2018

Evaluating The Biology And Ecology Of Sea Turtles In The Context Of Anthropogenic Climate Change

Elizabeth Michelle Bevan
University of Alabama at Birmingham

Recommended Citation

Bevan, Elizabeth Michelle, "Evaluating The Biology And Ecology Of Sea Turtles In The Context Of Anthropogenic Climate Change" (2018). *All ETDs from UAB*. 1159.
https://digitalcommons.library.uab.edu/etd-collection/1159

EVALUATING THE BIOLOGY AND ECOLOGY OF SEA TURTLES IN THE CONTEXT OF ANTHROPOGENIC CLIMATE CHANGE

by

ELIZABETH MICHELLE BEVAN

JAMES MCCLINTOCK, CO-CHAIR
THANE WIBBELS, CO-CHAIR
KEN MARION
SARAH PARCAK
DANIEL WARNER
DOUGLAS WATSON

A DISSERTATION

Submitted to the graduate faculty of The University of Alabama at Birmingham,
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy

BIRMINGHAM, ALABAMA

2018

EVALUATING THE BIOLOGY AND ECOLOGY OF SEA TURTLES IN THE CONTEXT OF ANTHROPOGENIC CLIMATE CHANGE

ELIZABETH MICHELLE BEVAN

BIOLOGY

ABSTRACT

This dissertation addresses several key gaps in our knowledge of how long-term threats, like climate change, impact the survival and reproduction of thermally-sensitive endangered sea turtles. Many aspects of the sea turtle life history, such as sex determination in hatchlings, are directly affected by environmental temperatures, making sea turtles crucial sentinels for monitoring the impacts of ecosystem variability. Chapter 1 re-evaluates the historic size of the Kemp's ridley sea turtle population in the context of current nesting trends at its primary nesting habitat in the western Gulf of Mexico to address recovery targets and the conservation status for this species. In Chapter 2, I use drone technology to investigate the rarely-observed courtship and mating behaviors of adult green sea turtles at offshore breeding habitat at Rancho Nuevo, Mexico in the Gulf of Mexico. Chapter 3 includes a comparison of sea turtle, crocodile, and shorebird behavioral responses to drones, which is critical information in establishing ethical and effective drone-use protocols for scientific research. Chapter 4 compares sand temperatures across much of the historic nesting range of the Kemp's ridley to examine the potential of these beaches to provide viable nesting habitat considering near-future climate change. The final chapter evaluates rising nesting beach temperatures as a factor driving a feminizing trend in hatchling sex ratios for the Kemp's ridley. Environmental temperatures influence the timing of important events for other life stages of sea turtles like reproductive activities for adults. Thus, my Ph.D. research is not only demonstrating the ability of novel technology to enhance sea turtle conservation, but is providing key insight into critical aspects of sea turtle life histories that occur at in-water habitats where sea turtles spend about 99% of their lives. Given an uncertain future, this research is generating pivotal information for the conservation and protection of the most endangered, data-limited, and geographically restricted species of endangered sea turtles in the world.

Keywords: Sea turtle, Kemp’s ridley, drone, unmanned aircraft, climate change, temperature-dependent sex determination (TSD)

DEDICATION

This achievement is entirely possible because of the family, friends, and true mentors who believed I would conquer; who offered their shoulders from which to stand; and who reminded me of the passion to which I must always be true.

ACKNOWLEDGEMENTS

I am eternally grateful to those who have opened the doors for accomplishing this milestone in my life, especially Thane Wibbels who provided the opportunity to pursue a higher level of excellence in my career; James McClintock who has offered continuous support of my academic achievements; special thanks to Sarah Parcak whose words of wisdom kept me focused; Ken Marion who always lent an ear to listen; Doug Watson and Dan Warner whose advice and guidance have helped keep this dissertation on track; and the UAB Department of Biology for giving me the home from which to pursue these academic goals.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figures *Page*

INTRODUCTION

ESTIMATING THE HISTORIC SIZE AND CURRENT STATUS OF THE KEMP'S RIDLEY SEA TURTLE (*LEPIDOCHELYS KEMPII*) POPULATION

USING UNMANNED AERIAL VEHICLE (UAV) TECHNOLOGY FOR LOCATING, IDENTIFYING, AND MONITORING COURTSHIP AND MATING BEHAVIOR IN THE GREEN TURTLE (*CHELONIA MYDAS*)

