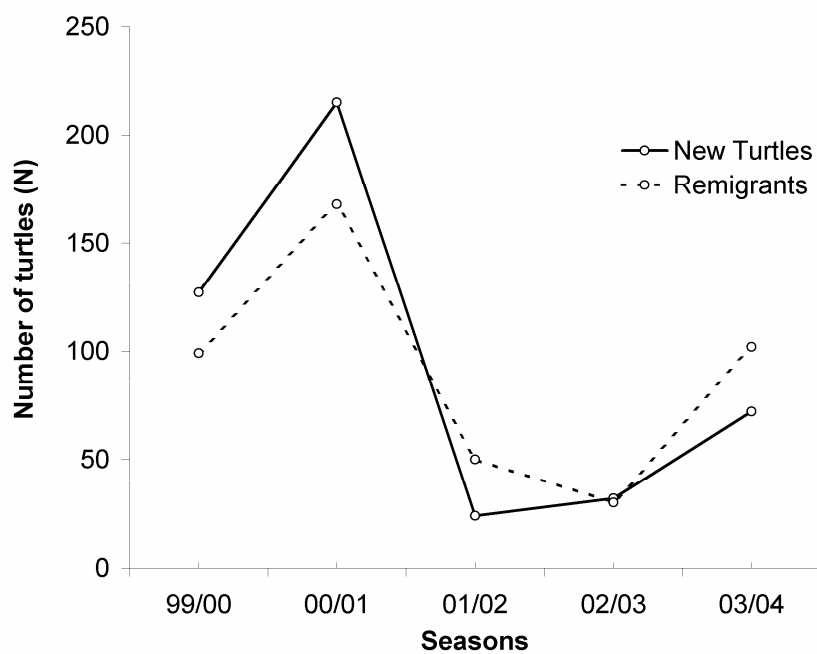


**Figure 1.** Map of Parque Nacional Marino Las Baulas in Guanacaste, Costa Rica.

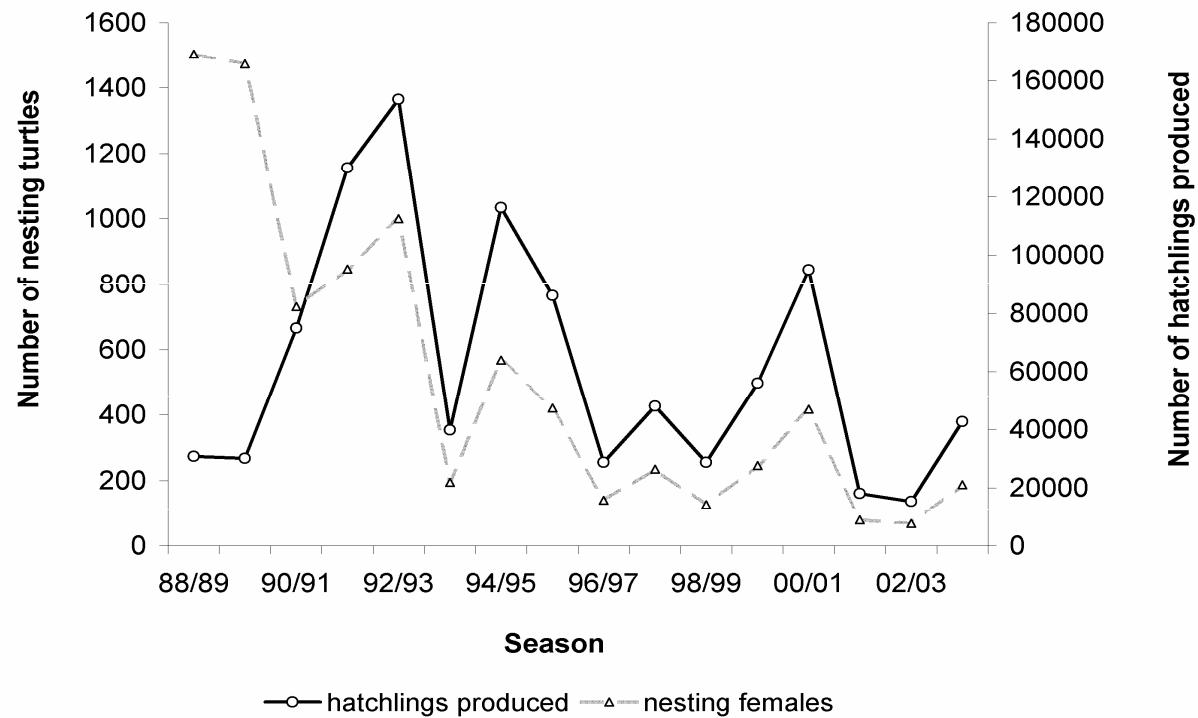




**Figure 2.** Number of nesting leatherback turtles at Parque Nacional Marino Las Baulas in Costa Rica from 1988-89 to 2003-2004 seasons. Numbers from 1988-1989 to 1992-1993 are based on estimations from body pit counts. We calculated annual number of turtles based on monthly distributions (see Reina et al. 2002 for details). A correction of 10% has been added to number of identified turtles from 1988-1989 to 1996-1997 to account for females that could have nested only in Playa Langosta.



**Figure 3.** Number of new recruits to the population and number of remigrant leatherback turtles per season at Parque Nacional Marino Las Baulas from 1999-2000 to 2003-2004.



**Figure 4.** Number of nesting leatherback turtles and number of hatchlings produced at Parque Nacional Marino Las Baulas from 1988-1989 to 2003-2004 seasons. Poaching levels were considered 90% in 1988-1989 and 1989-1990, 50% in 1990-1991, 25% in 1991-1992 and 1992-1993, and 0 % from 1993-1994 to 2003-2004.

**CHAPTER 3: Egg poaching: A major factor in the population decline of leatherback turtles, *Dermochelys coriacea*, at Parque Nacional Marino Las Baulas, Costa Rica**

**ABSTRACT**

The nesting population of leatherback turtles (*Dermochelys coriacea*) at Parque Nacional Marino Las Baulas declined from 1500 turtles per year to about 100 in 19 years. Egg poaching was the most important single cause of the decline. We analyzed the effect of high levels of poaching and incidental fishery mortality on the population. We modeled the population response to different levels of egg poaching: 90%, 75%, 50% and 25% and the effect of eradicating poaching at different times during the population decline. We compared effects of 90% poaching to those of 20% adult mortality, as these were the impacts that we measured on the population at Las Baulas. There was a typical stepwise decline in number of nesting turtles at all poaching intensities. Extirpation times for different levels of poaching ranged from 45 to 282 years. The nesting population declined slower and survived longer with 20% adult mortality (146 years) than it did with 90% poaching (45 years). Time that elapsed until poaching stopped determined the average population size at which the population stabilized, ranging from 90 to 420 nesting turtles. Saving clutches naturally lost to the sea would be effective in restoring a leatherback population if adult mortality rates were low, and would have a greater impact in recovering populations with short remigration intervals between nesting seasons and a large proportion of natural loss of clutches to tidal inundation. Because poaching is the most important cause of the leatherback decline at Las Baulas, beach protection is critical for survival of this population. However, current high mortality rates of adults will

prevent population recovery. Therefore, protection must focus both on the beach and in the ocean.

## **INTRODUCTION**

Long-lived species are usually characterized by high survival of late stages and high mortality of early ones, delayed sexual maturity, and higher fecundity in older females than in younger ones (Stearns 1992). Population biology frequently uses life history theory to understand responses of a stable population to changes in its different life stages. In general, populations of long-lived vertebrates are believed to be most sensitive to variations in the survivorship of adults (Congdon et al. 1993; Heppell et al. 1996). Consequently, populations could suffer more from an increase in adult mortality than from increasing mortality of younger stages at the same rate of change. Therefore, adult animals are more important than their offspring in keeping a population stable. This is especially true when populations are declining and in need of recovery. Based on these principles, it is typically recommended that conservation efforts focus on protection of late stages and that management be directed to ensure the survival of adult animals (Crouse et al. 1987; Heppell et al. 1996). However, it is also acknowledged that protection of all life stages is necessary for the survival of natural populations (Congdon et al. 1993; Crouse 1999).

Poaching of young and adults is one of the greatest threats to survival of populations of plants and animals (Manel et al. 2002). Poaching is related to population declines and high probability of extinction across taxa, including neotropical parrots (Wright et al. 2001), tigers (Kenney et al. 1995) and giant pandas (Zhou & Pan 1997).

Intensity and duration of poaching are both critical factors in the process of extinction (Kenney et al. 1995).

Leatherback turtles (*Dermochelys coriacea*) are long-lived vertebrates and are critically endangered (Hilton-Taylor 2000). This is especially true in the Eastern Pacific Ocean where populations have been greatly reduced in the last 20 years (Spotila et al. 1996; Spotila et al. 2000). It is commonly accepted that a species such as the leatherback cannot sustain any level of harvest of adults and late juveniles in their populations (Congdon et al. 1993; Spotila et al. 1996). However, population responses to heavy harvest on early stages have yet to be explored.

### **Population background**

Leatherback turtles that nest at Parque Nacional Marino Las Baulas (PNMB) in Costa Rica constitute the last remaining large nesting population of the species in the Eastern Pacific Ocean. The total length of its three beaches is 6 km and the main nesting beach is Playa Grande (3.6 km). The population declined by 95% from the 1988-1989 nesting season to the 2003-2004 season (Spotila et al. 1996; Spotila et al. 2000; Santidrián Tomillo et al. 2007). There are two main hypotheses proposed to explain the decline of leatherback turtles at Las Baulas. These are (1) high rate of interaction with fisheries such that the decline is due to mortality of late stages (Spotila et al. 2000; Lewison et al. 2004b; Kaplan 2005) and (2) egg poaching such that the decline is the result of mortality of early stages (Pritchard 1996). In addition to the two main threats, there are also new pressures on the population such as development on the nesting beaches (Spotila & Paladino 2004; Clune 2005) and the more frequent occurrence of El Niño events since 1980 (Saba et al. 2007). Thousands of seabirds (Lewison & Crowder

2003; Tuck et al. 2003), mammals (Lewison et al. 2004a) and sea turtles (Lewison et al. 2004b) are killed every year due to longlines and other fisheries in the world's oceans. Bycatch of leatherback turtles in longlines and coastal gill net fisheries is reducing their populations in the Pacific Ocean (Kaplan 2005; Lewison & Crowder 2007). In addition, annual mortality rate of nesting leatherbacks at Las Baulas is 22% (Santidrián Tomillo et al. 2007). This is considerably higher than the 11% estimated for the increasing population of leatherback turtles nesting at St. Croix, US Virgin Islands (Dutton et al. 2005).

The oldest memories of poaching at Las Baulas go back to the 1950s when people noticed leatherbacks nesting at Playa Grande for the first time. There were only two or three families living around the area between the 1950s and the 1970s that went occasionally to the beach and took 1-2 clutches of eggs for their own consumption (Rodríguez and Rosales, personal communication). We estimated that the level of poaching at this time was <1% and therefore, the impact of poaching on the population was very low. A road opened early in the 1970s facilitating beach access and people soon started to arrive from nearby villages and from more distant locations, such as the cities of Santa Cruz and San José. A systematic system of poaching was well established by 1975. Poachers divided the beach into small sections and removed 90% of eggs while wholesalers transported eggs by trucks to big cities for commercialization. Intense poaching lasted until 1990-1991, when the Park was established (Santidrián Tomillo et al. 2007). Thus, heavy poaching lasted for approximately 15-20 years. Beach protection was fully enforced after 1993-1994 and poaching was reduced to <1% a year.

The general aim of this study was to assess the impact that high levels of egg poaching over 15-20 years had on the leatherback population nesting at Las Baulas. We ran simulations to test the response of a stable population to 90% poaching and therefore, to test the effect of prolonged and heavy pressure on early life stages. We looked in detail at the effects on the population of (1) continuous poaching at the 90% level, (2) lower intensities of poaching, (3) eradicating poaching at different times after it started and (4) relocation of eggs threatened by the ocean after poaching stopped. Then, we simulated the response of a stable population to 20% annual adult mortality, the population response to a combination of 90% egg poaching and 20% adult mortality and the effect of egg relocation under these conditions. Finally, we compared the effect of egg relocation and 20% adult mortality on (1) populations with different remigration interval between seasons and (2) populations that naturally lose 10% or 20% of eggs to tidal inundation.

## **METHODS**

We conducted several interviews with the oldest residents at Playa Grande and the nearby town of Matapalo to reassess the intensity of poaching since leatherback nesting was discovered. We determined that intense poaching took place at the 90% level between the early 1970s and the time Las Baulas became a National Park in the early 1990s. Based on that, we simulated the response of a stable population to the effect of (1) 90% egg poaching, (2) 20% adult mortality and (3) both 90% poaching and 20% mortality of adults.

We created a Leslie matrix for a stable population, built on a life table similar to the one used by Spotila et al. (1996) but including more recent data (Table 6). Average



number of eggs per clutch, estimated clutch frequency, percentage of female hatchlings (Binckley et al. 1998), emergence success and survival of hatchlings on the beach were based on data collected from 1993-1994 to 2006-2007 and in more detail from 2004-2005 through 2006-2007. We considered that 10% of eggs were lost every season due to tidal inundation (Santidrián Tomillo et al. 2007). We estimated annual survival of adults (90%) based on a stable population of leatherback turtles (Spotila et al. 1996). It was similar to the 89% for the nesting population at St. Croix (Dutton et al. 2005). We based age at sexual maturity (11 years) on Zug and Parham (1996). Turtles were considered juveniles from the time hatchlings reached the water until they reached sexual maturity. We calculated annual survival of juveniles (60.9%) given the other values (Spotila et al. 1996). Population growth rate = 0. These variables produced a stable population.

We looked in more detail at the structure of the nesting population to be able to compare model results to what we actually observed on the beach. We divided nesting turtles into five nesting stages: first time, second time, third time, fourth time and fifth time nesters. Therefore, in any season there were turtles that came to nest for the 1st time (1st time nesters), turtles nesting for the 2nd time (2nd time nesters), etc. We have not observed a turtle nesting for more than five seasons, although this may be limited by the length of the study. Thus, we considered only five nesting stages. We assumed an average remigration interval for model purposes of 4 years (Reina et al. 2002; Saba et al. 2007). Consequently, we assumed a reproductive life of 20 years (Spotila et al. 1996; Hughes et al. 1996) and also assumed the same fecundity and survival at all nesting stages.

## Simulations

*Effect of poaching.* We first simulated the effect of removing 90% of the eggs laid every year on a stable population. We set the simulation starting with 1000 nesting turtles a year. We looked specifically at the effect of egg poaching on the total number of nesting turtles and on the different nesting stages. We calculated extirpation time for the population at this level of poaching. Second, we ran the same simulation for poaching at 75%, 50% and 25% levels and looked at the overall effect on the number of nesting turtles per year. Then, we calculated extirpation time for each poaching intensity. Extirpation was considered at 10 or fewer nesting females per year. Third, we repeated the simulation at 90% poaching for a given period of time after which we stopped poaching. We reduced poaching in the following way: to 50% the first year, to 25% the two following years and to 0% from the next year forward. This followed how poaching was actually eradicated at Las Baulas (Santidrián Tomillo et al. 2007). We simulated stopping poaching at different times based on the characteristic stepwise decline that occurred in the first simulation at the 90% level of poaching. In these simulations we stopped poaching when the number of nesting turtles dropped for the first, second, third and fourth time in order to determine the response of the population to a removal of the human predation pressure on the eggs. Finally, we simulated the effect of relocating the eggs that otherwise would be lost to tidal inundation.

*Fisheries versus egg poaching.* First, we simulated the effect on a stable population of decreasing the annual survival of adults from 90% to 80%. Second, we simulated the effect of reducing the annual survival of adults to 80% and increasing the level of poaching from 0% to 90%. In this case, we kept 20% adult mortality and 90%

poaching until the number of nesting turtles dropped for the second time. Then, we stopped poaching by reducing it at the same rate as mentioned above. Thereafter, we kept 20% continuous annual mortality rates of adults and 0% poaching. Finally, we simulated the effect of egg relocation. In the case of 90% poaching to the second drop and 20% adult mortality, relocation started after poaching was eradicated but high mortality of adults continued. We calculated the extirpation times under all the above conditions.

*Effect of egg relocation - Length of remigration interval and proportion of egg loss naturally.* We compared two populations of leatherback turtles with corresponding remigration intervals of two and four years. Both populations were considered to nest five seasons and had equal production of hatchlings. Annual survival of juveniles for the two year remigrant population was 59.3%. We assumed that the populations were stable at 400 nesting turtles per season, to recreate the nesting numbers of a population stabilized after poaching. In addition, we considered that the populations could lose either 10% or 20% of eggs to tidal inundation under natural conditions. Then, we compared the effect of egg relocation on each population and their responses to increased adult mortality.

