DEPREDATION OF OLIVE RIDLEY AND LOGGERHEAD TURTLE CLUTCHES ON BEACHES WITH AND WITHOUT PREDATOR MANAGEMNT

by

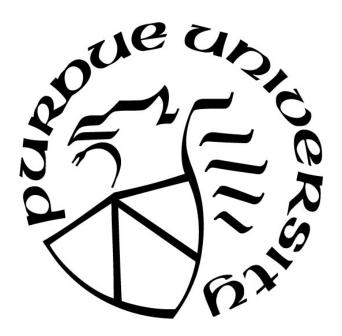
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Dedicated to Gra	ndma Dorothy Stoltz who con	tinually fostered my love	of the natural world.
Dedicated to Gra	ndma Dorothy Stoltz who con If it were not for you, I wou		
Dedicated to Gra			

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I would first like to thank Dr. Paladino for introducing me to sea turtle conservation by giving me the opportunity to work with The Leatherback Trust in Costa Rica and for taking me on as a graduate student. I would like to thank Dr. Gillespie for allowing me to work in his lab through undergrad and for his support and advice as I completed my first original research. Thank you to my committee members: Dr. Bergeson, Dr. Marshall, Dr. Paladino, and Dr. Pfaller for their support and assistance through this plan of study. Dr. Marshall I would also like to thank for his help in making sure I was always on track with the correct requirements and paperwork and for helping me through the extremely frustrating (yet rewarding) process of learning how to apply statistics and use R Studio.

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TABLE OF CONTENTS

		RES	
ABST	RACT		7
CHAP	TER 1.	INTRODUCTION	8
CHAP	TER 2.	METHODS	. 11
2.1	Species		. 11
2.2	Study A	reas	. 11
2.3	Nest Me	onitoring and Data Collection	. 12
	•	s	
2.5	Statistic	s	. 13
CHAP	TER 3.	RESULTS	. 15
CHAP	TER 4.	DISCUSSION	. 23
REFEI	RENCES		. 27

LIST OF FIGURES

Figure 1- Annual predation rate of sea turtle clutches at sites in Costa Rica (Playa Cabuyal and Playa Grande) and the USA (Vero Beach and Wassaw Island)
Figure 2- Statistical models of annual predation rate/km on the four beaches: (A) Playa Cabuyal, (B) Playa Grande, (C) Vero Beach, and (D) Wassaw Island
Figure 3- Mean annual predation rate per km of sea turtle nests at sites in Costa Rica (Playa Cabuyal and Playa Grande) and the USA (Vero Beach and Wassaw Island)
Figure 4- Mean predation density (A) and egg loss (B) of sea turtle nests at sites in Costa Rica (Playa Cabuyal and Playa Grande) and the USA (Vero Beach and Wassaw Island)
Figure 5- Percentage of predation events by different predator species on olive ridley (Lepidochelys olivacea) nests at Playa Cabuyal
Figure 6- Percentage of predation events by different predator species on olive ridley (Lepidochelys olivacea) nests at Playa Grande
Figure 7- Percentage of predation events by different predator species on loggerhead (Caretta caretta) nests at Vero Beach
Figure 8- Percentage of predation events by different predator species on loggerhead (Caretta caretta) at Wassaw Island

ABSTRACT

Management of predation on sea turtle nesting beaches is vital to conservation efforts for the vulnerable loggerhead turtles (*Caretta caretta*) and olive ridley turtles (*Lepidochelys olivacea*). Sea turtles increasingly face threats from invasive and human-tolerant mammalian predators as human disturbances on nesting beaches rises. The intensity of mammalian predation has increased in Las Baulas National Park in Costa Rica which is an important nesting site for several species of threatened and endangered sea turtles. I analyzed loggerhead and olive ridley nest predation on four beaches in the United States and Costa Rica that were chosen for variations in degree of human disturbance and management strategies. My objectives were to 1) determine if egg predation rates differ at the four sites, 2) determine the most destructive predators at each location, and 3) suggest management options to alleviate mammalian threats to turtle clutches on Playa Grande and Playa Cabuyal in Costa Rica. My results show that the beaches without a nest protection or predator control program had very high rates of predation. Invasive mammalian predators and mammalian predators associated with human disturbance were the most destructive at the four sites. I recommend that regulations regarding dogs and the take of eggs from the beach are enforced at Playa Cabuyal and that physical nest protection is rapidly implemented at Playa Grande. I also recommend that the National Park consider managing raccoon predation by removing problem individuals, but caution that they do so in a way that maintains the animals' role in the ecosystem.