MEASURING BEHAVIORAL RESPONSES OF SEA TURTLES, SALTWATER CROCODILES, AND CRESTED TERNS TO DRONE DISTURBANCE TO DEFINE ETHICAL OPERATING THRESHOLDS

COMPARISON OF BEACH TEMPERATURES IN THE NESTING RANGE OF THE KEMP'S RIDLEY SEA TURTLE IN THE GULF OF MEXICO, MEXICO AND USA

PREDICTED HATCHLING SEX RATIOS OF THE KEMP'S RIDLEY SEA TURTLE AT RANCHO NUEVO, MEXICO: IMPACTS OF A WARMING NESTING HABITAT

INTRODUCTION

Humans have a profound impact on the environment. Anthropogenic activity has been the leading cause of increasing carbon and greenhouse gas emissions due to our reliance upon fossil fuels, which exerts a cascade of impacts on the marine environment (Hansen et al. 2005). Rising concentrations of carbon dioxide (CO_2) in the atmosphere warms our global air and ocean temperatures by trapping heat, leading to sea level rise, greater levels of precipitation, and increased intensity of storms (Pachauri et al. 2014). High concentrations of atmospheric CO_2 concurrently increase the rate at which CO_2 dissolves into water, which disassociates into carbonic acid, and ultimately leads to increasingly acidic oceans. A more acidic ocean can negatively affect the health and survival of a number of organisms, particularly species that form shells or are comprised of calcium carbonate (Kroeker et al. 2010). Rising sea surface temperatures can cause shifts in habitats for cold and warm-water species (Walther et al. 2002, Perry et al. 2005, Pachauri et al. 2014), affect migratory routes for a number of species, and result in changes in resource distribution. One of the more concerning factors contributing to the issue of climate change, is the rate at which these changes are happening. Ice cores and other long-term climate records reveal evidence of a climate that has gone through periods of warming in the past. However, human activities have exacerbated the rate of climate change such that it may be difficult or impossible for many species and ecosystems to adapt to these rapid changes (Clark et al. 2008). These symptoms of a rapidly warming and acidifying ocean, are particularly troubling for the marine environment, not in the least because of the implications for a variety of marine life, including long-lived sea turtles.

Many aspects of the biology and physiology of all sea turtles, such as reproductive timing, metabolism, and sex determination, are temperature-dependent (Lutz et al. 2002). Therefore, climate change can be a potent factor influencing the survival and reproduction of all sea turtles, yet the long-generation time for sea turtles makes it unlikely that these species will be able to adapt to the impacts of future climate change (Poloczanska et al. 2009, Fuentes and Hawkes 2011). The Kemp's ridley sea turtle (*Lepidochelys kempii)* is an example of an excellent indicator for monitoring the impacts of increasing environmental temperatures on the biology and ecology of sea turtles due to its geographically restricted distribution relative to other sea turtle species. The Kemp's ridley was once abundant in the Gulf of Mexico. In the mid 1900's, immature Kemp's ridleys were frequently encountered in the Gulf of Mexico, but information on adults was scarce. At that time, there was no documentation on nesting in this species. This prompted some fishermen to develop the misconstrued notion that the Kemp's ridley was a hybrid of two other sea turtle species, such as the loggerhead (*Caretta caretta*) and the hawksbill (*Eretmochelys coriacea*), the loggerhead and the green (*Chelonia mydas*), or the green and the hawksbill, earning the Kemp's ridley the nickname "bastard turtle" (Garman 1880, Carr 1942, Carr 1952, Braun-McNeill et al. 2007). The "riddle of the ridley" was finally revealed to the scientific community in 1963 when Hildebrand discovered a historic film showing a mass nesting of Kemp's ridleys on a remote beach in the western Gulf of Mexico near Rancho Nuevo, Tamaulipas, Mexico (Hildebrand 1963). That film had been recorded by Andres Herrera in June of 1947 and showed an estimated 40,000 Kemp's ridley females nesting during a single "arribada" (mass nesting event) (Hildebrand 1963). The arribada in the Herrera film provided a historic benchmark for evaluating the potential impacts of a variety of stressors such as fishing-related mortality, changes in food resources, and the impacts of climate change on the Gulf of Mexico ecosystem. Unfortunately, the astonishing abundance of turtles in the Herrera film was no longer evident when scientists began surveying the beach at Rancho Nuevo in the 1960's (Adams 1966, Chavez et al. 1968, Chávez et al. 1968b, Marquez 1994). The ridley population had declined dramatically since the 1947 Herrera film, and continued this trend for the next two decades. By the mid 1980's, the numbers of nesting females had dwindled to less than 300 females for an entire nesting season (Heppell et al. 2007).