### **Nesting population at Las Baulas**

Details of field methodology are described by Reina et al. (2002). We individually marked leatherbacks with permanent PIT (passive integrated transponder) tags since 1993-1994. Estimations of number of nesting turtles from 1988-1989 to 1993-1994 were based on body pit counted (Reina et al. 2002; Santidrián Tomillo et al. 2007). We recorded 100% of leatherbacks that nested at Las Baulas by maintaining beach coverage of 90% (Reina et al. 2002). We considered a turtle to be a new recruit to the population if

it was unmarked from 2000-2001, when enough seasons had passed since saturation tagging started.

## **RESULTS**

### **Simulation of effect of egg poaching**

There was a rapid stepwise decline in number of nesting turtles when the population suffered 90% poaching of eggs for an extended period of time. There was a delay of 11 years from the initiation of intense poaching until the population dropped for the first time. This delay was the time lag from when eggs were laid until the resulting turtles reached sexual maturity and reproduced for the first time. There was a first big drop in total number of nesting turtles as a result of the large drop in recruitment. Then, there was a second reduction in total number of nesting turtles four years after the first drop, due to a drop in second time nesters. The same occurred every four years: there was a decline in the total number of nesting turtles because of corresponding drops of third, fourth and fifth time nesters (Fig. 5a). The largest drop was the first one because new nesters were the largest percentage in the stable nesting population and in the actual population at Las Baulas (Table 7).

There was also a stepwise nesting population decline at poaching intensities lower than 90% but the drops were not as large and the overall decline was smoother and slower (Fig. 5b). The same delay of 11 years occurred in all cases. At 90% poaching the population disappeared after 45 years, while at 75%, 50% and 25% poaching, the population disappeared after 64 years, 116 years and 282 years respectively.

The model predicted that the population stabilized when poaching stopped (Fig. 6a). There was a delay in all cases after poaching stopped. The population continued to decline until recruitment was normal again and then the number of nesting turtles stabilized. When poaching was stopped after the number of nesting turtles declined for the first time, second time, third time and fourth time, the nesting population stabilized at around 420, 260, 150 and 90 nesting turtles per year respectively. When relocation of eggs started, the number of nesting turtles increased rapidly after a time lag of 11 years (Fig. 6b).

### **Simulation of fisheries versus egg poaching**

There was an immediate population response to the increase in adult mortality due to simulated bycatch in a fishery. There was no delay in the decline, as observed when the pressure came from egg poaching. Number of nesting turtles decreased as soon as the fishing pressure started. However, the decline was smoother and slower than it was with 90% poaching (Fig. 7a). When annual adult mortality rates were 20% and egg poaching was 0%, the population was extirpated in 146 years. With 90% poaching and 20% adult mortality, the nesting population showed an immediate decline from the increase of adult mortality and then a delay of 11 years until the drops from poaching started. Poaching of eggs was stopped in this case at the second drop. However, the number of nesting turtles continued to decline. The population under these conditions lasted longer than it did with 90% continuous poaching but eventually disappeared in 86 years because it could not sustain adult mortality rates of 20% (Fig. 7a). Relocation of eggs slowed down the decline but was insufficient to recover the population (Fig. 7b). The population lasted 179 years with 20% adult mortality, no poaching and egg relocation. When adult mortality

was 20%, egg poaching 90% to the second drop and egg relocation started after poaching, the population was extirpated in 101 years.

### **Simulation of effects of egg relocation - length of remigration interval and proportion of egg loss naturally**

Relocation of eggs succeeded in increasing the number of turtles when mortality rates of adults were those of a stable population (10%), and it resulted in a faster increase in populations with a natural egg loss of 20% and with a two year remigration interval (Fig. 8). Relocation of eggs was unsuccessful in recovering populations when adult mortality increased to 20%. Extirpation times for an initial population of 400 turtles and 10% natural egg loss were 200 and 145 years for corresponding remigration intervals of two and four years (Fig. 8a). Extirpation times for populations of 20% egg loss were 384 and 209 years for two and four year re-migrants (Fig. 8b).

### **Nesting population at Las Baulas**

The nesting population of leatherback turtles at Las Baulas, declined from about 1500 to about 100 turtles between 1988-1989 and 2006-2007 (Fig. 5c). Despite the variability in the annual number of nesting turtles due to environmental factors, there was an apparent stepwise decline in number of nesting turtles. There were high rates of recruitment in the last three years (Table 7) and the observed stepwise decline in the population was similar to that predicted by the model for the cases with 90% continuous poaching, with or without 20% adult mortality.

## DISCUSSION

Our simulations indicate that egg poaching was the most important cause for the decline in the nesting population of leatherback turtles at PNMB. This is counterintuitive given data (Congdon et al. 1993) and mathematical models (Heppell et al. 1996) that indicate that populations of long lived animals are more sensitive to changes in adult mortality than to changes in hatchling and juvenile mortality. Indeed our simulations indicated that the leatherback population would decrease more rapidly with 20% adult mortality than with 25% egg poaching. However, the effect of 90% egg poaching was overwhelming.

When eggs are taken, and after the time to reach sexual maturity, there is a decrease in recruitment because those eggs never develop into adults. Then, there is a drop in other nesting stages with a four year lag as a result of lack of recruitment. At Playa Grande, for 15-20 years, 90% of eggs were removed for human consumption. As a result the nesting population dropped in less than 20 years, from about 1500 turtles in the late 1980s, to about 100 turtles in 2001-2005 (Fig. 5c). We began collecting data in 1988-1989 when poaching was ongoing for about 15 years. Thus, the population was probably already reduced by this time. It is hard to determine accurately the stage of the stepwise decline at which the population was in 1988-1989. If sexual maturity is 11 years, as assumed, the number of nesting turtles could have already dropped for the first, second or even third time.

In addition, if a population suffers egg removal for an extended period of time, the proportion of nesting stages changes. After there is a drop in recruitment, the nesting population gets old, because there is a higher proportion of late stages. Consequently,

apparent annual mortality rate increases because old turtles die and there is no recruitment. A nesting population that suffers from poaching will show significant changes in the proportion of nesting stages through time. In the case of the population at PNMB, when we started PIT tagging in 1993-1994 most of the turtles were old and there were probably few recruits. Now 17 years after poaching was reduced and 14 years after it stopped there is normal recruitment because new turtles are coming from eggs laid after implementation of beach protection. Proportions of second time nesters are similar to those of a population with no poaching. It will still take 10-15 years before the nesting population structure is not affected by past poaching. Even if high environmental variability affects the number of nesting females per season (Saba et al. 2007), the proportion of nesting stages in a population with no poaching will be similar to those estimated based on the life table of a natural population (Table 7).

Extirpation times vary with levels of poaching. Although all levels of poaching affect a population, the population response to different poaching levels varies greatly. The simulated population lasted 237 years longer with 25% poaching than it did with 90% poaching. When poaching of eggs begins in a stable population, time elapsed from egg poaching to extirpation will be determined by poaching intensity: the higher the intensity, the faster the extirpation. If poaching stops, the population will stabilize (as long as there are no additional pressures) and the time passed will determine size of the nesting population. A nesting population of 400 turtles a year can respond better to additional anthropogenic impacts than a population of 50 turtles. However, any population that recovers from poaching may still be vulnerable to extinction due to environmental stochasticity (Kenney et al. 1995).



In the case of leatherback turtles that nest at Las Baulas, poaching stopped after 15-20 years of high intensity. The number of turtles had probably already dropped 2-3 times when this happened. There are currently about 100 turtles nesting per year. If poaching stopped 5-10 years earlier, the population could have stabilized at about 200-400 nesting turtles. If poaching continued 5-10 more additional years, the annual number of turtles on the beach could have been as low as 20-40 females. If poaching continued any longer the population would have followed the same course that the leatherback population at Terengganu, Malaysia (Chan & Liew 1996). At a constant rate of 90% poaching, the population would have disappeared by year 2020.

Leatherback turtles that nested at Terengganu, Malaysia, were members of the largest population of leatherback turtles in the world. The population was, however, practically depleted by the mid-1990s. The main reason for the nearly total extirpation was decades of egg poaching. Other causes were bycatch of turtles by fisheries, unnatural production of sex ratios in hatcheries and unregulated coastal development (Chan & Liew 1996). A combination of egg poaching and fisheries also caused the rapid decline of leatherback turtles on the Pacific coast of Mexico (Sarti et al. 2007), which replaced Terengganu as the largest population in the World (Pritchard 1982). The population at PNMB also faced, and is facing, all those threats, except for the negative effect of hatcheries, but has not collapsed. Two crucial events that did not happen in Malaysia may have tipped the scale at Las Baulas towards survival. First, establishment of an effective national park guaranteed full beach protection and eradicated poaching. Second, poaching was eradicated before it was too late. Protection and the time taken to be accomplished have given leatherbacks at PNMB an opportunity to recover.

The population of leatherback turtles that nests at PNMB is still far from stable. One problem has been solved with the eradication of poaching but other threats remain. Fishing is probably the biggest current threat to its survival. The response of a stable population to fishing differs from that of egg poaching. When adult mortality is increased, the number of nesting turtles declines immediately, because reduction is produced by direct removal of adult turtles (Fig. 7). When poaching occurs, there is a delay related to the time to develop from egg to reproductive female. The same time lag happens from the time poaching stops until the population recovers. We chose to test 90% poaching of eggs and 20% adult mortality because those were the levels of impact estimated for the population at Las Baulas. In our simulation, extirpation took place 101 years later with 20% adult mortality than with 90% poaching. However, extirpation occurred 136 years earlier with 20% adult mortality than it did with 25% poaching. The impact of killing adult turtles is higher than the impact of removing their eggs. However, the impact of poaching was greater than that of fishing at Las Baulas, because of the much higher intensity of poaching.

Relocation of sea turtle eggs at risk of tidal inundation is a common practice to increase the number of hatchlings produced. Several nesting beaches where leatherbacks nest are high energy beaches of high erosion and consequently, high rate of egg loss (Eckert 1987; Leslie et al. 1996). Other beaches, such as those at PNMB, are relatively more stable and therefore, lose a smaller proportion of eggs to tidal inundation. Relocation is more efficient when populations naturally lose higher proportions of eggs, because there is a greater proportional increase in number of hatchlings. The population

of leatherbacks at St. Croix, US Virgin Islands, with natural loss of eggs of 40%, is currently increasing as a result of egg relocation (Dutton et al. 2005).

Duration of remigration interval between nesting seasons also affects effectiveness of egg relocation. North Atlantic populations of leatherback turtles have shorter remigration intervals than Pacific ones (Wallace et al. 2006) and relocation of eggs has a larger effect in recovering those populations. Relocation of eggs cannot recover nesting populations when adult mortality is high. Thus, even if beach protection is successful, every nest laid on the beach hatches and eggs laid under the high tide line are relocated, the population will not survive unless the mortality rates of adults are reduced to those of a stable population.

The effects of direct take and fishery bycatch on adult mortality of other long-lived species are also much greater than those of harvesting young. In sooty shearwaters, *Puffinus griseus*, bycatch of adults has a 10-fold greater effect than an equivalent level of chick harvest, although chick harvest can also have a great impact (Hunter & Caswell 2005). When pressure on late stages is caused by increasing adult mortality in long-lived species, selection may favor early maturation (Reznick et al. 1990). However, it takes many generations for organisms to adapt to such a change and human impacts can cause extirpation during the lifetime of a single generation. History provides tragic examples of extinction due to human exploitation. Elimination of bison, white (polar) bear and elk from Eastern North America are well known. Likewise bison, wolves, and bears were eliminated from most of Europe. The great auk was exterminated from North America through a combination of hunting adults and collecting eggs and “eggers” eliminated numerous colonies of sea birds along the coast of North America. The last colony of great

auks at Eldey was eliminated by 1843 as eggs and stuffed adults went into natural history collections in Europe (Mowat 1984).

Management plans for protection of long-lived species must implement protection of early as well as late stages. In the case of sea turtles, it is necessary (1) to guarantee protection on the beach that counteracts human impacts such as poaching, light pollution, development and uncontrolled tourism and (2) to protect sea turtles from bycatch, direct capture and contamination in the ocean. Conservation must prioritize protecting sea turtles in their natural habitat, and other activities such as clutch relocation should only be applied when needed (Frazer 1992). Egg relocation increases hatchling production. However, hatching success could be lower in relocated than *in situ* nests (Eckert & Eckert 1990). Therefore, only nests clearly laid below the high tide line should be relocated. Leatherbacks at Las Baulas have declined by 95% in less than 20 years. Clutch relocation can extend the life of the population in the face of high adult mortality. This can buy time for implementation of conservation methods at sea. The recovery plan for U.S. Pacific leatherback populations lists among conditions to de-list the species as Endangered, that nesting populations should (1) be constituted by 5000 nesting females per year over a period of six years, and (2) show stable or increasing trends over a period of 25 years (NMFS & USFWS 1998). The population of leatherback turtles that nest at PNMB is far from achieving either aim. Currently, there are about 100 nesting turtles per year (2% of the levels aimed at by U.S. standards) and the trend has yet to be reverted. Therefore, even if some threats to the population have been eliminated, the population will still remain endangered for an extended of time.

Sea turtle populations will not be maintained without beaches to lay eggs, where eggs can develop and hatchlings can find their way to the ocean, and cannot survive if adults are killed by fisheries at sea. Therefore, we conclude that pressure on both early and late stages can result in population declines of long-lived species and we recommend protection of all stages when human actions are diminishing their populations.

**Table 6.** Life table calculated for a stable population of leatherback turtles based on reproductive characteristics of females that nest at Las Baulas Park in Costa Rica and survival of their hatchlings. Age at first reproduction is 11 years and remigration interval between nesting seasons is 4 years. Life table is based on 1000 hatchlings

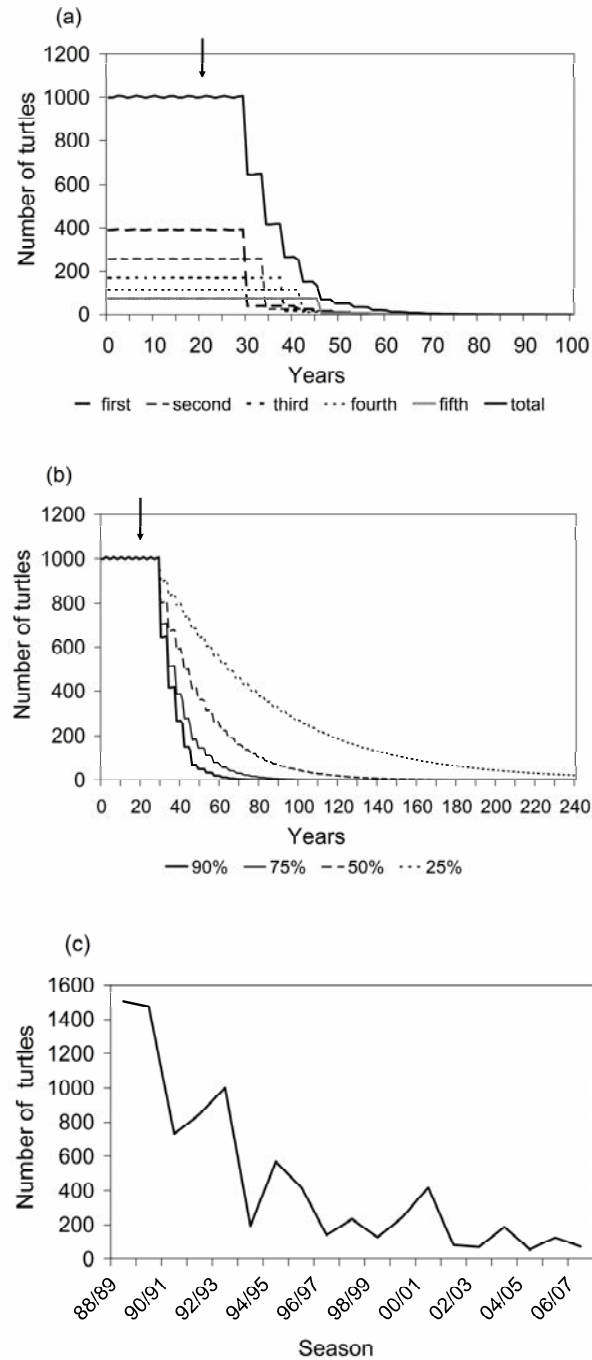
Turtle characteristics		Average production per female in a season	
Number of eggs per clutch		62	
Estimated Clutch Frequency		6.6	
Proportion of female embryos		0.75	
Total female eggs produced			<b>307</b>
Emergence success		0.38	
Female hatchlings emerged			<b>117</b>
Survival rate on the beach		0.87	
Female hatchlings that reach the water			<b>101</b>

Age	Annual survival	Annual fecundity	Number of individuals
0	0.609	0	1000
1	0.609	0	609.0
2	0.609	0	370.9
3	0.609	0	225.9
4	0.609	0	137.6
5	0.609	0	83.8
6	0.609	0	51.0
7	0.609	0	31.1
8	0.609	0	18.9
9	0.609	0	11.5
10	0.609	0	7.0
11	0.9	307	4.3
12	0.9	0	3.8
13	0.9	0	3.5
14	0.9	0	3.1
15	0.9	307	2.8
16	0.9	0	2.5
17	0.9	0	2.3
18	0.9	0	2.0
19	0.9	307	1.8
20	0.9	0	1.7
21	0.9	0	1.5
22	0.9	0	1.3
23	0.9	307	1.2
24	0.9	0	1.1
25	0.9	0	1.0
26	0.9	0	0.9
27	0.9	307	0.8