CHAPTER 1. INTRODUCTION

Effective conservation methods for species that are threatened by extinction must correctly identify and alleviate threats to their populations. In anthropogenically altered areas, threats due to habitat loss and predation are particularly damaging and often occur in tandem (Engeman et al. 2006, Pauliny et al. 2008, Roosenberg et al. 2014). Human development can cause reduction or degradation of available habitat for the predator and prey species and can lead to increased predation pressure (Andrén et al 1985). Human disturbance is also suggested to attract generalist predators such as red foxes (*Vulpes vulpes*) and racoons (*Procyon lotor*) by providing an additional, stable food source (Whitcomb et al. 1981, Andrén al 1985, Engeman et al. 2006). Predators drawn to human disturbances can be damaging to populations of endangered egg-laying species nesting in anthropogenically altered habitats (Engeman et al. 2005, Pauliny et al. 2008). Often, species in disturbed areas are forced to occupy relatively undisturbed patches of suitable habitat which can make predation of these small pockets devastating to population levels (Andrén 1994, Pauliny et al. 2008).

Predation is an important factor in nest success for egg-laying animals such as birds and turtles and is an important source of early mortality. Managing predation on nesting beaches has been vital to the successful conservation of endangered species and has been effective at maintaining annual predation rates below 15% (Engeman et al. 2005, NMFS and USFWS 2008, Butler et al. 2020). Popular methods of predation management for shorebird and sea turtle nests include nest exclosures, protective cages and screens, regulations for beach-goers, and direct control of predator populations either by reduction, removal or the targeting of problem individuals (Dutton et al. 2005, Isaksson et al. 2007, Barton and Roth 2010, Engeman et al. 2010, O'Connor et al 2017, Korein et al. 2019, Butler 2020). In the absence or cessation of predator management, predation rates can be as high as 80-100% annually (Hopkins et al. 1978, Stancyk et al. 1980, Engeman et al. 2010). On Playa Grande, a sea turtle nesting beach in Costa Rica, nest predation rates have recently increased in the absence of predator management.

Costa Rica supports important nesting beaches for the critically endangered population of East Pacific leatherbacks (*Dermochelys coriacea*) (Wallace et al. 2013), as well as endangered green (*Chelonia mydas*) (Seminoff 2004) and vulnerable olive ridley turtles (*Lepidochelys olivacea*) (Abreu-Grobois and Plotkin 2008). Las Baulas National Park, where Playa Grande is

located, is the principal nesting site for East Pacific leatherback turtles and nest counts suggest a decreasing trend (Spotila et al. 2000). Therefore, hatchling production at this site is critical for the survival of the population. The annual percentage of nest predation has increased in Las Baulas National Park which is cause for concern. Human habitation and day-use are important drivers of predation on nesting beaches (Engeman et al. 2006; Ficetola 2008). Animals, such as raccoons, that benefit from human disturbance and dogs that accompany beach goers are key predators of these endangered turtles. Because depth is an important factor affecting predation risk (Leighton et al. 2009), the eggs of smaller species, such as olive ridleys and green turtles, may be more vulnerable to predation than those of leatherbacks (Leighton et al. 2009) since their egg chambers are shallower.

In the 2019-2020 season at Playa Grande nearly all olive ridley clutches were relocated to a beach hatchery since the majority left on the beach were predated (pers obs.). Olive ridley are the most vulnerable to predation of the species to nest on Playa Grande, but even a leatherback nest, with the deepest egg chamber of any living sea turtle species, was found to be predated in a recent nesting season (pers obs.). Due to the recent rise in predation rates on Playa Grande, more vigorous egg loss monitoring and predator observation protocols are being put into practice by researchers and predator management is being considered. Predator management and *in situ* protection of nests would be less disruptive to the natural incubation process than relocating all atrisk nest to a protected hatchery. There is currently no predation management conducted on sea turtle nesting beaches in and around Las Baulas National Park and *in situ* nests are left unprotected. On several beaches in the United States, however, predator populations are managed by hunting and trapping and nests are protected using cages or screens (Dodd and Mackinnon 2003; Engeman et al. 2010; Engeman et al. 2012; Engeman et al. 2016; Kurz et al. 2012; Welicky et al. 2012; Butler et al. 2020). If implemented, a predator management program should greatly decrease egg mortality in Las Baulas National Park.

The goal of this study is to assess the need for a predator management program on Playa Grande and Playa Cabuyal in Costa Rica and to determine what measures of protection would be the most practical and beneficial at each site. To achieve this goal, the objectives of this study were to determine if rates of nest predation differ at four study sites: Playa Cabuyal, Playa Grande, Vera Beach (Florida, USA), and Wassaw Island (Georgia, USA). These sites were chosen for variations in degree of human disturbance and management strategies and to determine the most destructive

predators at each location. Predation is predicted to be higher at sites where *in situ* nests are left unprotected and at sites with no predator management. Predation is also predicted to be higher at sites with heavy human disturbance. Results of this study will help assess the viability of predator management and *in situ* nest protection as conservation measures on Playa Grande.