The drastic decline of the ridley resulted from a variety of threats. Historically there was intense exploitation of eggs on the primary nesting beach during and prior to the 1960's (Hildebrand 1963, Adams 1966). Additionally, since Kemp's ridleys feed primarily on benthic crustaceans, there has been a high rate of mortality from incidental capture in shrimp trawls that has significantly hindered the recovery of this species (Marquez 1994). Ridleys were also captured in large gill nets along the northern Gulf of Mexico, along with green turtles off the western coast of Florida up through the 1950's, and were frequently caught on hook and line in both recreational and commercial fishing activities (Braun-McNeill et al. 2007). The drastic decline of the Kemp's ridley population prompted intense conservation efforts which started in the mid 1960's and have continued to the present. In 1966, a Kemp's ridley conservation program was initiated by the Mexican government that included the protection of nesting females, banning the harvest of eggs, and movement of nests to protected egg hatcheries or “egg corrals” (Chavez et al. 1968 a, b; Marquez 1994). In 1978 the conservation program was expanded to a binational collaboration between the United States and Mexico due to the continued decline of the Kemp’s ridley and the growing knowledge that a majority of their life history in foraging grounds and developmental habitats is spent in U.S. Gulf coastal waters (Marquez 1984, Fontaine et al. 1989, Woody 1989). The binational collaboration resulted in enhanced protection of nesting females, nests, and hatchlings at Rancho Nuevo, and eventually led to the implementation of turtle excluder devices (TEDs) in the shrimping industry in the Gulf of Mexico (Carr 1942, Renaud and Center 1990, Crowder et al. 1995, Lewison et al. 2003).

In addition to those major efforts, an experimental attempt to start a second nesting colony for ridleys on the Padre Island National Seashore in Texas was conducted from 1978 to 1988 (Shaver and Wibbels 2007). Up to 2,000 eggs were transported yearly to Padre Island for “imprinting” and incubation, since Padre Island had been suggested to be the northern extreme of the natural nesting range of the Kemp’s ridley (Werler 1951). Hatchlings from Padre Island were then reared or “headstarted” at the NMFS laboratory in Galveston, Texas until almost a year old, then released into the Gulf of Mexico. Due to the high mortality rates of sea turtles in the Gulf of Mexico prior to the implementation of turtle excluder devices on shrimp nets, data on the effectiveness of imprinting and headstarting remained inconclusive (Adams 1966, Ogren 1989, Allen 1990, Wibbels 1992), although there have been numerous nests of headstarted ridleys documented on Padre Island (Shaver and Wibbels 2007). Imprinting efforts were ended in 1988 and starting in 1989 all hatchlings remained in Mexican sand during incubation before a subset was sent to Texas for headstarting. This protocol was continued with Kemps ridley hatchlings until the program's end in 1992 (Shaver and Wibbels 2007).

Although the Kemp's ridley was on the brink of extinction by the mid 1980's, the comprehensive conservation efforts initiated a gradual recovery of this species from the mid 1990's through 2009 (Figure 1). However, beginning in 2010, the species deviated from the upward trajectory seen in the previous 2 decades, possibly due to a variety of factors, including the Deep Water Horizon Oil Spill and cold stunning events that occurred in 2010. Since 2010, the annual number of nests has fluctuated between approximately 13,000 to over 27,000 (Burchfield, *pers. comm*), but has not returned to the exponential recovery observed in the previous two decades and the reasons for the lack of recovery are unknown (Caillouet 2011, 2014).