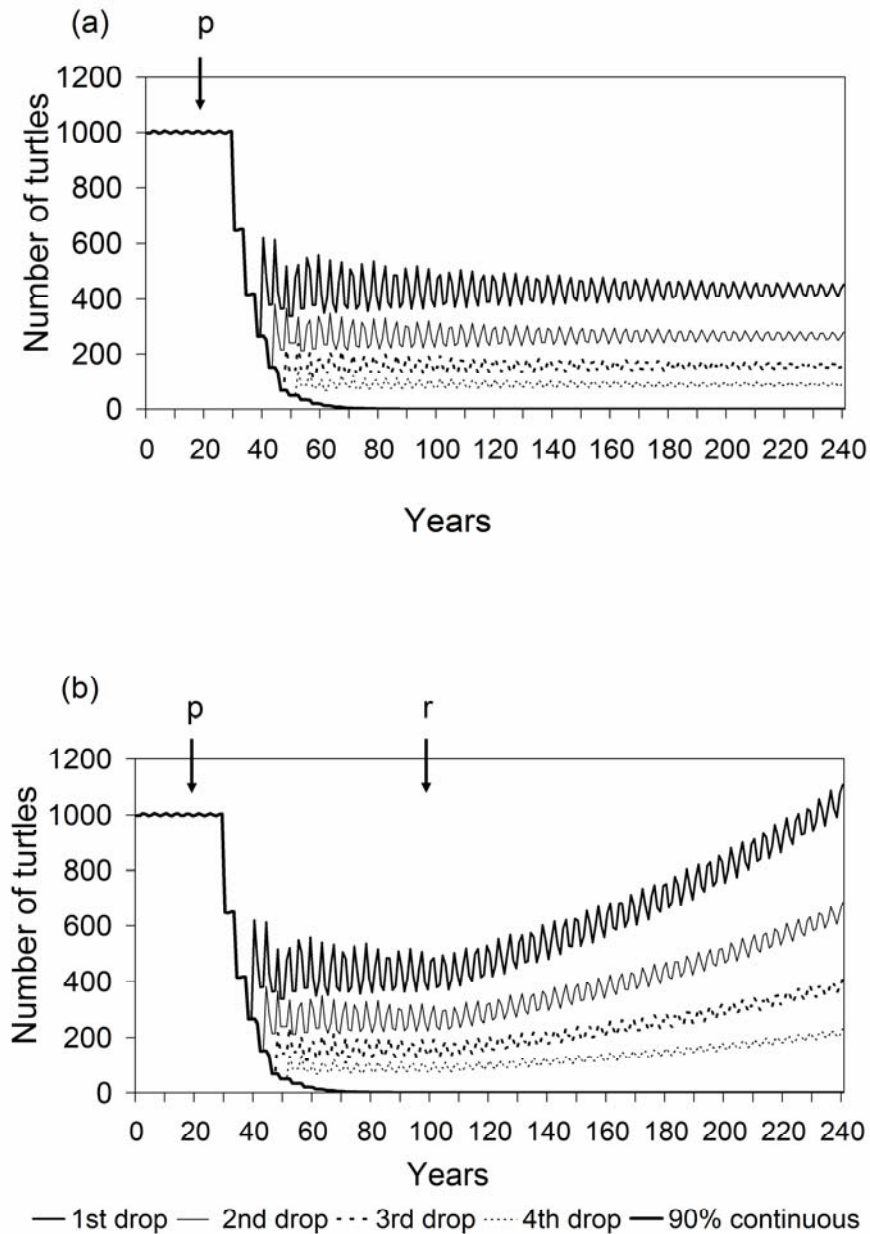
**Table 7.** Percentage of leatherbacks of different nesting stages measured in seasons 2004-2005, 2005-2006 and 2006-2007 at Las Baulas Park in Costa Rica and estimated for a stable population based on the life table in Table 6.

Nesting stages	Season			Estimated
	2004-2005	2005-2006	2006-2007	
First time nesters	35%	36%	51%	39%
Second time nesters	22%	33%	16%	26%
Third time nesters	35%	19%	16%	17%
Fourth time nesters	8%	9%	14%	11%
Fifth time nesters	2%	3%	3%	7%

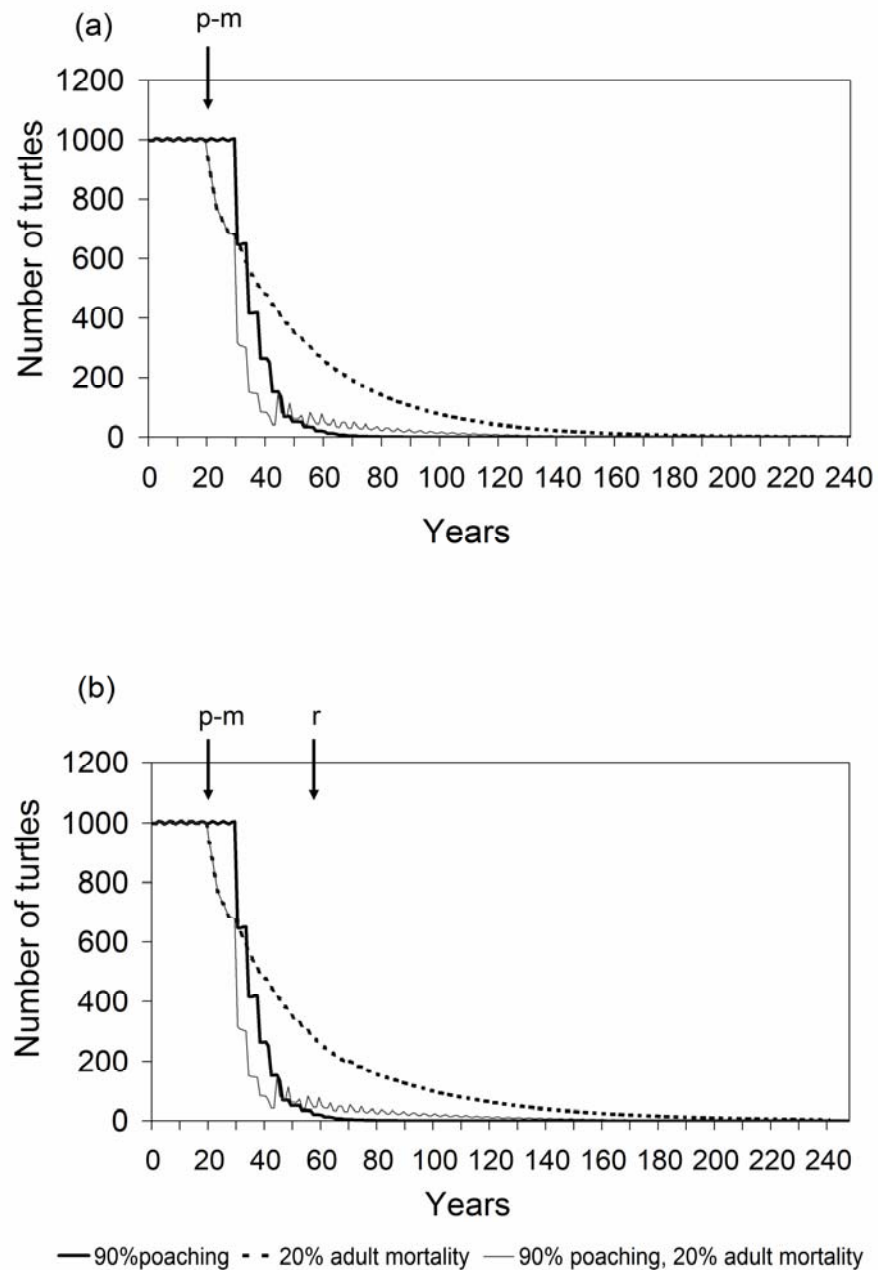


**Figure 5.** Number of nesting turtles through time. Arrows mark the time when poaching starts. **5a.** Effect of 90% poaching on the total number of nesting turtles and number of first, second, third, fourth and fifth time nesters. **5b.** Total number of nesting turtles through time for different intensities of egg poaching: 90%, 75%, 50% and 25%. **5c.** Actual number of nesting turtles per season at Parque Nacional Marino Las Baulas, between 1988-1989 and 2006-2007.

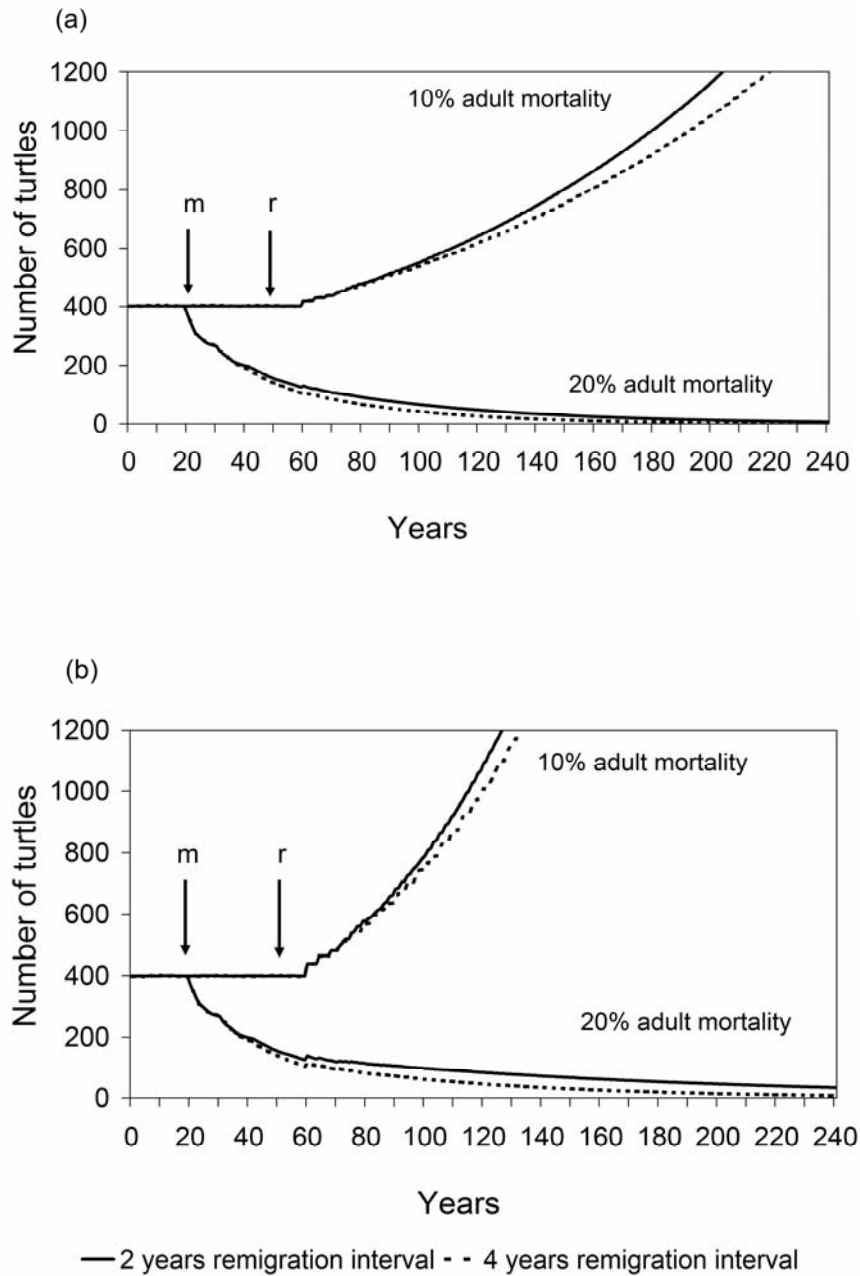




**Figure 6.** Total number of nesting turtles through time. 90% poaching starts at year 20. Then, poaching is stopped after the first, second, third and forth drop. “p” and the arrow mark the time when poaching starts. “r” marks the time when relocation starts. **6a.** There is no egg relocation **6b.** Relocation of 10% of eggs starts at year 100. Population parameters as in Figure 5.



**Figure 7.** Total number of nesting turtles through time. The population is subject to (1) 90% continuous poaching, (2) 20% annual adult mortality and (3) 90% poaching to the second drop and 20% adult mortality. “p, m” and the arrow mark the time when poaching, adult mortality or both, start. “r” marks the time when relocation starts. **7a.** There is no egg relocation. **7b.** Relocation of 10% of eggs starts at year 60. Population parameters as in Figure 5.



**Figure 8.** Number of nesting turtles through time. The effect of relocation on stable populations (10% mortality) is compared to the effect of relocation on populations with increased adult mortality (20% mortality). “r” marks the time when relocation starts. “m” marks time when annual mortality of adults is increased to 20% on the corresponding populations. Solid line shows populations with 2 years remigration interval and dashed line, populations with 4 years remigration interval. **8a.** Populations lose naturally 10% of eggs laid to tidal inundation. **8b.** Populations lose naturally 20% of eggs laid.

## CHAPTER 4: The walk to the water: the process of departure from the nest in hatchling leatherback turtles

### ABSTRACT

The process of departure of hatchling sea turtles from the nest is directed by the high probability of being predated on the walk to the water. During this process hatchlings must move rapidly, find the water and reduce the time spent on the beach. Hatchling leatherback (*Dermochelys coriacea*) turtles at Playa Grande, Costa Rica, spent 34 min visible during the process of departure from the nest to the water, covered a distance of 46.8 m and moved at a rate of  $3.11 \text{ m min}^{-1}$ . During the process of departure 12% of hatchlings were predated, 83% reached the water and 5% were potentially predated. The main predators of hatchling leatherbacks at Playa Grande were ghost crabs (*Ocypode occidentalis*), great blue herons (*Ardea herodias*) and yellow-crowned night herons (*Nycticorax violaceus*) during the night, and crested caracaras (*Polyborus plancus*) during the day. Straightness of tracks increased as the process of departure progressed from an average of 0.71 by the nest to an average of 0.90 near the high tide line and straightness was lower in areas of higher exposure to light pollution. Dispersion of tracks at the beginning and the end of the process of departure increased with number of hatchlings. Hatchlings “dilute” the predation risk by emerging in groups and by dispersing on the walk to the water. Further studies should continue to explore the effect of dispersion on the predation risk.

## INTRODUCTION

Sea turtles are marine animals highly adapted to the aquatic environment (Lutcavage & Lutz 1997) that spend over 99% of their lives in the ocean. However, they are still dependent on a terrestrial environment for a short period of time of their lives. There are three situations-stages at which sea turtles fully depend on land: (1) females need to lay eggs on tropical and sub-tropical beaches around the world (Miller 1997), (2) eggs develop buried deep in the beach for about 50-70 days (Ackerman 1997) and (3) hatchlings emerge from the nest and shortly and rapidly depart from the beach to the ocean (Carr & Ogren 1960). After reaching the ocean, female turtles will only return to the beach to nest for a short period of time and male hatchlings will never come back again.

The period of time hatchling turtles spend on the beach has received some attention. Most hatchlings emerge at night, because emergence from the nest is inhibited by high temperature, (Mrosovsky 1968; Drake & Spotila 2002). After hatchlings emerge, they move rapidly to the water displaying a typical behavior called frenzy that allows them to reduce the time exposed to predators (Dial 1987). Hatchlings typically emerge in several groups (Carr & Hirth 1961; Bustard 1967), crawl to the ocean and once in the water, they swim actively in a frenzy-swimming that lasts for approximately 24 hours (Wyneken & Salmon 1992). Frenzy-swimming has also been explained as a mechanism to reduce inshore predation (Salmon & Wyneken 1987). Therefore, frenzy behavior starts after hatchlings emerge from the nest, occurs on the beach to escape from land predators, and continues in the ocean to escape from aquatic predators.

Although predation of sea turtle hatchlings on the beach is assumed to be high, most studies on predation have focused on nests (Fowler 1979; Bouchard & Bjorndal 2000; Tiwari et al. 2006) rather than on hatchlings. Mammals prey on hatchlings, although they constitute a greater threat to nests (Stancyk 1979), and birds and crabs are also common predators on sea turtle hatchlings (Fowler 1979; Stancyk 1979).

Synchronous hatching and emergence in groups that occur in some reptile species may dilute predation risk (Spencer et al. 2001). The dilution effect refers to the lower probability of an individual being predated when part of a group than as an individual and has been extensively studied in ecology (Foster & Treherne 1981; Dehn 1990; Wrona & Dixon 1991). In general, the larger the group is, the lower the predation risk per individual. However, grouping also increases the detection effect by predators (Dehn 1990), a risk that sea turtle hatchlings must face during the process of departure from the nest. For example, Wyneken et al. (1998) observed that predatory fish were more abundant in waters near beach hatcheries where a high number of hatchlings were released than at other locations. In general, hatchling sea turtles have efficiently evolved to avoid predation on the beach: (1) by hatching and emerging synchronously in groups to dilute the predation risk, (2) by emerging from the nest at night and (3) by rapidly crawling down the beach while displaying a frenzy behavior.