CHAPTER 2. METHODS

2.1 Species

The species in this study were loggerhead turtles (*Caretta caretta*) and olive ridley turtles (*Lepidochelys olivacea*). Loggerhead turtles nest on both Wassaw Island and Vero Beach and olive ridley turtles nest on Playa Cabuyal and Playa Grande. There were more available data for these two species than there were for other turtles that were less common on their respective beaches.

2.2 Study Areas

I chose four study sites based on the relative degree of human disturbance, management strategies with respect to predator control and nest protection, and data availability.

Playa Cabuyal (10.6755° N, 85.6531° W) has 1.4 km of nesting habitat and is a remote beach on the north coast of Guanacaste province in Costa Rica. Playa Cabuyal is an important nesting beach for eastern Pacific leatherback, green, and olive ridley turtles and there are currently no predator management or nest protection strategies in place. The beach is undeveloped except for one house, a parking lot, and guard shack, and is sparsely populated by humans except for on weekends and holidays. At-risk nests were relocated to more suitable locations on the beach, however, this was done rarely and none of the nests were protected and there was no beach hatchery as there was on Playa Grande. This beach is monitored during the nesting season from October to March. The most important animal predators on the beach were dogs and there were many instances of human poaching.

Playa Grande (10.3355° N, 85.8472° W) has 3.6 km of nesting habit in Las Baulas National Marine Park in Guanacaste, Costa Rica, and is an important nesting beach for eastern Pacific leatherback, green, and olive ridley turtles. Playa Grande is a popular tourist destination with heavy human habitation behind the beach. There are currently no predator management strategies in place. Clutches that were deposited below the tideline or that were at high risk of loss were relocated to a beach hatchery and monitored until emergence. Relocated clutches in the hatchery were protected with screens and patrolled at night to guard against predators. Clutches left *in situ* were unprotected, though biologists patrolling nightly on the beach chased away observed predators and

recorded predated nests. This beach is monitored during the nesting season from October to March. The most important predators on the beach were racoons and dogs.

Vero Beach (27.6386° N, 80.3973° W) in Florida, USA, has a total of 38.6 km of nesting habitat and is a high-density nesting beach for loggerhead turtles in the United States. The beach and surrounding ecosystems have become stressed by human development. Coastal Connections, Inc., is a conservation organization founded in 2017 as part of Indian River County's Habitat Conservation Plan for sea turtles to protect Vero Beach. This beach is monitored during the nesting season from May to October. The most important predators on Vero Beach included raccoons and dogs (Cope 2015).

Wassaw Island (31.9055° N, 80.9794° W) has 10.8 km of nesting habitat, is the least developed of Georgia's barrier islands (Georgia DNR) and has been managed by the US Fish and Wildlife Service as a National Wildlife Refuge since 1969 (Seabrook, 2018 and Georgia DNR). The Caretta Research Project has conducted sea turtle research and conservation on Wassaw Island since 1973 (Pfaller et al. 2013). Sea turtle nests were protected with mesh screens and predator populations were managed by hunting and trapping to ensure that the annual rate of mammalian nest predation was below 10% (NMFS-USFWS 2008). This beach is monitored during the nesting season from May to August. The most important egg predators on Wassaw Island are raccoons and red foxes (*Vulpes vulpes*) (Butler et al. 2020).

2.3 Nest Monitoring and Data Collection

Data from Playa Cabuyal and Playa Grande were provided by Dr. Bibi Santidrian Tomillo (The Leatherback Trust), data from Vero Beach were provided by Quinten Bergman (Coastal Connections, Inc.) and data from Wassaw Island were provided by Dr. Joseph Pfaller (Caretta Research Project). At Playa Cabuyal and Playa Grande, data that were recorded included nest depth, location and the date when the nest was laid. The number of eggs laid were recorded for most nests and nest excavations were conducted at the end of the incubation period to determine causes of embryo mortality. The number of estimated eggs excavated was used, where possible, to estimate egg loss for the study sites in Costa Rica since egg loss due to predation was not usually recorded. In 2017, researchers on Playa Grande began more vigorous predator observation and egg mortality tracking due to increased predation rates. The data received from Vero Beach and Wassaw Island included a detailed loss report that documented egg and hatchling mortality as well

as the predators responsible. Those data also included the date the nest was laid and, where applicable, the loss date for that nest.