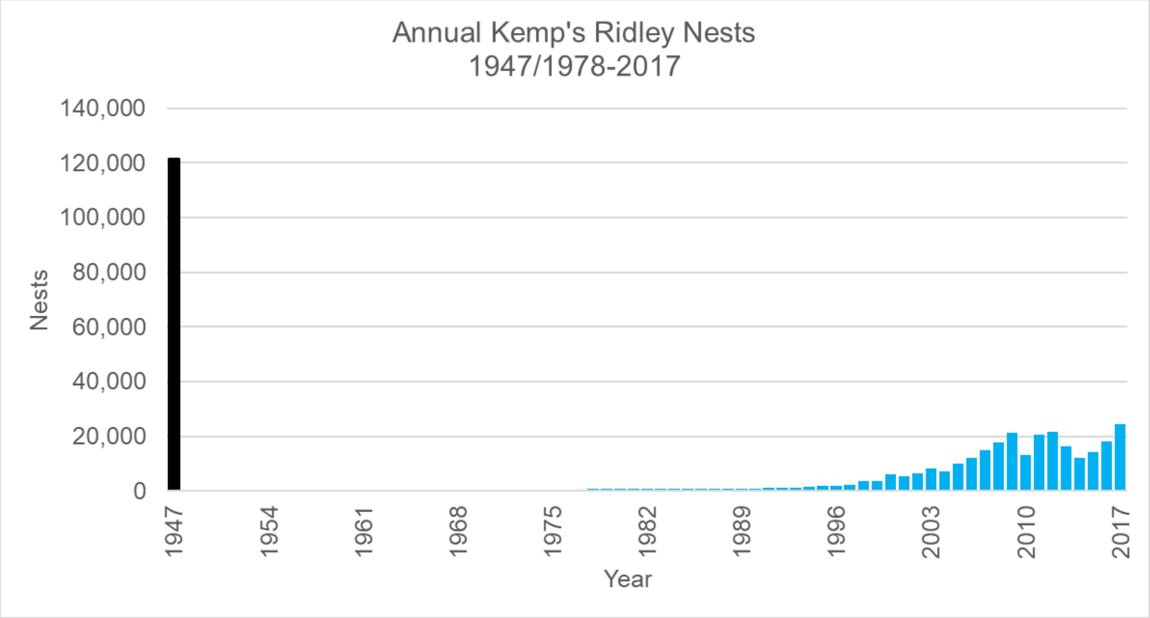

Figure 1. Annual Kemp's ridley nests, the estimated benchmark in 1947 (black) from Bevan et al. 2016 and observed nesting from 1978-2017 (blue) (Peña, *pers. comm.*).

Biology and Ecology

As adults, the grey-colored Kemp’s ridley is the smallest of all sea turtle species and nesting females have straight carapace lengths of approximately 60 to 75 cm, and weigh approximately 40 to 50 kg (Chavez et al. 1968, Chávez et al. 1968b, Pritchard and Marquez 1973) The Kemp’s ridley is an opportunistic feeder, feeding primarily on tunicates and crustaceans, particularly shrimp and crabs (Marquez 1994, Witzell and Schmid 2005). Though there may be differences in diet between life history stages, Kemp’s ridleys show a strong preference for benthic crabs (primarily spider (*Libinia sp.*), purse (*Persephona sp.*), calico (*Hepatus sp.*) or blue (*Callinectes sp*.) crabs) and generally feed in waters less than 50 meters deep (Ogren 1989). The Kemp’s ridley is generally thought to reach sexual maturity at a relatively early age due to its high protein diet of crustaceans and high metabolic rate (Marquez 1994). A variable range of 10-17 years has been accepted for age to maturity in the Kemp’s ridley, though estimates of 10-13 years predominate in most studies (Marquez 1994). However, growth rate, activity levels, and age to maturity estimates vary and may reflect the particular habitat of the turtle and such factors as environmental temperature (Pritchard and Marquez 1973, Schmid and Witzell 1997, Snover et al. 2007), which makes the Kemp’s ridley in the Gulf of Mexico particularly vulnerable to increasing water temperatures due to global climate change. The swimming speed and behavior of the Kemp’s ridley are affected by temperature, which partially determine its geographic distribution (O'Hara 1980) and could contribute to the improbability of the Kemp’s ridley adapting to warming ocean and beach temperatures. Since the majority of the species nests in the western Gulf of Mexico, it is unlikely that enough of the species could shift to nesting on significantly cooler beaches (e.g. on beaches in the northern Gulf of Mexico, along temperate regions of the Atlantic coast, etc.) in only a few generations.