In addition, there is a very important factor that takes place during the process of departure from the nest. In order to leave the beach rapidly, hatchlings must be able to efficiently locate the water first. The mechanism by which hatchlings find the ocean and orient themselves is well documented. While on the beach hatchlings are attracted by the brightness and the lower elevation of the water. Then, after reaching the ocean, they

follow the direction of the waves (Lohmann & Lohmann 1996). If hatchlings encounter difficulties in finding the ocean, their departure from the beach is delayed and therefore, the probability of being predated increases. Artificial lights from development behind or near nesting beaches are known to have a negative effect on hatchling orientation (Witherington & Bjorndal 1991). Hatchlings are attracted by these lights, move towards them and often die from dehydration or are depredated upon (Peters & Verhoeven 1994; Lorne & Salmon 2007). Good orientation plays an important role in the process of departure from the nest since it increases the probability of surviving to the next stage. In addition, turtles showing a poor orientation on the beach may not be able to orient themselves once in the water, which ultimately might affect the ability of the female turtle to find her way back to the beach after reaching sexual maturity (Lorne & Salmon 2007).

The focus of this study was to determine the role of predation in the departure of leatherback turtle (*Dermochelys coriacea*) hatchlings from the nest to the water. We carried out a natural experiment by measuring time spent by hatchlings in the departure process, distance covered, rate of movement, patterns of movement and predation of hatchlings. We then analyzed how factors that affected the process of departure interacted and determined the success of hatchlings in reaching the water.

## METHODS

We conducted this study at Playa Grande, Parque Nacional Marino Las Baulas, Costa Rica, during 2004-2005 and 2005-2006 nesting seasons. We divided the 3.6 km beach into 50 m sections and marked locations of nests. We placed a thermocouple into

each nest as turtles laid eggs to record temperatures during incubation, which in addition helped us to find nests. We measured distance from the nest to the closest marker to the north and south. We monitored temperatures during incubation and when nests were expected to hatch, we checked them daily at sunrise, before sunset and several times during the night.

### **Process of departure from the nest**

We performed direct observations at night in 2004-2005 and 2005-2006, during which we recorded times of activity and predation. We used a military night vision scope to be able to see the hatchlings without the need of a light. Nests that were expected to hatch were monitored during the night starting shortly after sunset. During each observation, there was only one observer located 15 to 20 m away from the nest to avoid interaction with predators. We only followed visually the first emergent group of hatchlings from each nest. We calculated that 87% and 78% of the total number of emerged hatchlings from study nests in 2004-2005 and 2005-2006 were in the first group of emergents. This percentage was based on the average number of hatchlings seen during the first observation related to the calculated number of hatchlings emerged (average number of eggs per clutch multiplied by average emergence success for the season). We recorded observations on predation and times of activity. We counted and measured hatchling tracks coming from the nest after hatchlings left the beach.

*Duration, distance covered and rate of movement.* We annotated times when a depression in the sand occurred over the nest, once hatchlings were visible, when hatchlings started moving and when they reached the water. Once all hatchlings were gone, we measured the distance from the nest to the water line. We calculated the rate of



movement on the beach by dividing the distance covered by the time taken by the first hatchling to reach the ocean and leave the beach. Rate of movement was only estimated in 2005-2006.

*Patterns of movement.* We measured straightness of tracks and dispersion in 2005-2006. We measured tracks left by hatchlings at the end of the direct observations after all hatchlings entered the ocean. Additionally, we measured tracks early in the morning when nests that hatched the previous night had been missed by the night observer. For each nest, we calculated straightness indexes of tracks at two locations to compare the beginning and the end of the departure process: (1) within the first meter of the emergence location and (2) within the last meter of the high tide line. We measured a meter in a straight line from the nest towards the ocean and then made two parallel lines to the shore, first through the center of the emergence location and second, one meter away from the nest (Fig. 9). Then, we repeated these measurements at the entering location through the high tide line and one meter away inland. We measured the total distance covered by 5 hatchlings in between the two lines at each location. Then, we calculated the straightness index of each track by dividing one meter by the actual distance covered by the hatchlings between the two lines. Finally, we calculated an average straightness index per nest at the emergence location and at the entering location. In addition, we measured hatchling dispersion at two locations: by the nest and by the high tide line. We used the line parallel to the shore one meter away from each location and measured the greatest distance between tracks along each line. Finally, we counted the number of tracks coming from the nest.

*Predation.* We recorded every time a hatchling was predated, the time at which it happened, and the predator species. Once all hatchlings were gone we checked for unnoticed predation. We considered hatchlings as potentially predated when they stayed upside down and could not right themselves and when they got stuck in vegetation or at other obstacles and could not escape. In addition to night observations, we recorded predation when it was directly observed during the morning walk and in the afternoon. We also recorded any signs of predation when we found tracks from an emerged nest missed by the night observer and all hatchlings were gone.

We made direct observations on 23 nests in 2004-2005 and 24 nests in 2005-2006, from which we recorded predation and duration of activities. In addition, we measured tracks to estimate straightness indexes and dispersion from 38 nests in 2005-2006. Distributions of variables were tested for normality using the Kolmogorov-Smirnoff test. Straightness indices were arcsin transformed prior to analysis. Nonparametric tests were used when assumptions of normality were not met.

## RESULTS

The highest number of nests laid by female leatherbacks at Playa Grande concentrated around the central part of the beach in 2004-2005 and 2005-2006 (Fig. 10).

*Duration, distance covered and rate of movement.* Leatherback hatchlings took 34 min to reach the ocean after they were visible at the nest. Hatchlings spent longer time visible in 2004-2005 (range: 19 to 73 min) than in 2005-2006 (range: 8 to 51 min) but the difference was not significant (independent t-test:  $t_{21} = -1.966$ ;  $P = 0.063$ ). Equally, the time elapsed between each pair of activities was always longer in 2004-2005 (Table 8)

but in no case significant. The distance covered by the hatchlings on their way to the water ranged from 16 to 107 m ( $X \pm SD = 46.8 \pm 30.2$  m). The rate of movement from the nest to the water ranged from 1.80 to 6.00 m min<sup>-1</sup> ( $X \pm SD = 3.11 \pm 1.29$  m min<sup>-1</sup>).

*Patterns of movement.* Tracks were significantly straighter within the last meter before the high tide line than within the first meter of departure from the nest (paired t-test:  $t_{37} = -6.631$ ,  $P < 0.01$ ). Straightness index by the nest was  $X \pm SD = 0.71 \pm 0.19$  and by the high tide line  $0.90 \pm 0.09$ . Therefore, hatchling tracks became straighter and less variable as the departure process progressed.

Tracks by the nest were straighter towards the south part of the beach than towards the north (linear regression:  $R^2 = 0.14$ ,  $P < 0.05$ ). Similarly, tracks by the high tide line were straighter towards the south (linear regression:  $R^2 = 0.14$ ,  $P < 0.05$ ) (Fig. 11a). Dispersion by the high tide line was also related to the location on the beach, being greater towards the north (linear regression:  $R^2 = 0.14$ ,  $P < 0.05$ ). However, dispersion by the nest was not significantly affected by location on the beach (Fig. 11b).

The straightness index by the nest was negatively correlated with both dispersions: by the nest (Spearman correlation:  $r_s = -0.681$ ,  $P < 0.0001$ ) and by the high tide line ( $r_s = -0.475$ ,  $P < 0.005$ ). The number of tracks was not significantly related to the straightness indices either by the nest ( $R^2 = 0.16$ ,  $P = 0.085$ ) or by the high tide line ( $R^2 = 0.012$ ,  $P = 0.598$ ). However, there was a significant positive relationship between the number of tracks and dispersion by the nest (linear regression:  $R^2 = 0.54$ ,  $P < 0.001$ ) and the high tide line (linear regression:  $R^2 = 0.35$ ,  $P < 0.01$ ) (Fig. 11c).

*Predation.* On average, 83% of all hatchlings seen after emergence reached the ocean in 2004-2005 and 2005-2006; 12% of hatchlings were predated and 5% were

potentially predated, because they were trapped on the vegetation, on logs or upside down and were not capable of righting themselves (Table 9). Seventy four percent of nests seen at the first emergence had some predation and 26% of nests had no predation for at least the first emergent group. Number of hatchlings predated per nest in 2004-2005 and 2005-2006 was  $X \pm SD = 2.5 \pm 2.9$  and  $1.4 \pm 1.1$  respectively and the number of hatchlings per nest that reached the water was  $X \pm SD = 11.4 \pm 12.5$  and  $19.3 \pm 17.8$ . There were no significant differences in the number of hatchlings that reached the water (Mann-Whitney  $U$  test:  $U = 164.5$ ,  $N_1 = 23$ ,  $N_2 = 20$ ,  $P = 0.11$ ), were predated ( $U = 198.5$ ,  $N_1 = 23$ ,  $N_2 = 20$ ,  $P = 0.43$ ) and potentially predated ( $U = 212$ ,  $N_1 = 23$ ,  $N_2 = 20$ ,  $P = 0.61$ ) between 2004-2005 and 2005-2006.

The most common predator of hatchling leatherback turtles was the ghost crab (*Ocypode occidentalis*). Ghost crabs took hatchlings from 12 of 23 nests in 2004-2005 and from 15 of 24 nests in 2005-2006 (Table 10). Nocturnal birds that predated hatchlings included yellow-crowned night herons (*Nycticorax violaceus*) and great blue herons (*Ardea herodias*). Crested caracaras (*Polyborus plancus*) ate hatchlings early in the morning near sunrise, between 0500 and 0600 hours. In addition, there were unidentified diurnal predators that attacked hatchlings when hatchlings emerged late in day, before sunset. When this happened we found hatchlings partially eaten but did not see the predator. Thus, we could reconstruct the number of hatchlings killed for those nests but could not identify the predator species. There were 2 nests in 2004-2005 and 1 in 2005-2006 with this characteristic type of predation. Ghost crabs took 1 to 3 hatchlings per nest and night birds and diurnal predators took 1 to 9. Ghost crabs accounted for 48.3% of all hatchlings predated, night birds accounted for 26.4% and diurnal predators

accounted for 25.3%. However, crabs predated a larger proportion of nests (27) compared to night birds (8) and diurnal predators (8). During our observations, mammals did not predate hatchlings. However, in prior years raccoons did predate leatherback hatchlings. The number of hatchlings predated by crabs (Mann-Whitney  $U$  test:  $U = 181.5$ ,  $N_1 = 23$ ,  $N_2 = 20$ ,  $P = 0.21$ ) and night birds ( $U = 189.5$ ,  $N_1 = 23$ ,  $N_2 = 20$ ,  $P = 0.15$ ) was not significantly different for the two seasons studied. The number of hatchlings predated by crabs increased with the total number of hatchlings seen during the process of departure ( $R^2 = 0.11$ ,  $P < 0.05$ ).

There were more hatchlings seen per nest towards the north end of the beach than towards the south (linear regression:  $R^2 = 0.12$ ,  $P < 0.05$ ) and more hatchlings that reached the water (linear regression:  $R^2 = 0.11$ ,  $P < 0.05$ ) towards the north. However, the total number of hatchlings predated was not correlated to the location of the nest on the beach (spearman correlation:  $r_s = 0.007$ ,  $P = 0.965$ ). More hatchlings were predated by yellow-crowned night herons towards the south end of the beach (linear regression:  $R^2 = 0.13$ ,  $P < 0.05$ ).

We found 250 nests that emerged the previous night during 49 morning walks in 2005-2006. From 33 of them (13%) there was at least 1 hatchling still on the beach. Crested caracaras flew along the beach between 0500 and 0600 hours nearly every morning. However, predation could not always be determined if we were too far from the nest. Frigatebirds (*Fregata magnificens*) also took hatchlings on two different occasions, once hatchlings were already in the water. In addition to natural predators, domestic animals frequently attacked hatchlings on the beach. Nineteen nests were excavated by

dogs after hatchlings emerged and 2 domestic cats took at least 1 hatchling from a nest located close to one of the beach entrances.

In addition to hatchlings killed by predation, 56 hatchlings from 4 different nests desiccated in 2005-06 because of daytime emergence. Hatchlings were at various distances from the nest and variable directions.

## **DISCUSSION**

A female leatherback turtle nests 7 times in a season and spends approximately 1 and ½ hours on the beach each time (Reina et al. 2002). If she nests 5 seasons in her life she will spend about 52 and ½ hours nesting. If she lives 30 years, she will spend 0.02% of her life nesting. Incubation takes about 60 days (Bell et al. 2003), which is about 0.55% of the life of that female. If emergence takes 4 days, this requires 0.04% of her life. The process of departure to the water lasts on average 34 min which is about 0.0002% of her life. Although the departure process takes as little as 0.0002% of their lives, 12% to 17% of the hatchlings die on the way to the ocean. Therefore, adaptations to reduce the probability of mortality on the beach are highly valuable because of the high risk of mortality on the walk to the water.

Since mortality during the departure is high, hatchlings must reduce the time exposed to predation to a minimum. We found that leatherback hatchlings at Playa Grande spent about 20 min visible on the beach before they moved to the water. By being motionless hatchlings become an easy target to predators. However, very few predation events occurred before hatchlings moved. Most predation that took place by the nest occurred during the day, either early in the morning or just before sunset. Only one

predation event took place around the nest during the night and the predator was a night heron. Great blue herons are mainly crepuscular, but also diurnal and nocturnal feeders, and yellow-crowned night herons are crepuscular and nocturnal feeders. Both yellow-crowned night herons and great blue herons are visual predators and the nocturnal vision capability is good in both species but best in yellow-crowned night herons (Rojas et al. 1999). However, detecting hatchlings on top of the nest in the dark is probably difficult for any visual predator if hatchlings are not moving. Therefore, once hatchlings move, they must do it rapidly because the probability of detection increases.

Leatherback hatchlings reduce the predation risk first by dilution and second by dispersion to compensate for the detection effect from grouping. However, dispersion will be limited by the necessity to reduce the time spent on the beach. Hatchlings reduce time spent on the beach and, therefore, predation risk by moving straight to the water but also reduce the predation risk by dispersing. The dilution effect makes a hatchling less likely to be predated if it is part of a group. However, group size also increases probability of detection. Birds at night frequently fly and rest on the beach. If the bird is flying, it is more likely that it will detect a large group of hatchlings running to the ocean than a smaller one. Therefore, detection risk increases with group size. Ghost crabs are sensitive to noise and vibration (Horch 1971) and the effect of a group of hatchlings should be more easily detected by crabs than the effect of a single hatchling. Normally, once hatchlings start moving, ghost crabs arrive in the area shortly after. There was a positive relationship between total number of hatchlings coming from a nest and number predated by crabs.

The occurrence of animal aggregations that reduce the risk of predation is known for many species. For example, the dilution effect in groups reduces predation on marine insects by small fish (Foster & Theherne 1981). Attacks on large groups of marine insects are less successful because of predator confusion. Mormon crickets have a lower probability of being predated when migrating in large groups (Sword et al. 2005). Aggregations of ungulates are related to the risk of predation and to the quality of the feeding habitats (Kie 1999). Grouping in aphids is a successful strategy to reduce the risk of predation (Turchin & Kareiva 1989). In this case, aggregation is advantageous only in the presence of predators. Predators also responded to aggregating, but grouping is still beneficial as a result of the dilution effect. Another benefit derived from aggregation is the confusion effect. The confusion effect refers to the higher difficulty of capturing a prey if it is surrounded by other individuals (Schradin 2000). The confusion effect has been reported frequently together with the dilution effect (Foster & Theherne 1981; Sword et al. 2005; Wrona & Dixon 1991).

Dispersion of hatchlings on the walk to the water increased with the number of tracks, both near the nest and by the high tide line. Two hypotheses could explain the behavior of dispersion during the process of departure. First, the probability of being predated could vary for different locations. For example, if the core of the group had a higher probability of being predated, some hatchlings would disperse from the group to increase their chances of surviving. Second, dispersing and increasing the distance from each other would make a predator less efficient at capturing multiple hatchlings and additionally it would spend more energy doing so. Consequently, the total number captured by a single predator would be lower if hatchlings disperse and, therefore, the



probability of being predated per individual would be even lower. Therefore, dispersion provides an additional advantage for surviving on the walk to the water.