2.4 Analysis

The primary objective of this study was to determine whether nest predation rates were different at the four chosen sites, each differing in predation management. I used three measures to meet this objective: annual predation rate (the percentage of nests with documented predation events), predation density (the number of predation events per kilometer), and egg loss (the number of eggs destroyed per km). Annual predation rate can be used to assess the success of nest protection measures (Engeman et al. 2006). I adjusted annual predation by beach length to account for the size differences between the sites by dividing each value by the length of the beach in kilometers. I calculated predation density by dividing the number of marked nests predated per year by the length of the beach in kilometers. Egg loss was directly recorded for Vero Beach and Wassaw Island and, where data were available, I estimated egg loss for Playa Cabuyal and Playa Grande by subtracting the number of eggs excavated from the number of eggs laid. Missing data entries contributed to extreme biases in these analysis for Playa Cabuyal and Playa Grande.

To determine the most important nest predators on each beach, I calculated the percent of total predation events attributed to each predator species for which predation events were recorded. Whether or not nest screens will be beneficial at the Costa Rican sites depends on how effectively they are expected to function against the most prevalent predators found on these beaches. To test the effectiveness of nest protection and predator management, I compared the two sites in Costa Rica with no management to the two sites in the United States that each had their own management program in place.

2.5 Statistics

Generalized additive models (GAM) were used for each beach to determine if year in the study period had a significant effect on annual predation and predation density. The GAMs were calculated using either annual predation/km or predation density as dependent variables and smoothed year as the independent variable. General additive models are able to deal with more complex, non-linear relationships than other regression types and are data rather than model-driven.

This allowed for a clear depiction of data that were not forced into a certain type of distribution. GAMs were estimated for all sites except Vero Beach. There were not enough data for a GAM to be estimated for Vero Beach, so I used a generalized linear model instead. GAM analysis was conducted using the *mgcv* package using a tensor product smoothing factor and Gaussian model family and generalized linear models were conducted using *base* package in R version 4.0.5 with alpha = 0.05 (Wood 2006, Wood et al. 2016, R Core Team 2021).

In order to test for differences between sites, I analyzed egg loss, annual predation/km, and predation density using a mixed effects ANOVA model with year as a random effect and site as a fixed effect using the *car*, *lme4* and *multcomp* packages in R version 4.0.5 with alpha=0.05. (Fox and Weisberg (2019), Bates et al. 2015, Hothorn et al. 2008).

CHAPTER 3. RESULTS

Playa Cabuyal and Playa Grande had the highest annual predation rate of the four sites and had major shifts in predation rates around 2014 (Fig.1). At Playa Cabuyal, the annual predation rate was initially the highest (between 20 and 55%) then sharply decreased to 20% in 2014 and stayed consistently high, never dropping below 20% (Fig.1). At Playa Grande, the annual predation rate was initially low (<20%) and similar to that at Wassaw Island, where nests are screened from predators (Fig.1). GAM analysis shows that predation increased significantly at Playa Grande throughout the study period (Fig.2B, F= 16.74, p<0.05) and, after 2014, was the highest of the four sites (Fig. 1). Annual predation did not significantly increase or decrease at Playa Cabuyal (Fig.2A), Vero beach (Fig.2C) or Wassaw Island (Fig.2D). For annual predation/km and predation density, the random effect year did not add to the ANOVA models, so I used fixed effect ANOVAs instead with site as a fixed effect. Fixed effects ANOVAs show that annual predation/km was significantly higher at Playa Cabuyal and Playa Grande than at the other sites (Fig.3, F= 14.63, p<0.05). At Vero Beach, annual predation was very low (<5%) (Fig. 1) and annual predation/km was not significantly different from that at Wassaw Island (Fig. 3). The annual predation rate at Wassaw Island was also relatively low and stayed near the site's conservation goal (<10% annual predation) (Fig. 1). The average annual predation between 2011 and 2014 was highest at Playa Cabuyal (36%) and lowest at Wassaw Island (12%). The average annual predation at Playa Grande during this period was 15% and there were no data available for Vero Beach. The average annual predation between 2015 and 2020 was highest at Playa Grande (81%) and lowest at Vero Beach (2%). The average annual predation at Playa Cabuyal and Wassaw Island was 27% and 8%, respectively. Between the two time periods annual predation increased by 66% at Playa Grande and decreased by 9% at Playa Cabuyal and by 4% at Wassaw Island.

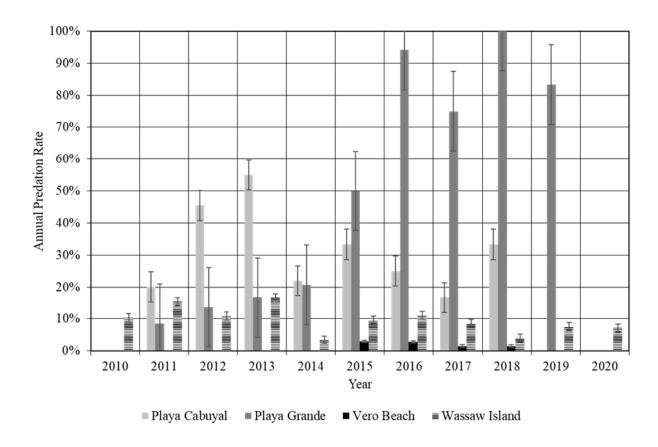


Figure 1- Annual predation rate of sea turtle clutches at sites in Costa Rica (Playa Cabuyal and Playa Grande) and the USA (Vero Beach and Wassaw Island). Annual predation rate was calculated for each site by taking the percentage of total annual nests that were predated.

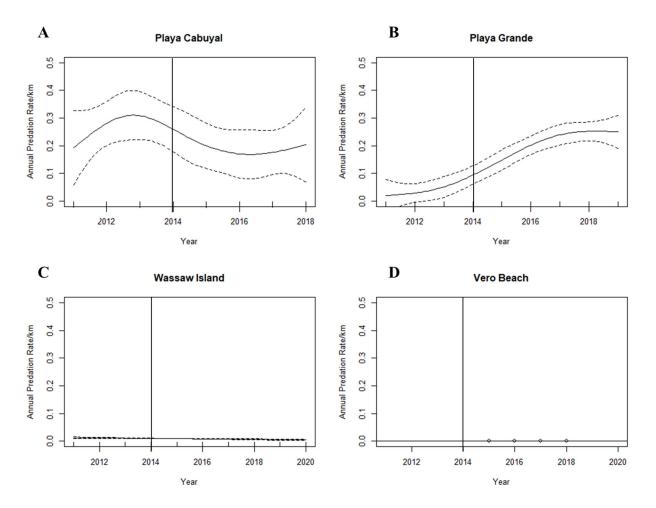


Figure 2- Statistical models of annual predation rate/km on the four beaches: (A) Playa Cabuyal, (B) Playa Grande, (C) Vero Beach, and (D) Wassaw Island. The cutoff between 2011-2014 and 2015-2020 is shown by a vertical line on each panel. Generalized additive models were estimated for Playa Cabuyal, Playa Grande, and Wassaw Island. Due to insufficient data, a generalized linear model was used for Vero Beach.

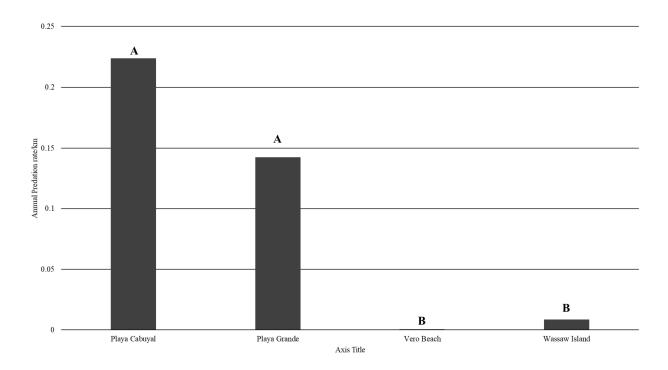


Figure 3- Mean annual predation rate per km of sea turtle nests at sites in Costa Rica (Playa Cabuyal and Playa Grande) and the USA (Vero Beach and Wassaw Island). Bars represent the mean annual predation rate divided by the length of the beach in km. Letters above the bars indicate significant differences from a fixed effects ANOVA.

Predation density was the highest at Playa Cabuyal and the lowest at Vero Beach throughout the study period (Fig.4). Predation density did not significantly differ at Playa Grande or Wassaw Island (Fig.4), nor did it significantly increase or decrease at either of these sites. Predation density was only significantly different at Playa Cabuyal (Fig.4, F= 6.39, p<0.05) and showed an increasing trend throughout the study period. Egg loss/km was significantly higher on Playa Cabuyal (F= 7.17, p<0.05) than the other three sites which were not significantly different from each other (Fig.4).