The distance between high and low tide at Playa Grande ranges between 50 m and over 100 m (Reina et al. 2002). Consequently both time spent on the beach and distance covered by hatchlings is highly variable. Hatchlings that emerge when the tide is high benefit from a short distance to the water and, therefore, a shorter time on the beach. On the other hand, hatchlings that emerge when the tide is receding, could ride it out, swimming faster and getting away from the beach rapidly, reducing the risk of predation in the water. Additionally, emerging early in the night is also beneficial since it gives hatchlings more time to get away from the beach before the daylight predators are active (Spotila et al. 1996). Therefore, there is not a clear advantage in either emergence pattern at Playa Grande. Emergence times of loggerhead turtles (*Caretta caretta*) in Melbourne beach, Florida, follow a normal distribution with peak time between 2300 and 2400 hours (Witherington et al. 1990). Glen et al. (2006) found emergence peak of green turtle (*Chelonia mydas*) hatchlings between 2000 and 2100 hours. Drake & Spotila (2002) reported that most nests in a hatchery at Playa Grande emerged between 1830 and 2100 hours. In the three studies emergence was related to sand temperatures.

Leatherback hatchlings moved slower than loggerhead hatchlings in Florida (Dial 1987). Hatchling loggerheads during the frenzy moved at  $6.5 \text{ m min}^{-1}$  ( $5.2$  to  $7.0 \text{ m min}^{-1}$ ). Maximum rate of movement of leatherbacks at Playa Grande was  $6.0 \text{ m min}^{-1}$  and mean was  $3.1 \text{ m min}^{-1}$ . This difference might be partly a result of the selection by Dial for turtles that maintained constant hatchling frenzy locomotion and traveled directly to the water. In addition, we did not measure the actual speed of the turtles. Instead, we

measured the rate of movement between two points: from the nest to the water, regardless of the straightness of the route followed. Therefore, our values do not correspond to the actual speed at which the animal moved. Rate of movement of both leatherback and loggerhead hatchlings were below the reported speeds for ghost crabs. During the times crabs are moving, they reach speeds of about  $4.8 \text{ m min}^{-1}$  but under stress can reach speeds as high as  $49.8 \text{ m min}^{-1}$  (Weinstein 1995). Therefore, ghost crabs can easily overrun their prey.

Hatchlings follow paths consistently straighter once they are near the high tide line than when they are around the nest. Therefore, their ability to find the water and to follow the shortest possible way to the ocean improves as the process of departure progresses. We also found straighter tracks coming from nests laid towards the southern part of the beach. Because of the shape of the beach, hatchlings at the north end have a higher exposure to the lights coming from the town of Tamarindo, which is located to the south (Fig. 12). Despite the conservation efforts of the Las Baulas National Park to protect leatherback turtles from development (Steyermark et al. 1996), light pollution at Tamarindo has considerably increased in the last ten years and continues to rise yearly. The town of Tamarindo has become a developed island surrounded by Las Baulas National Park, and has no controlling rules for the illumination at night.

Despite the higher concentration of nests that are laid every year around the central part of Playa Grande (Fig. 10), we found that predation in general was not related to the location along the beach. Predation by yellow-crowned night herons, however, was greater towards the south end. This could be related to the shortest distance between the

southern end and the Estuary, where yellow-crowned night herons are frequently seen during the day (Fig. 12).

Mammals did not predate on hatchlings during the night observations. Dogs seldom go on the beach at night. However, dogs did disturbed hatchlings from 8% of nests during the day at dawn or dusk. The presence of the observer may have prevented other mammals from approaching the nest. This is unlikely since raccoons frequently jump over the fence of the hatchery located at Playa Grande, with people inside and generally act fearlessly. A second possibility is that raccoons are not as interested in hatchlings as they are in eggs as reported by Stancyk (1979). A third explanation comes from the opportunistic nature of raccoons as predators (Garmestani & Percival 2005). Since the number of female leatherbacks has decline by 95% since the late 1980s (Santidrián Tomillo et al. 2007), the production of hatchlings has also declined and the probability of being on the beach when hatchlings emerge from a nest is very low. Consequently, raccoons do not visit the beach frequently at night.

In conclusion, despite the short duration of the process of departure from the nest, hatchlings are highly adapted to this activity, which is driven by the urge to reach the water to avoid predation. Thus, hatchling sea turtles are an excellent model to test dilution, detection, confusion and dispersion. Hatchlings “dilute” the predation risk by emerging and running in groups and by dispersion. In addition to natural predators, hatchlings face new threats during the process of departure from the nest. These are mainly disorientation caused by light pollution and predation by domestic animals, which need to be controlled given the status of leatherback turtles as critically endangered. The patterns followed by hatchlings during the process of departure need further exploration

to better understand the mechanisms that drive dispersion on the beach and whether or not similar patterns continue once in the water.

**Table 8.** Time elapsed between activities of leatherback turtle hatchlings on Playa Grande, Costa Rica, during the process of departure from the nest to the water.

Season	N	Mean time between two activities (min) $\pm$ SD			
		Depression in sand – hatchling visible	Hatchling visible – hatchling moving	Hatchling moving – hatchling reaching water	Hatchling visible – hatchling reaching water
2004-05	17 $\pm$ 16	43 $\pm$ 26	21 $\pm$ 17	19 $\pm$ 8	41 $\pm$ 18
2005-06	25 $\pm$ 19	32 $\pm$ 28	18 $\pm$ 17	16 $\pm$ 13	26 $\pm$ 17
Average	21	37	20	17	34

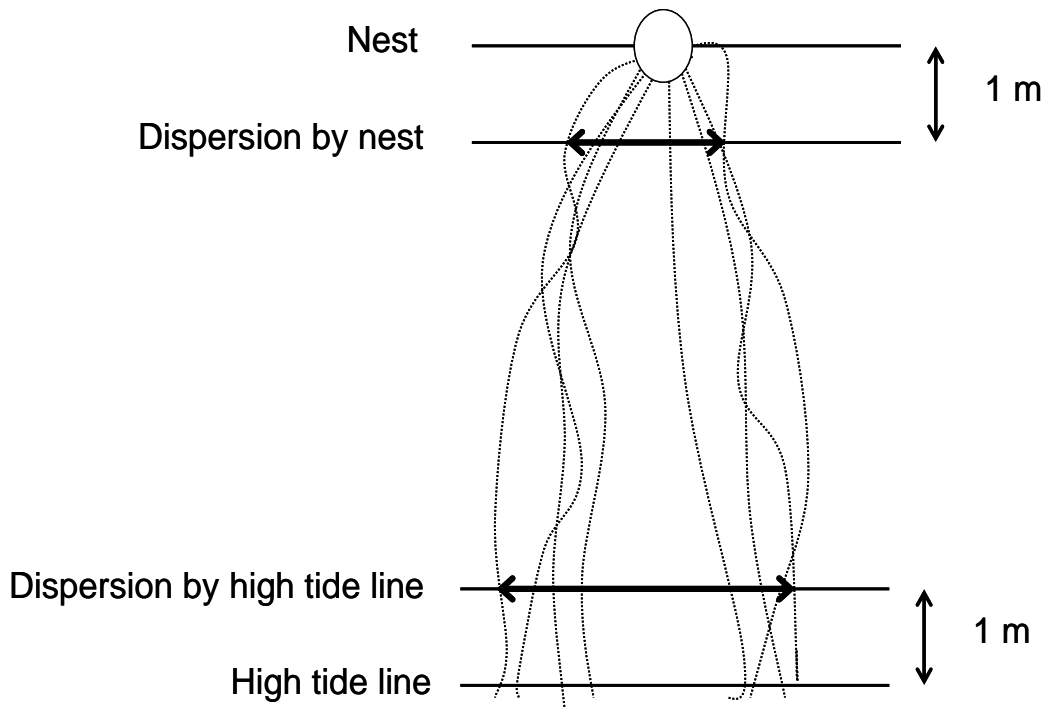
**Table 9.** Number and percentage of leatherback hatchlings seen during direct observations at Playa Grande, Costa Rica, that were predated, potentially predated and that reached the water in 2004-2005 and 2005-2006.

Season	Number of hatchlings	Number of nests	Hatchlings to the water		Hatchlings predated		Hatchlings potentially predated	
			#	%	#	%	#	%
2004-2005	337	23	263	78.0%	58	17.2%	16	4.7%
2005-2006	442	24	386	87.3%	33	7.5%	23	5.2%
Total	779	47	649	83.3%	91	11.7%	39	5.0%

**Table 10.** Predation of leatherback turtle hatchlings on Playa Grande, Costa Rica, in 2004-2005 and 2005-2006.

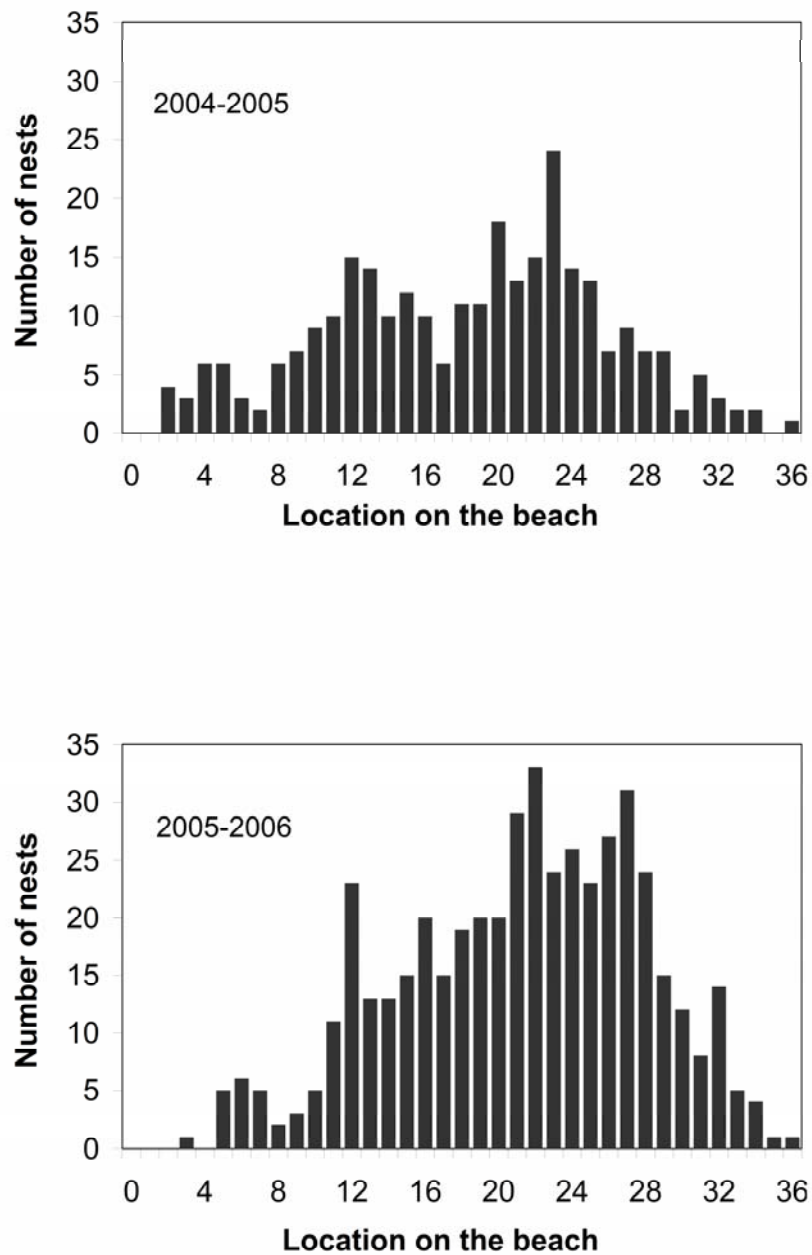
	Number of hatchlings		Nests with predation	
	2004-2005	2005-2006	2004-2005	2005-2006
ghost crab	20	24	12	15
yellow-crowned night heron	11	2	4	1
great blue heron	9	1	1	1
unidentified night heron	1	0	1	0
total night birds	21	3	6	2
crested caracara	6	5	1	4
unidentified diurnal predator	11	1	2	1
total diurnal predators	17	6	3	5
domestic animals	-	-	-	20*

\*19 nests were disturbed by domestic animals but predation of hatchlings was not quantified

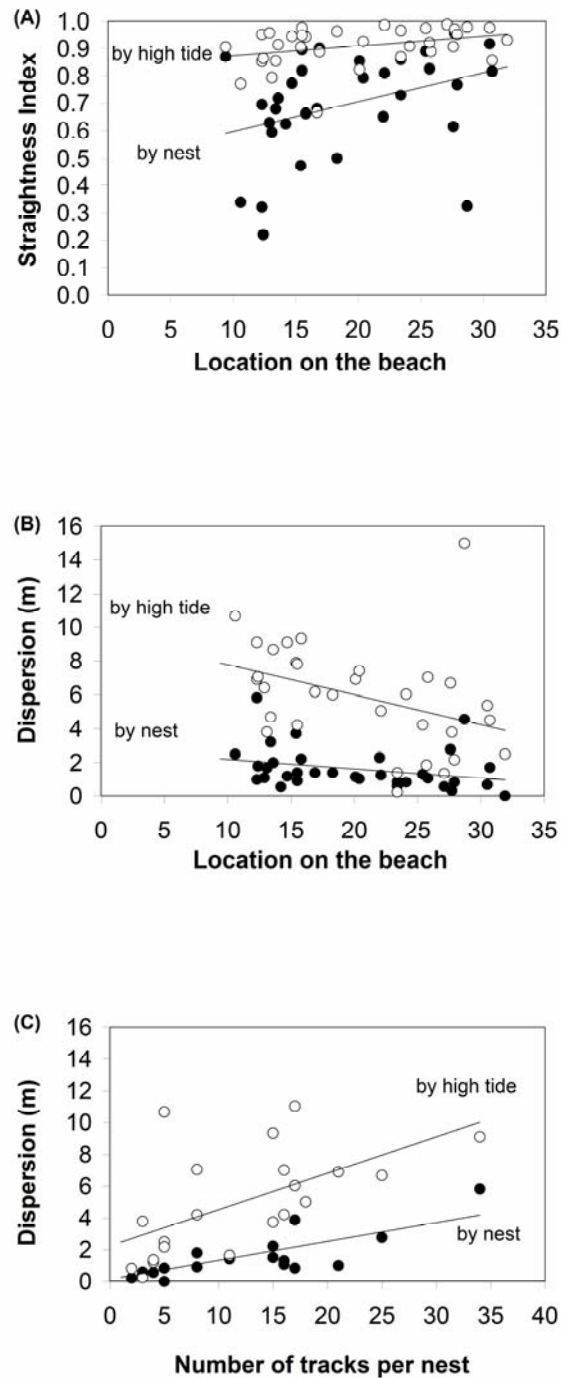


**Figure 9.** Diagram of hatchling tracks of leatherback turtles coming from the nest at Playa Grande. Dispersion was measured along the line located 1 m from the nest and 1 m from the high tide line. Straightness was calculated by measuring the distance covered of 5 tracks: (1) in between the nest and the first line located 1 m away and (2) in between the high tide line and the line located 1 m away inland. The straightness index of each track at each location was estimated by dividing 1 m by the distance covered by the track between the two lines.

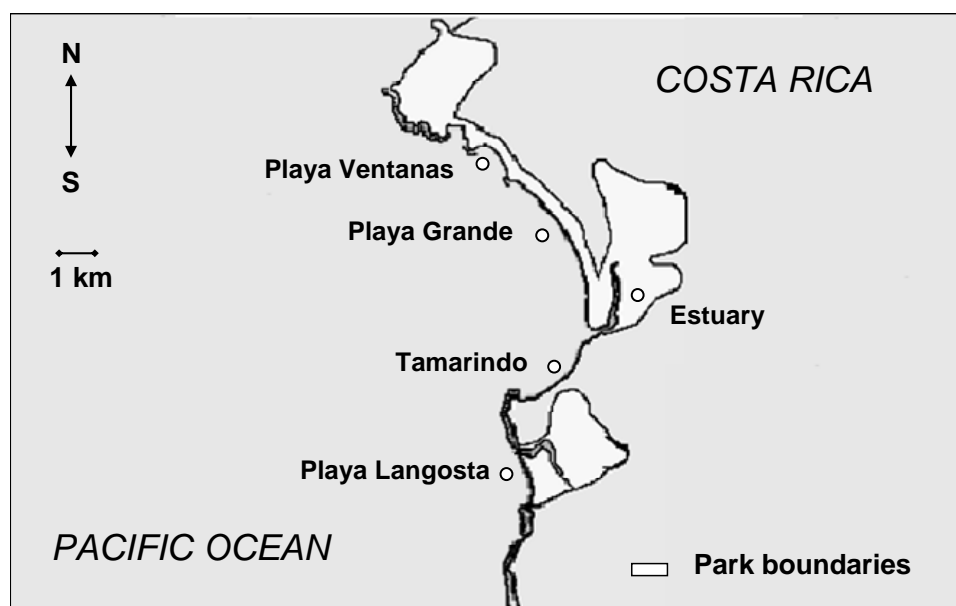




**Figure 10.** Distribution of leatherback turtle nests laid on Playa Grande along the beach in 2004-2005 and 2005-2006. **10a.** Number of nests per location in 2004-2005. **10b.** Number of nests per location in 2005-2006.