Throughout the study period at Playa Cabuyal, human poaching accounted for over 40% of the total nest predation events and over 90% of predation in 2011 and 2014 (Fig.5). It is likely that in 2012 and 2013, given the relatively high annual predation rates for these years, poaching accounted for the majority of predation, but this is uncertain since those data were not recorded in those years. Domestic dogs were also important predators on Playa Cabuyal and accounted for nearly all non-human mammalian predation events (Fig.5). On Playa Grande, humans were the dominant predator of sea turtle clutches, accounting for between 30 and 70% of total nest

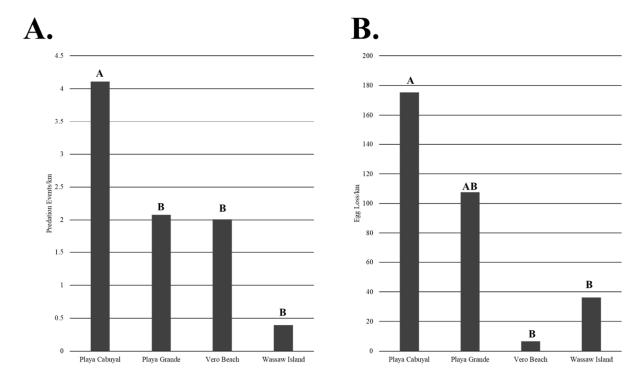


Figure 4- Mean predation density (A) and egg loss (B) of sea turtle nests at sites in Costa Rica (Playa Cabuyal and Playa Grande) and the USA (Vero Beach and Wassaw Island). Egg loss and predation density data were analyzed using a mixed effects model and fixed effects ANOVA respectively. Bars represent the mean values of each parameter. Letters above the bars indicate significant differences.

predations until 2013 (Fig.6). When human poaching declined in 2013, raccoons started to account for the majority of the predation events on Playa Grande, contributing to half of all predation events by 2014 (Fig.6). Until 2017, over a third of predation events had no data on predator species recorded and in 2016 no data were taken on nest predators despite increases in predation rates. Starting in 2017, however, data on nest predators were more reliably recorded as well as more extensive observations on predator sightings. Dogs and crabs did not appear to be important predators on this beach; however, they could account for some of the unknown predation events (Fig.6). Raccoons on Playa Grande made up the majority of predation events throughout the study period (Fig.6). Domestic dogs occasionally will dig up a nest and human poaching was an issue in several years, but raccoons accounted for over 50% of predated nests on Playa Grande since 2014 (Fig.6).

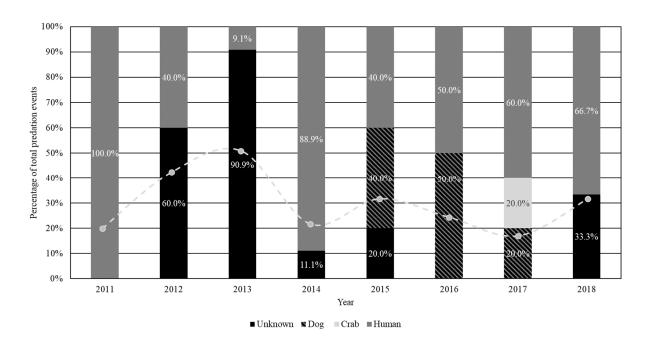


Figure 5- Percentage of predation events by different predator species on olive ridley (Lepidochelys olivacea) nests at Playa Cabuyal. Bars represent the percentage of total predation events attributed to each predator species and the dashed line shows the annual percentage of nests predated.

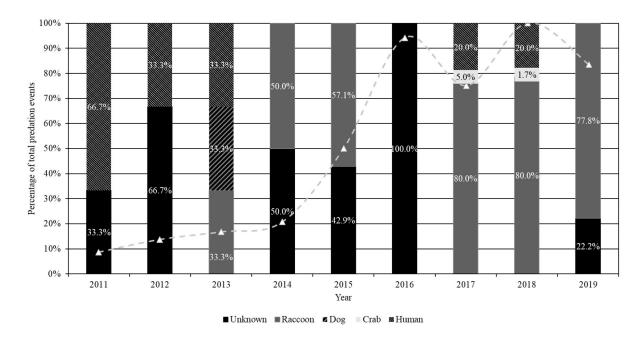


Figure 6- Percentage of predation events by different predator species on olive ridley (Lepidochelys olivacea) nests at Playa Grande. Bars represent the percentage of total predation events attributed to each predator species and the dashed line shows the annual percentage of nests predated.

At Vero Beach, dogs accounted for the majority of nest predation events (44.0%) in 2015, followed closely by ghost crabs (36.0%) (Fig.7). Dog predation quickly dropped below 30% in 2016 and was nonexistent in 2017 and 2018 (Fig.7). Ghost crabs and raccoons as dominant predators alternated between years; when ghost crab predation rates were high (above 40%), raccoon predation rates were low (below 20%) and vice versa (Fig.7). The dominant mammalian predators on Wassaw Island were raccoons and foxes (Fig.8). Fire ant and ghost crab predation was relatively low and fire ant predation events were below 10% for the majority of the years (Fig.8). Ghost crab predation was below 25% of total predation events until 2018 (Fig.8). Between 2018 and 2020, ghost crabs accounted for the majority of all nest predation events (Fig.8), although in most cases the number of eggs lost during ghost crab predation events was very small (<5 eggs/nest). With the exception of 2014 and 2018, predation rates of mammalian predators exceeded those of invertebrate predators (ghost crabs and ants) (Fig.8). Raccoons and foxes were the most prevalent mammalian predators, with minks only accounting a single predation event in 2018 (Fig.8). Raccoons and foxes alternated between being the most prevalent predator for a given year (Fig.8).

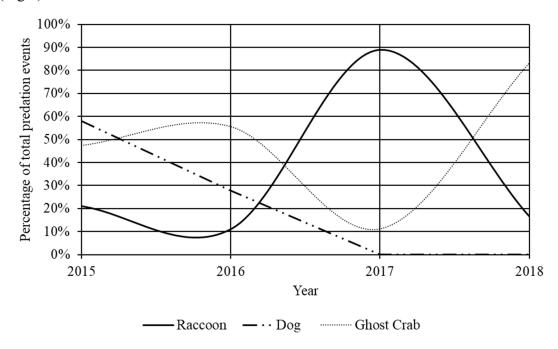


Figure 7- Percentage of predation events by different predator species on loggerhead (Caretta caretta) nests at Vero Beach.

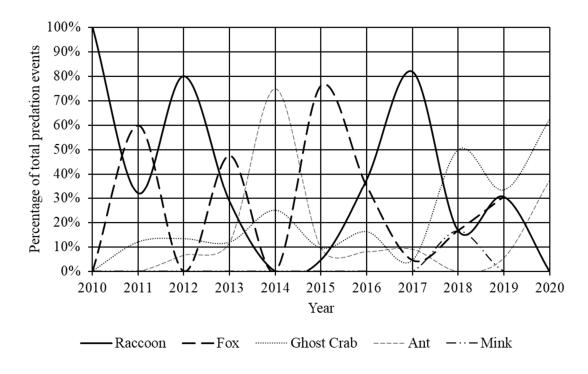


Figure 8- Percentage of predation events by different predator species on loggerhead (Caretta caretta) at Wassaw Island.

CHAPTER 4. DISCUSSION

Beaches where there were no nest protection or predator control programs (Playa Cabuyal and Grande) had higher annual rates of predation than beaches with protective measures (Vero and Wassaw). However, predation density was not always significantly higher at the less managed sites. At Playa Grande the significant increase in annual predation rate, despite constant levels of predation density, indicates relatively constant predation, but a decrease in the number of nests laid. There was an increasing trend in predation density at Playa Cabuyal that could be cause for future concern. At Vero beach annual predation and predation density were the lowest of all four sites. The decrease in predation density at Vero Beach indicates decreasing predator numbers and, due to a drastic decrease in dog predation events after 2016, could be the result of fewer people bringing unleashed dogs to the beach. Vero Beach did not employ nest protection during the study period and their predator management only involved the removal of problem individuals (Quinten Bergman, pers. comm.). There were few predation incidents involving humans or domestic dogs, indicating that regulations put in place on this beach to protect nesting sea turtles were being followed by beach-goers. Larger, wild predators such as foxes and coyotes that are important predators on other nesting beaches would find Vero Beach difficult to access due to the level of development on and around the beach while raccoons, although well-suited to this human-dense area, are often removed. Animals, such as raccoons and skunks, that would typically be a problem on this beach are considered nuisance animals and are therefore dealt with by local animal control agencies after complaints by residents (Quinten Bergman). At Wassaw Island annual predation and predation density were relatively low, as expected due to its undeveloped state, predator management, and nest protection program. Raccoons and foxes were the most important nest predators at Wassaw Island and in-situ nests were physically protected from them using mesh screens while populations of predators were managed by hunting and trapping (NMFS-USFWS 2008). Raccoons were the dominant predator on Wassaw Island from 1973 until 2011 when red foxes had arrived (Dr. Joseph Pfaller, pers. comm.). Non-native mammalian predators, such as foxes, and animals closely associated with human disturbances, such as raccoons and domestic dogs, were responsible for the majority of predation events at the four sites.