**Figure 11.** Straightness index and dispersion of tracks of leatherback turtle hatchlings at Playa Grande. **11a.** Straightness index of hatchling tracks by the nest and by the high tide line along the beach **11b.** Dispersion of hatchling tracks by the nest and by the high tide line along the beach. **11c.** Dispersion of hatchling tracks by the nest and by the high tide line in relation to the number of tracks.



**Figure 12.** Map of Parque Nacional Marino Las Baulas in Guanacaste, Costa Rica.

## **CHAPTER 5: Nest success and reproductive success of leatherback turtles are driven by environmental variability**

### **ABSTRACT**

Reproductive success of leatherback turtles (*Dermochelys coriacea*) depends on environmental variability. High temperatures in the nest during incubation reduced hatching success and proportion of hatchlings emerged, and affected development both early and late during the incubation process. There was a seasonal effect on nest success with more hatchlings being produced at the beginning of the season, because of higher hatching success, than towards the end. Hatching/emergence success and proportion of hatchlings emerged differed between seasons and was strongly related to local weather conditions. In particular, total rainfall in the two months before nests were laid and ambient temperature during the two months of incubation explained 82% of the variation in monthly emergence success. Overall, seasons with high levels of rain and low temperatures had higher emergence success than dry and hot seasons. Predicted emergence success from 1976 to 2006 based on local weather, was also related to global weather in the Pacific Ocean. El Niño Southern Oscillation (ENSO) was related to predicted emergence success, with El Niño years corresponding to seasons of low emergence success and La Niña years corresponding to seasons of high emergence success. Total production of hatchlings increased with number of seasons female turtles had nested and was related to an increase in number of eggs and clutches and the early arrival of turtles that had nested multiple seasons. The environmental variability effect on hatchling production and ultimately, recruitment to the nesting population, may constitute

an additional threat to the nesting population of leatherback turtles at Parque Nacional Marino Las Baulas.

## INTRODUCTION

Leatherback turtles (*Dermochelys coriacea*) exhibit the greatest reproductive investments among reptiles (Wallace et al. 2007). Females lay on average 60-80 eggs per clutch and 7 clutches during a nesting season (Van Buskirk & Crowder 1994, Boulon et al. 1996, Reina et al. 2002). In addition, they reproduce multiple seasons during their life with an interval of 2-3 years in Atlantic populations (Girondot & Fretey 1996, Dutton et al. 2005) and 3.7 years in Eastern Pacific ones (Reina et al. 2002). High investment in reproduction is usually associated with low survival of early stages (Stearns 1989). Mortality of eggs and hatchlings is high in sea turtles. Loss of clutches, embryonic mortality during development, unsuccessful emergence and predation reduce overall offspring survival and that, ultimately conditions the reproductive success of female turtles.

Nest success can be quantified by looking at (1) hatching success of the clutch (proportion of eggs that develop into hatchlings), (2) emergence success (proportion of eggs that result in emerged hatchlings) and (3) proportion of hatchlings emerged (proportion of emerged hatchlings in relation to the number of hatchlings hatched). Hatching success of leatherback turtle nests is low, approximately only half of the eggs laid develop into hatchlings (Bell et al. 2003), unlike other sea turtles species that are characterized by higher survival of eggs (~80%) (Miller 1997). Hatchling sea turtles die in the nest before emergence is complete (Fowler 1979) and after emergence, hatchlings

still face high risk of predation, both on the beach and once in the water (Fowler 1979, Stancyk 1979, Gyuris 1994).

Abiotic factors such as temperature and humidity affect developmental success in both freshwater turtles (Packard et al. 1988, Packard et al. 1999, Tucker & Paukstis 2000) and sea turtles (Davenport 1997). Temperature in sea turtles determines sex during the middle third of incubation (Morreale et al. 1982), accelerates development (Miller 1997), increases embryo abnormalities (Billet et al. 1992), affects size of hatchlings (Booth et al. 2004, Reece et al. 2002) and decreases activity of hatchlings due to thermal inhibition (Drake & Spotila 2002). Additionally, high temperatures reduce proportion of hatchlings emerged (Matsuzama et al. 2002).

Humidity also increases hatching success in olive ridley turtles (*Lepidochelys olivacea*) (López-Castro et al. 2004) and hatchling size in loggerhead turtles (*Caretta caretta*) (Reece et al. 2002). On the other hand, some studies have found no apparent effect of temperature/humidity on nest success. For example, Hewavishenthi and Parmenter (2000) found that hatching success in flatbacks (*Natator depressus*) was not influenced by hydric environment and Matsuzama et al. (2002) found no relationship between temperature and hatching success. Factors other than temperature and humidity also affect nest success. For example, beach location (Caut et al. 2006), clutch size (Hewavishenthi & Parmenter 2002), sand compaction (Peters et al. 1994) and fungal infection ((Phillott & Parmenter 2001) all affect hatching and emergence successes.

Although overall hatching success of leatherback turtle nests is low (~50%), this is highly variable. Several studies on leatherback nests have been carried out to explain the low levels of hatching success at Playa Grande, Parque Nacional Marino Las Baulas

(PNMB), in Costa Rica. Bell et al. (2003) found that high embryonic mortality and not unfertilized eggs (~90-95% of eggs were fertilized) caused low hatching success. Wallace et al. (2004) found no relationship between hatching success and temperature in hatchery conditions at PNMB. However, Bilinski et al. (2001) found hatching success of eggs incubated in artificial conditions to be related to temperature. Wallace et al. (2004) also showed that PO<sub>2</sub> decreased as number of metabolizing embryos increased but was not related to hatching success. Ralph et al. (2005) found differential hatching success within a nest, with lower success at the center of the nest and higher towards the sides. Despite the long-term research on nests at PNMB, factors affecting hatching success of *in situ* leatherback nests remain unknown. Studies at PNMB were always conducted in “non-natural” relocated nests at the hatchery or in incubators. Furthermore, these studies were limited to nests relocated during the first two months of the season, so information on the last part of the season was lacking. Thus, variability in nest success along the season has yet to be analyzed, as well as between seasons and in natural *in situ* conditions.

Environmental variability is known to affect recruitment in sea turtle populations. Erosion can cause high loss of nests on some beaches (~45-60%) (Eckert 1987) and tidal inundation prevents development when clutches are washed by high tides (Leslie et al. 1996). High variability in nest success due to environmental variability could affect the overall reproductive success of leatherback turtles at PNMB. To increase lifetime reproductive success turtles may increase number of eggs per clutch, number of clutches per season, number of seasons nested or nest success by increasing hatching/emergence success.

The focus of this study was to determine factors affecting hatchling production through the analysis of nest success, and ultimately, the contribution of nest success to the reproductive success of female leatherback turtles. First, we looked at “in situ” effects on the success of leatherback turtle nests by looking at the effects of incubation temperature, location on the beach, distance to vegetation, distance to high tide line and number of eggs laid in a clutch. Second, we analyzed seasonality in nest success through the season and between seasons and the effects of local and global weather on the overall success of nests. Finally, we looked at the contribution of nest success to the reproductive success of leatherback turtles at PNMB.

## **METHODS**

We conducted the study at Playa Grande, the main nesting beach at Parque Nacional Marino Las Baulas, on the Pacific coast of Costa Rica. The beach is 3.6 km long. We divided the beach in 36 sections of 100 m with markers from North to South to determine the part of the beach where turtles laid clutches. Then, we subdivided each section in two 50 m sections. We collected data during three seasons: 2004-2005, 2005-2006 and 2006-2007. We marked a total of 417 nests (114, 172 and 131 in 2004-2005, 2005-2006 and 2006-2007 respectively).

### **“In situ” effects on nest success**

We marked nests when we found turtles on the beach before they had laid or were already laying eggs. We counted number of eggs when possible and deposited a thermocouple into the nest to record temperatures. We located the tip of the thermocouple in the center of the clutch and the connector at the surface of the sand. We measured the



distance from the top of the nest to the two closest markers on the beach to determine its location. Additionally, we measured the distance from the nest to the vegetation and to the latest high tide line. We recorded temperatures using a thermocouple reader every two days during the incubation period.

Once hatchlings were observed or tracks were found coming from nests, we excavated nests two days after the first observance. When there were no signs of emergence 70 days after the nest was laid, we excavated it. Because the average incubation period at Playa Grande was 60 days and the longest recorded 69 days, we considered that after 70 days, a nest with no signs of emergence had either 0% emergence success or the emergence event had been missed.

During excavations we counted number of shells, number of unhatched eggs and number of dead and live hatchlings. We distinguished 4 developmental stages in unhatched eggs based on Leslie et al. (1996): (0) there were no signs of development, (1) there were signs of development such as blood vessels or a black spot but the embryo was not visible, (2) embryo was visible but had no pigmentation and (3) embryo had pigmentation. Additionally, we considered an unhatched egg to be of “unknown stage” when we could not determine the developmental stage at which the egg had died. We combined stages 0 and 1 in early developmental stages and considered stage 3 as the only late environmental stage. We calculated hatching success by using the formula:  $H = S/(S+U)$ , where S was number of shells and U, number of unhatched eggs. We calculated emergence success by using the formula:  $E = (S-(L+D))/(S+U)$ , where L was the number of live hatchling left in the nest and D was the number of dead hatchlings found in the

nest. Finally, we calculated proportion of hatchlings emerged by using the formula:  $P = (S - (L + D)) / S$ .

### **Seasonality in nest success: weather effects**

To analyze seasonality in nest success we compared hatching success, emergence success and proportion of hatchlings emerged by date nests were laid along the season. We gathered local weather data from a weather station located at the Liberia airport, 55 km in straight line from Playa Grande. We obtained rain accumulation and average ambient temperature per month between 1976 and 2006. We compared average hatching/emergence success per month in each season, to the rain accumulated in the three previous months, two previous months, previous month, current month and in the two months of incubation (month laid and following month). We also compared average ambient temperature during the two incubation months to monthly hatching/emergence success.

We used the regression equation that explained the greatest variation in nest success, obtained from the local weather data, to predict the average emergence success between seasons 1976-1977 and 2006-2007. Then, we compared the predicted emergence success to annual Multivariate ENSO Index (MEI) to relate emergence success to global weather patterns in the Pacific Ocean. We chose to use MEI because of the known influence of El Niño/La Niña events in ecological processes.

### **Reproductive success: hatchling production**

We conducted a long-term population study on the leatherback turtles that nest at PNMB since the late 1980s (Steyermark et al. 1996, Spotila et al. 2000, Reina et al. 2002,

Santidrián Tomillo et al. 2007). As part of this bigger project, we identified every turtle that came to the beach to nest with Pit tags (passive integrated transponder). Saturation tagging started in 1993-1994. Therefore, every turtle that nested at Playa Grande since 1993-1994 was identified with a permanent tag. This methodology allowed us to track the fate of nests laid by individual females within and between seasons.

We calculated total production of hatchlings per female in each season. We obtained total production for a female by multiplying average number of eggs of all her clutches by her estimated clutch frequency (ECF) (description of ECF in Steyermark et al. 1996) and by the average hatching success of her nests. We only included females for which we had at least three nests successfully excavated. We calculated production of hatchlings for 33 females in 2004-2005, 25 in 2005-2006 and 21 in 2006-2007. We compared total production of hatchlings by date nests were laid along the season, to determine any seasonal effects on hatchling production. Finally, we compared number of eggs, ECF and hatchling production according to the number of seasons females had nested.

All statistical tests were made using SPSS. We used Kruskal-Wallis test to compare differences in nest success between seasons, and regressions to quantify the effects of different variables on nest success and reproductive success. Hatching success, emergence success and proportion of hatchlings were arcsin transformed before analysis.

## RESULTS

### “In situ” effects on nest success

There were significant differences between seasons in hatching success ( $KW = 57.752$ ,  $df = 2$ ,  $p < 0.001$ ), emergence success ( $KW = 63.332$ ,  $df = 2$ ,  $p < 0.001$ ) and proportion of hatchlings emerged ( $KW = 25.800$ ,  $df = 2$ ,  $p < 0.001$ ). Average hatching successes were 32.3% ( $n = 114$ , range: 0%-91%), 55.6% ( $n = 172$ , range: 0%-95%) and 38.4% ( $n = 130$ , range: 0%-88%) in 2004-2005, 2005-2006 and 2006-2007 respectively. Average emergence successes were 26.6% ( $n = 114$ , range: 0%-89%), 50.9% ( $n = 170$ , range: 0%-94%) and 31.4% ( $n = 130$ , range: 0%-82%) in 2004-2005, 2005-2006 and 2006-2007 respectively. Proportions of hatchlings emerged were 70.7% ( $n = 75$ , range: 0%-98%), 84.5% ( $n = 103$ , range: 0%-98%) and 69.8% ( $n = 97$ , range: 0%-98%) in 2004-2005, 2005-2006 and 2006-2007 respectively.

The most important factor affecting emergence success across seasons was the maximum temperature during the first quarter of the incubation period (stepwise regression:  $R^2 = 0.291$ ,  $p < 0.001$ ) (Fig. 13). Within seasons, the most important factors affecting hatching success were maximum and mean temperatures during the first quarter of the incubation period in 2004-2005 (stepwise regression:  $R^2 = 0.247$ ,  $p = 0.01$ ), maximum temperature during the third and fourth quarters of the incubation period (stepwise regression:  $R^2 = 0.211$ ,  $p = 0.002$ ), and maximum temperature during the first quarter in 2006-2007 (stepwise regression:  $R^2 = 0.241$ ,  $p < 0.001$ ). The most important factors affecting proportion of hatchlings emerged were the total number of hatchlings hatched and the mean and maximum temperature during the last quarter of the incubation period (stepwise regression:  $R^2 = 0.479$ ,  $p < 0.001$ ). Number of hatchlings hatched

explained most of the variation in proportion of hatchlings emerged ( $R^2 = 0.328$ ,  $p < 0.001$ ).

Maximum temperature during the first quarter of the incubation period affected number of dead embryos in early stages in 2004-2005 ( $R^2 = 0.159$ ,  $p = 0.001$ ) and 2006-2007 ( $R^2 = 0.071$ ,  $p = 0.011$ ) but not in 2005-2007 ( $p = 0.446$ ). Mean temperature during the last quarter of the incubation period affected number of dead embryos in late stages in 2004-2005 ( $R^2 = 0.230$ ,  $p < 0.001$ ), 2005-2006 ( $R^2 = 0.215$ ,  $p < 0.001$ ) and 2006-2007 ( $R^2 = 0.397$ ,  $p < 0.001$ ) (Fig. 13).

Number of eggs did not affect hatching success ( $p = 0.752$ ) and hatching success was not significantly affected by the distance to the vegetation in any season ( $p = 0.513$ ,  $p = 0.630$  and  $p = 0.970$  for 2004-2005, 2005-2006 and 2006-2007 respectively), nor by the distance to the high tide line ( $p = 0.922$ ,  $p = 0.099$  and  $p = 0.691$  for 2004-2005, 2005-2006 and 2006-2007 respectively). Nests laid towards the North had a higher hatching success than those laid towards the South in 2004-2005 ( $R^2 = 0.042$ ,  $p = 0.029$ ), but did not significantly vary along the beach in 2005-2006 and 2006-2007 ( $p = 0.544$  and  $p = 0.119$  respectively).

### **Seasonality in nest success: weather effects**

There was a seasonal effect on hatching success and on the proportion of hatchlings emerged. Both hatchlings produced and hatchlings emerged were lower as the season progressed. The date at which nests were laid affected hatching success in 2004-2005 ( $R^2 = 0.143$ ,  $p < 0.001$ ), 2005-2006 ( $R^2 = 0.102$ ,  $p < 0.001$ ) and 2006-2007 ( $R^2 = 0.155$ ,  $p < 0.001$ ). Equally, date laid affected the proportion of hatchlings emerged in

2004-2005 ( $R^2 = 0.154$ ,  $p < 0.001$ ), 2005-2006 ( $R^2 = 0.120$ ,  $p < 0.001$ ) and 2006-2007 ( $R^2 = 0.325$ ,  $p < 0.001$ ) (Fig. 14).

Average emergence success per month laid (October to January) across seasons was strongly related to the rainfall in the two months before nests were laid and to the ambient temperature during the two incubation months (stepwise regression:  $R^2 = 0.824$ ,  $p = 0.001$ ). Rainfall explained most of the variation ( $R^2 = 0.692$ ,  $p = 0.001$ ) (Fig. 15). Average Multivariate ENSO Index between August and January per season explained 50.7% of the variation in the predicted emergence success obtained from local weather data ( $R^2 = 0.507$ ,  $p < 0.001$ ) (Fig. 16). El Niño events (positive values) corresponded to years of low emergence success of leatherback nests at PNMB and La Niña events (negative values) resulted in higher emergence success (Fig. 17).