Despite its remote location, Playa Cabuyal had the highest annual predation early in the study period. However, very few predation incidents were attributed to natural predators. Disregarding the incidents for which the predator was unknown, almost all predation events were associated with humans and were either by poachers or domestic dogs. Several studies on Costa Rican nesting beaches have found dogs to be among the most prominent predators of sea turtle eggs (Fowler 1979, Burger and Gochfeld 2014, Korein et al. 2019). The presence of dogs may scare away natural egg predators, such as raccoons, though unlike raccoons, dogs play no natural role in the local food chain and managing them should be high priority (Korein et al. 2019). Putting into practice beach regulations regarding domestic pets and the taking or destruction of sea turtle nests would likely bring predation rates on Playa Cabuyal to a sustainable level comparable to a managed beach, like Wassaw Island, without the use of nest screens or predator removal. Nest protection screens could be employed to protect nests against dogs (Korein et al. 2019), but due to the large, cumbersome nature of physical nest protection measures, they may cause more harm at this site as they will be readily noticeable to poachers who are the main cause of clutch predation. More robust monitoring of egg loss and predator species could also be beneficial so that predation can be better evaluated in case of future increases in annual predation. Many of the nest predators throughout the study period were unknown or not recorded and data on eggs lost were difficult to estimate due to missing entries, leading to significant biases in the results of this study.

Raccoons are the most important predators of turtle eggs on Playa Grande and preventing them from accessing turtle nests should greatly increase hatchling production. Many of these predation events are by raccoons and their removal can dramatically increase hatchling recruitment (Butler et al. 2004, Feinberg and Burke 2003, Munscher et al. 2012). Raccoons seem to locate turtle nests by interpreting visual cues, such as soil and sand disturbance, and scent, either of developing hatchlings or ocean water (Burke et al. 2005).

On Playa Grande, the date on which a clutch was predated was often not recorded, but anecdotally raccoons are reported to predate nests shortly after deposition or near emergence. This is consistent with findings from other sea turtle nesting beaches (Fowler 1979, Stancyk et al. 1980, Mroziak et al. 2000). Raccoons do not only rely upon chemical cues, such as the odor of cloacal fluid and ocean water, to locate nests. Racoons on Boca Raton, FL, for example, have learned to associate protective cages with turtle eggs and will attack decoy nest cages (Mroziak et al. 2000). Raccoons are able to recognize shapes, such as a nesting turtle or nest protection

barrier, and associate them with reward and can locate recently deposited eggs by digging in newly disturbed sand from the female turtle's body pit, though nests reburied in fresh sand without visual and olfactory cues are rarely located by them (Fields 1932, Stancyk et al. 1980, Mroziak et al. 2000). Nest caging failed as a long-term solution to raccoon predation at Boca Raton and predation rates were similar with and without caging (Mroziak et al. 2000). Nest cages can be easily seen above the surface, however, and other studies have shown concealed nest screens to be very effective at reducing predation rates (Ratnaswamy et al. 1997, Kurz et al. 2012, Lei and Booth 2017, O'Connor et al. 2017, Korein et al. 2019). On some beaches, screening nests soon after they are laid has been shown to be more effective than lethal removal of predators (Ratnaswamy et al. 1997; O'Connor et al. 2017). Concealed nest screens are already implemented at Playa Grande in a beach hatchery; using these screens for protection of in-situ nests would free space in the hatchery for nests that are endangered by factors other than predation. The use of nest screens will also allow for nests that would otherwise need to be relocated to remain in-situ. In situ nest protection should be used over relocation whenever possible to avoid disrupting natural incubation processes.

Since physical nest protections retain the functionality of raccoons in the ecosystem and can have maximum effect more rapidly, they be more beneficial than a long-term lethal removal at Playa Grande. A trapping program to target problem individuals should be considered at Playa Grande, but since raccoons are considered a natural predator in Costa Rica their complete removal could have unexpected ecosystem level effects. Long-term removal of 50% of raccoons on another beach altered the demography of the raccoon population without increasing nest success (Ratnaswamy et al. 1997). In another study, where control was removed midway through the season, predation through just two months quickly outpaced predation for the entire two past seasons (Engeman et al. 2005). Raccoons are important seed dispersers and predators of other native species, including other sea turtle nest predators such as ghost crabs (Wilson 1993, Ratnaswamy and Warren 1998). If a trapping program were implemented it would need to be persistently applied to have the greatest long-term effect and could take several years to appreciably reduce annual predation (Ratnaswamy et al 1997) and sea turtle nest deposition rates are already declining rapidly at Playa Grande. Due to rapidly declining nest deposition rates on Playa Grande and heavy mammalian predation, management options, such as physical protection of nests, that can be more rapidly implemented should take precedence over a trapping program at

this time. Future studies on Playa Grande should estimate raccoon populations during periods where there are no nesting turtles as well as during the nesting season and determine what the raccoons are feeding on during each season.

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