### **Reproductive success: hatchling production**

There was a seasonal effect on hatchling production. Total production of hatchlings by females decreased as the date they laid the first nest was later in the season in 2004-2005 ( $R^2 = 0.351$ ,  $p < 0.001$ ) and 2005-2006 ( $R^2 = 0.354$ ,  $p = 0.002$ ) but was not significant in 2006-2007 ( $p = 0.089$ ) (Fig. 18). Hatching success, ECF and number of eggs explained 93.1% of the variation in hatchling production ( $R^2 = 0.931$ ,  $p < 0.001$ ). Hatching success and ECF explained 86.7% (stepwise regression:  $R^2 = 0.867$ ,  $p < 0.001$ ) and hatching success alone explained 72.4% of the variation in hatchling output ( $R^2 = 0.724$ ,  $p < 0.001$ ). Average number of eggs per clutch ( $R^2 = 0.055$ ,  $p = 0.037$ ), ECF ( $R^2 = 0.231$ ,  $p < 0.001$ ) and hatchling production ( $R^2 = 0.144$ ,  $p = 0.001$ ) all increased with number of seasons nested (Fig. 19). Time of arrival was also related to the number of seasons nested. Turtles that nested multiple seasons arrived earlier to nest than turtles that

nested a lower number of seasons in 2004-2005 ( $R^2 = 0.198$ ,  $p = 0.009$ ) and 2005-2006 ( $R^2 = 0.175$ ,  $p = 0.037$ ), but was not significant in 2006-2007 ( $p = 0.091$ ).

## DISCUSSION

### **“In situ” effects on nest success**

Temperature plays an important role in nest success of leatherback turtles at PNMB. Temperature during incubation is known to affect survival of eggs in different reptile species. For example, high temperatures reduce hatching success in snakes (Ji & Du 2001, Lin et al. 2005), lizards (Ji et al. 2002), freshwater turtles (Packard et al. 1987) and desert tortoises (Spotila et al. 1994). We found a thermal effect on development of leatherback turtle eggs at PNMB. Nests of leatherback turtles had lower hatching success at high temperatures. Moreover, eggs were sensitive to high temperatures at all stages during the incubation period since number of dead embryos in early stages was related to temperature during the first part of incubation, and number of dead embryos in late stages was related to temperature in the last part of incubation.

Temperature during the final part of incubation increases rapidly as a result of ambient temperature but especially due to high metabolic activity (Wallace et al. 2004). Under these conditions, late developmental stages and hatched hatchlings, should be expected to tolerate greater thermal changes and overall, higher temperatures. Most of the mortality in leatherback turtle eggs does in fact take place at the beginning of incubation (Bell et al. 2003). Thus, early developmental stages are possibly more sensitive to high temperatures than later ones, despite facing overall lower temperatures. However, factors other than temperature could additionally explain early mortality during incubation. For

example, fungal infection from early dead eggs can spread to viable eggs increasing mortality (Phillott & Parmenter 2001).

Hatchling sea turtles typically emerge synchronously from the nest (Bustard 1967). Synchronous emergence facilitates emergence by cooperation among hatchlings and reduces predation once hatchlings are on the beach (Carr & Hirth 1961, Bustard 1967). We found that proportion of hatchlings emerged increased with number of hatchlings. Therefore, high numbers of emerging hatchlings increased survival. Although number of hatchlings emerging was the main factor affecting survival to the surface, high temperature also played an important role, decreasing the proportion of hatchlings emerged. Hatchling leatherback turtles start exhibiting uncoordinated movements at 33.6°C and have critical thermal maxima (CTM) of 40.2°C (Drake & Spotila 2002). Although temperatures above the CTM are uncommon in the nest, temperatures higher than 33.6°C are frequent at the end of the incubation period. Thus, locomotion of hatchling might be limited by temperature, which in turn increases their mortality rates in the nest.

In general, temperature had an effect on hatching success and proportion of hatchlings emerged and therefore, on the overall success of nests. However, there were differences between seasons. We found that maximum temperature during the first quarter of the incubation explained most of the variation in hatching success in 2004-2005 and 2006-2007. However, hatching success in 2005-2006 was best explained by high temperatures in the latest part of the incubation period. Differences in weather between seasons could explain this differential effect on the hatching success. Total rainfall during the rainy season in 2005-2006 was 2031 mm and rainfall in 2004-2005



and 2006-2007 was 1525 and 1214 mm respectively. In addition, nest temperatures were lower in 2005-2006 than in both 2004-2005 and 2005-2006. Temperature in other reptile species has been found to affect negatively hatching success only when above certain values (Ji & Du, 2001, Lin et al. 2005). Therefore, low temperatures within the first part of the season and the higher rainfall could have resulted in an overall higher nest success in 2005-2006. Temperature during the third and fourth quarters of the incubation period explained most of the variation in hatching success because temperatures on the beach were higher at this time.

Hewavishenthi and Parmenter (2002) found that nest success of flatback turtles was not affected by position on the beach but was correlated to clutch size. We found that nest success of leatherbacks at PNMB was not related to clutch size and we only found hatching success to be related to location on the beach in 2004-2005. Playa Grande is a high energy beach. Therefore, beach characteristics vary from season to season. For instance, sections of the beach can have higher erosion than others in some years or have dryer environments which ultimately, affect hatching success. We found that distance to vegetation and to high tide line did not affect hatching success. Our study only considered measurement taken to the high tide line on the first day after nests were laid. High tides vary along the season at Playa Grande. Therefore, there could be an effect on hatching success that we were not able to quantify because we took a single measurement. Future studies should consider measuring daily variation in the distance from the nest to the high tide line. Other studies on sea turtles have found that humidity and distance to high tide line affect hatching success (López-Castro et al. 2004). Thus,

further analysis should also quantify the effect of humidity inside the nest on the hatchling success.

### **Seasonality in nest success: weather effects**

Ambient temperature and dryness increase from the beginning to the end of the nesting season at Playa Grande. Thus, the lower hatching success toward the end of the season is most likely explained by the higher temperatures given the effect of temperature on hatching success. Bell et al. (2003) suggested that even if fertility of leatherback eggs was usually high (~93%), it might be reduced in turtles that arrive later in the season. However, the effect of temperature that we found on hatching success, suggests that temperature, rather than lower fertility, explains the seasonality in hatchling production.

We found a strong relationship between hatching/emergence success and local weather conditions. Rainfall during the two months before nests were laid and temperature during the two months of incubation explained over 82% of the average emergence success at PNMB. Weather Indices such as the ENSO Index, facilitate comparison between various weather variables and ecological processes. However, sometimes there is not a direct relationship between local and global weather (Stenseth et al. 2003). We found that the predicted emergence success from local weather data was related to the global weather patterns of ENSO in the Pacific Ocean, and that ENSO Index explained 51% of the variability in this prediction.

The effects of global weather patterns on animal populations have been extensively studied. For example, hatching success and fledging success of northern fulmar (*Fulmarus glacialis*) relate to the North Atlantic Oscillation (NAO) (Thompson & Ollason 2001). Equally, breeding success of Galápagos penguins is lower during El Niño

years in the Pacific (Boersma 1978), as well as fecundity and survival of black-throated blue warblers (*Dendroica caerulescens*) (Silleet et al. 2000). Reproductive success of different seabird species at Christmas Island was also heavily reduced by the 1982-1983 El Niño event (Schreiber & Schreiber 1984). On the other hand, the effect of El Niño events on reproductive success of other species can be positive. For example, Galápagos finches increase reproductive success during El Niño years (Gibbs & Grant 1987, Grant et al. 2000). Our predicted emergence success from local weather data was also negatively affected by El Niño years. We predicted lowest emergence successes in 1982, 1987 and 1997, which coincided with three big El Niño events and predicted highest emergence success in 1999 during the latest big La Niña event. Therefore, ENSO affects recruitment into the population of leatherback turtles that nest at PNMB and consequently, on its population dynamics.

Environmental variability also affects other ecological processes in sea turtle populations. For example, duration of remigration interval between nesting seasons is related to ocean sea surface temperature (Solow et al. 2002). Equally, remigration probability of leatherback turtles at PNMB increases with cool La Niña events and decreases during warm El Niño events (Saba et al. 2007). Therefore, La Niña events correspond to periods of high productivity at PNMB because of high number of nesting turtles and high hatchling production. Consequently, population dynamics of leatherback turtles are characterized by fluctuations in number of nesting turtles because of highly variable reproductive success which depends on climatic conditions.

Finally, changes in climate over time can potentially affect reproductive success of leatherback turtles at PNMB. More frequent and stronger El Niño events will result

fewer turtles nesting, lower production of hatchlings and, after the time lag to reach sexual maturity, even lower numbers of nesting turtles. The population of leatherback turtles that nest at PNMB has declined by 95% as a consequence of fisheries and past egg poaching and is critically endangered (Spotila et al. 2000, Santidrián Tomillo et al. 2007). Thus, further reduction in recruitment in addition to the previous threats, will threaten their survival.

### **Reproductive success: hatchling production**

Turtles increase hatchling production through time by (1) increasing number of eggs per clutch, (2) number of clutches and (3) average emergence success by arriving earlier in the season. A combination of age and experience appears to result in the higher reproductive success over time. Number of eggs and ECF probably increases with age and early arrival with experience.

Early breeding has been associated with higher reproductive success in bird species (Price et al. 1988). For example, older male american redstarts (*Setophaga ruticilla*) arrive earlier to breeding grounds than younger ones and their reproductive success is both related to arrival time and age (Lozano et al. 1996). Quality of wintering habitat can also influence arrival time in american redstarts and therefore, reproductive success (Norris et al. 2004). Leatherback turtles that arrive early in the season to nest produce more hatchlings and therefore, have higher reproductive success. Cost-benefits associated with early arrival have been hypothesized to drive arrival time in bird species (Møller 1994). In the case of barn swallows (*Hirundo rustica*) the benefit obtained from early arrival was a higher reproductive success and the cost to pay was the variable

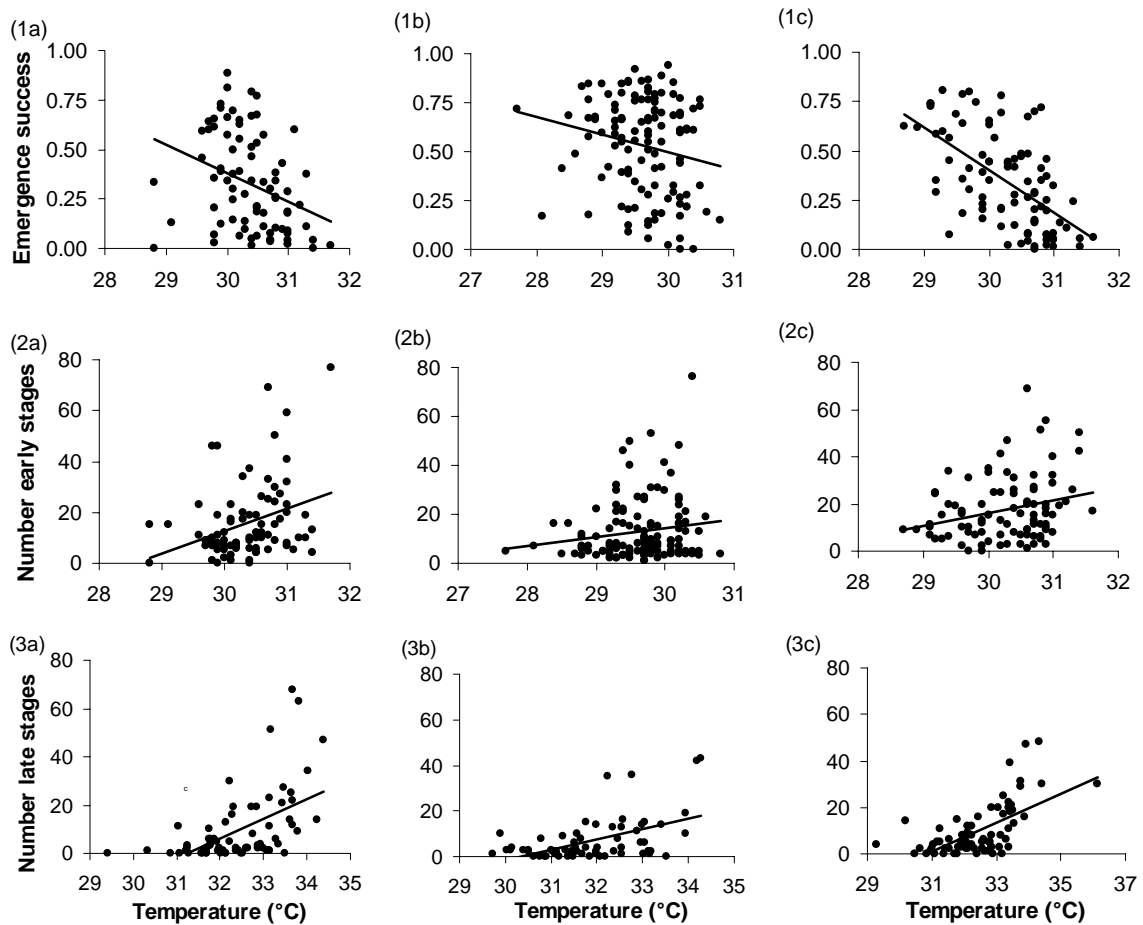
weather conditions at the breeding grounds and at grounds before migration (Møller 1994).

Benefits of early arrival of leatherbacks at PNMB are clearly increased hatchling production. Costs of early arrival could be related to weather conditions too. The nesting season at PNMB extends from early October to early March and the rainy season in Northwest Costa Rica extends from May-June to November. The rainiest months are September and October. Bad weather during the rainy season causes higher tides and greater erosion. Therefore, the probability of nests being washed away is higher at the beginning of the season. Because weather conditions vary from year to year, the optimal time of arrival might also vary between nesting seasons.

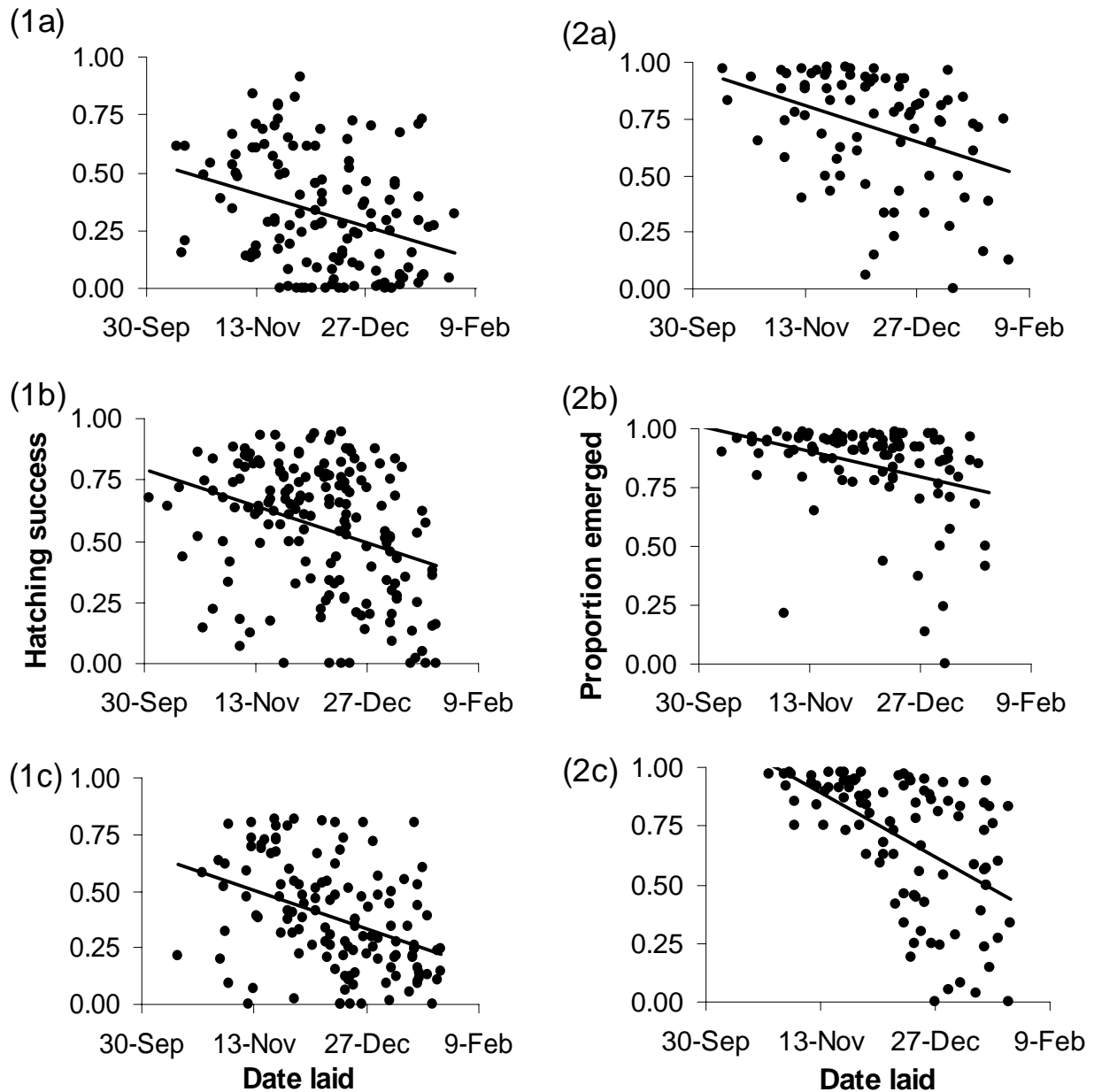
Little is known about male leatherback turtles. Only with the recent use of video cameras mounted on female turtles (crittercam) males have been observed around the nesting beaches (Reina et al. 2005). However, nothing is known about their migration patterns and therefore, the time of arrival to the nesting grounds. For example, in some bird species males always arrive earlier in the season than females (Cristol 1995). Time of arrival of female leatherback turtles related to the arrival of males may also be of importance, since appropriate arrival date could increase mating probability and quality of their offspring.

In conclusion, reproductive success of leatherback turtles at PNMB highly depends on weather conditions: (1) high *in situ* temperatures during incubation reduce nest success, (2) emergence success and hatchling production are driven by local environmental variability. Specifically, amount of rainfall and temperature affect production of hatchlings, with wet and cool seasons producing more hatchlings than dry

and hot seasons, and (3) emergence success at PNMB is affected by global weather patterns in the Pacific Ocean. El Niño years are of low success and La Niña years of higher reproductive success. Therefore, ENSO affects hatchling output and ultimately, recruitment to the nesting population of leatherback turtles at PNMB, which constitute additional threat to their survival.

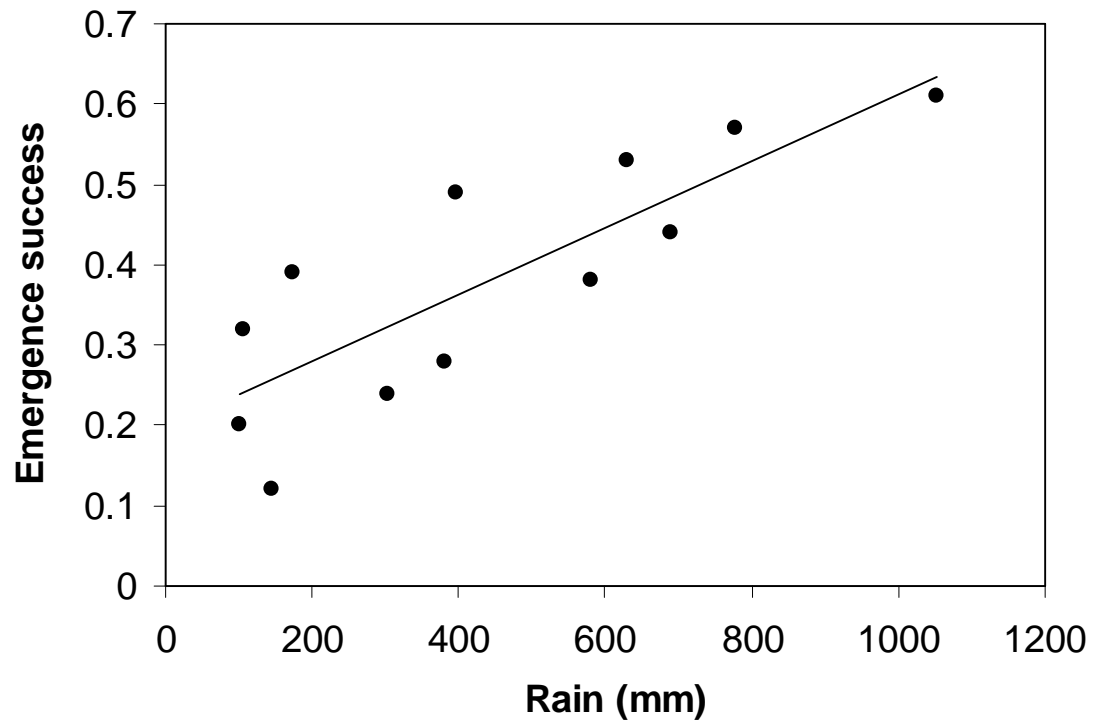


**Figure 13.** Effect of temperature during the incubation period on emergence success, number of early stage mortalities and number of late stage mortalities in leatherback turtle nests at Playa Grande, Costa Rica. **1.** Emergence success decreases as the maximum temperature during the first quarter of the incubation period increases. **2.** Number of dead embryos in early stages increases with the maximum temperature during the first quarter of the incubation period. **3.** Number of dead embryos in late stages increases with the average temperature during the last quarter of the incubation period. **Figures a, b and c** are seasons 2004-2005, 2005-2006 and 2006-2007 respectively.

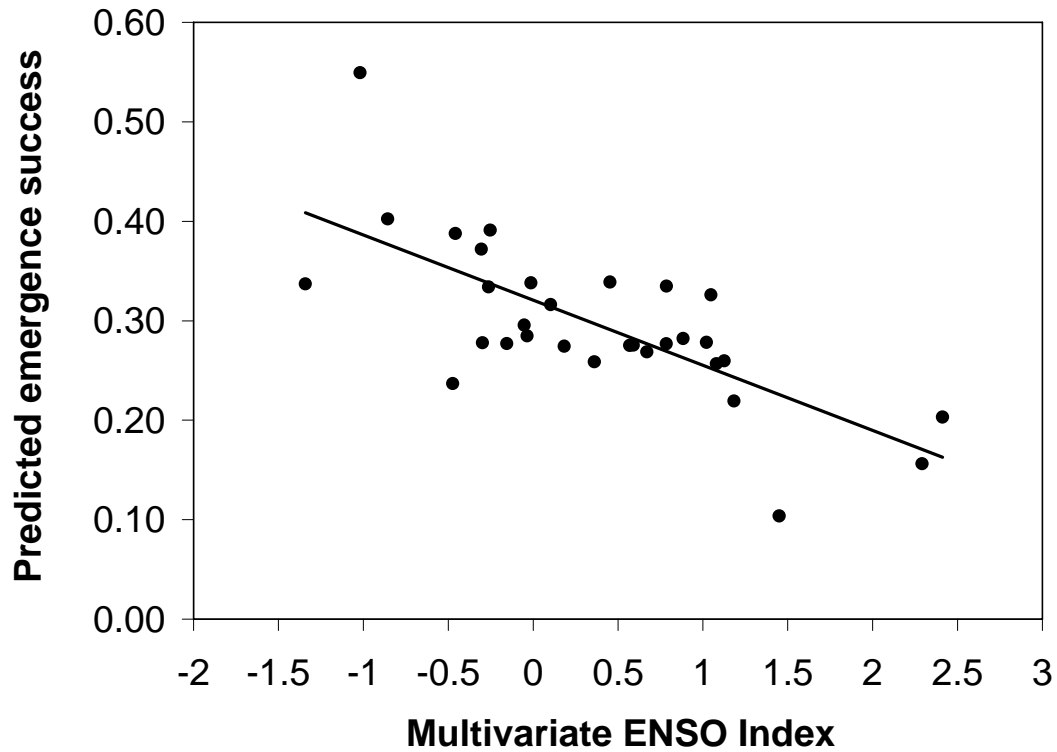


**Figure 14.** Seasonal effect on hatching success of leatherback turtle nests and on proportion of hatchlings emerged at Playa Grande, Costa Rica. **1.** Hatching success per date nests were laid. **2.** Proportion of hatchlings emerged per date nests were laid. **Figures a, b and c** are seasons 2004-2005, 2005-2006 and 2006-2007 respectively.

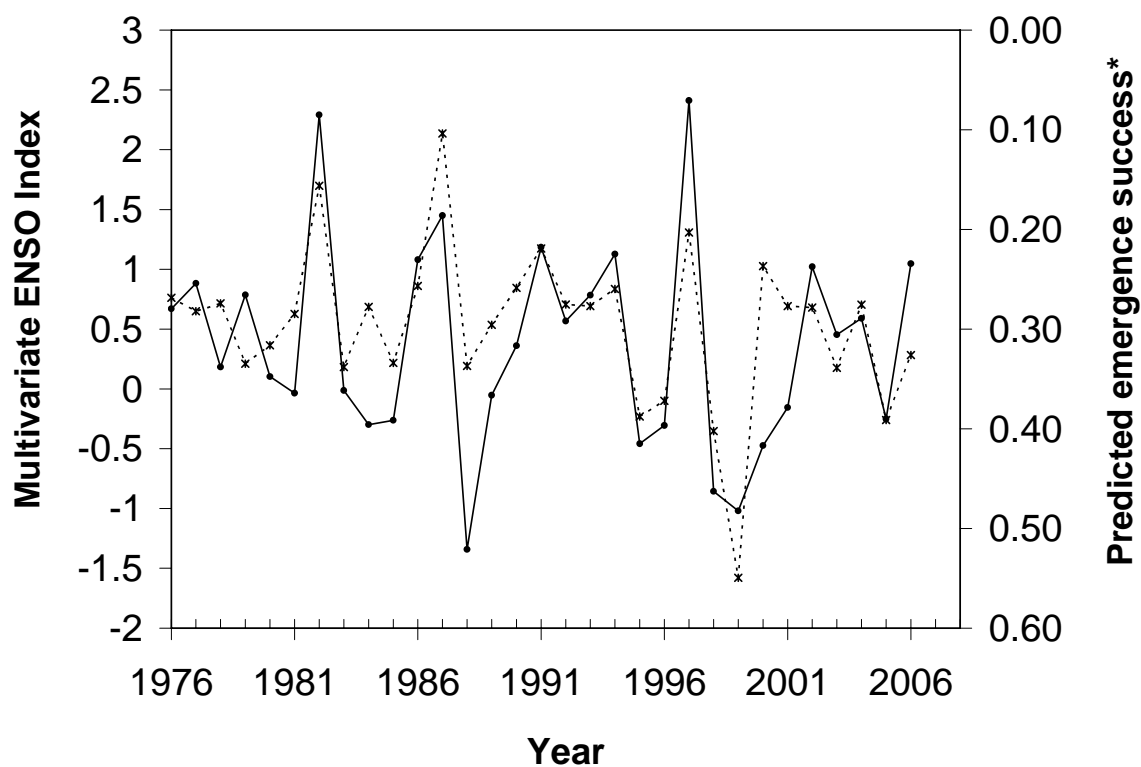




**Figure 15.** Average measured emergence success of nests per month these were laid (October-January) in 2004-2005, 2005-2006 and 2006-2007, related to the rainfall accumulated in the two previous months.

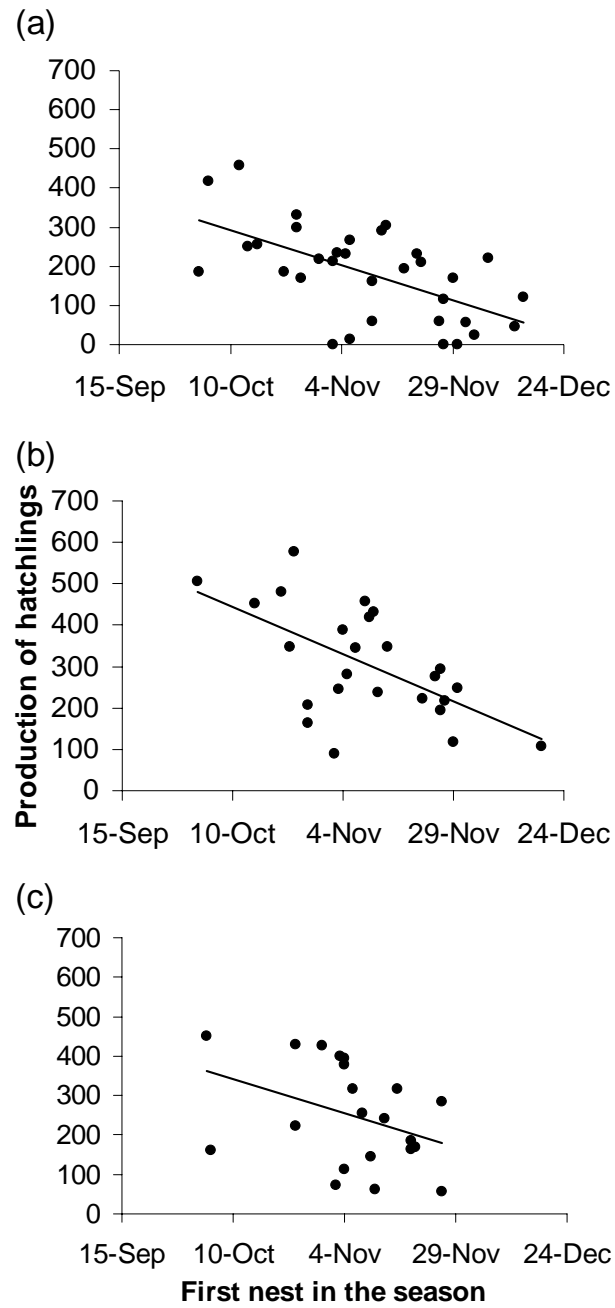


**Figure 16.** Predicted emergence success per season based on local weather data (rainfall in the two previous months and ambient temperature during the two months of incubation) of leatherback turtle nests at Playa Grande, Costa Rica in relation to the average Multivariate ENSO Index (August to January) for each season.

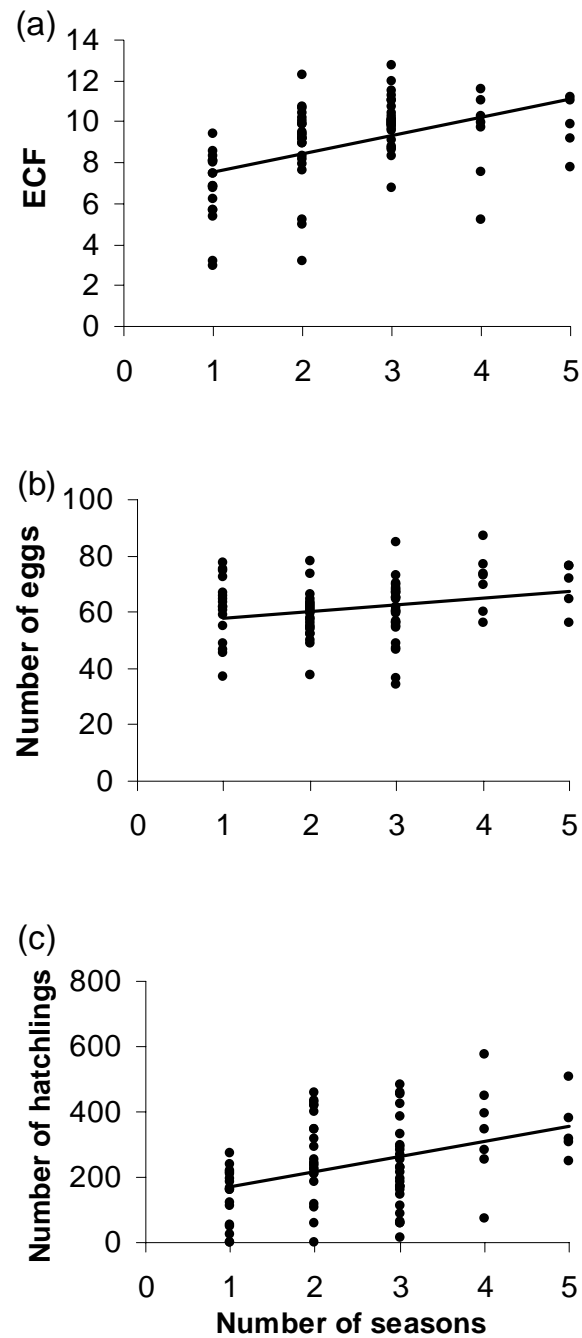


**Figure 17.** Predicted emergence success per season between 1976-1977 (1976 in graph) and 2006-2007 (2006 in graph), based on local weather data (rainfall and ambient temperature) of leatherback turtle nests at Playa Grande, Costa Rica and average Multivariate ENSO Index (August to January) for the same years. Solid line shows the average Multivariate ENSO Index through time and dashed line represents the predicted emergence success.

\* Note reversal of the scale.



**Figure 18.** Seasonal effect on the total production of hatchlings in a season by female leatherback turtles at Playa Grande, Costa Rica. Total production decreases as the date of arrival is later in the season. **Figures a, b and c** are seasons 2004-2005, 2005-2006 and 2006-2007 respectively.



**Figure 19.** Reproductive success of female leatherback turtles related to the number of seasons nested at Playa Grande, Costa Rica. **19a.** Estimated Clutch Frequency (ECF) increases with number of seasons. **19b.** Average number of eggs per clutch increases with number of seasons. **19c.** Number of hatchlings produced in the season increases with number of seasons.

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## VITA

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#### Professional experience

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2002	Research Assistant. Restoration of native vegetation. University of Alcalá de Henares, Madrid, Spain.

#### Publications

**Santidrián Tomillo, P.**, Saba, V.S., Piedra, R., Paladino, F.V. and Spotila, J.R. accepted. Egg poaching: A major factor in the population decline of leatherback turtles, *Dermochelys coriacea*, at Parque Nacional Marino Las Baulas, Costa Rica. Conservation Biology.

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#### Memberships

Society for Conservation Biology  
International Sea Turtle Society  
Sea Turtle Society of Greece