Distribution and Nesting Range

Unlike other sea turtle species, almost all Kemp's ridley nesting occurs in the western Gulf of Mexico from Texas to Campeche with the majority centered on a single, 30.2 km stretch of beach at Rancho Nuevo, in the state of Tamaulipas, Mexico (Marquez 1994). The nesting season occurs from approximately late March through July (Marquez 1994). Subadult Kemp's ridleys inhabit nearshore waters in the Gulf of Mexico and along the Atlantic coast of the U.S. (Chávez et al. 1968b, Marquez 1994), while adults remain mainly in the Gulf of Mexico (Marquez 1994). Hatchlings swimming offshore from the nesting beach ride the gyres of the Gulf of Mexico's currents, possibly associated with mats of seagrasses, until they reach approximately 1 to 2 years of age. Recent particle dispersion modeling supports the area off Tamaulipas, Mexico as a critical area for Kemp's ridleys as they move away from shore and into nearshore currents, thus beginning the pelagic stage of their life history (Putman et al. 2013). Putman et al. (2013) also suggests that there is significant variation in hatchling dispersal as well as later dispersal of juvenile Kemp's ridleys due to seasonal and annual variation in ocean currents (Putman et al. 2013). For example, some juveniles are periodically swept out through the Straits of Florida, into the Gulfstream, and up to New England, which is generally the northernmost extent of their range (Bleakney 1965). Ocean circulation generally favors the distribution of juvenile Kemp's ridleys to the northern Gulf, the eastern Gulf, and the western Atlantic, but dispersal to the south into the Bay of

Campeche, Mexico, may be less frequent (Putman et al. 2013). However, it is possible that climate change could alter ocean currents (Walther et al. 2002) and thus change the dispersal patterns of post-hatchling sea turtles. Historically, nearshore habitats, particularly areas associated with major river systems, have been documented as primary foraging areas for Kemp's ridleys, including Florida Bay, the Mississippi river region, and Campeche Sound (Marquez 1994). In particular, the northern Gulf of Mexico (NGOM) is rich with shrimp and portunid crabs associated with the Mississippi Delta and has been historically reported as a major foraging and developmental habitat for ridleys (Pritchard and Marquez 1973, Hildebrand 1982, Ackerman et al. 1985, Marquez 1994). The crustacean-rich feeding grounds of the NGOM also provide an important migratory corridor and foraging areas for adult Kemp's ridleys (Ackerman and Prange 1972, Putman et al. 2013). However, long-term environmental temperature changes in the Gulf of Mexico ecosystem can have a cascading effect, impacting the distribution of food resources, foraging habitat, and ultimate the distribution of larger marine megafauna (Perry et al. 2005, Parmesan 2006).

Arribada Nesting Behavior

Lepidochelys is the only genus known to exhibit synchronized nesting events termed "*arribadas",* involving hundreds to thousands of turtles nesting in a relatively short period of time (i.e. several hours to several days) and over a spatially restricted section of beach, although some turtles may nest alone (Pritchard and Marquez 1973, Eckrich and Owens 1995). These events average approximately 25 days apart, but this timing can be unpredictable (Bernardo and Plotkin 2007). The density of each arribada is also variable. As the Kemp's ridley neared extinction in the mid-1980s, arribadas involved relatively small numbers of turtles (tens to hundreds of nesting turtles) nesting over a wide stretch of beach (i.e. 20 km or more). With the gradual recovery of the species, periodic, large arribadas of much higher nesting density (i.e. thousands of nesting turtles distributed over only several hundred meters of beach) now occur in addition to low nesting density arribadas. Though various physiological and environmental factors have been suggested as possible factors cueing an arribada, such as strong winds, tidal cycles, (Chávez et al. 1967, Pritchard and Marquez 1973, Witzell et al. 2005) or small changes in water temperature (Aguilar 1987), the exact stimuli controlling this phenomenon remain unknown (Pritchard and Marquez 1973, Bernardo and Plotkin 2007). With changes in the severity and occurrence of these environmental conditions due to climate change, it is possible that the cues that female turtles use to coordinate arribadas could also change.

Synchronized nesting in ridleys is thought to be an adaptive response to this pressure in which predators are satiated by an overwhelming abundance of prey in a short period of time, termed the "predator satiation hypothesis" (PSH) (Hendrickson 1980, Eckrich and Owens 1995, Bernardo and Plotkin 2007). The combined odors of many females and nests at the same time make singling out any one particular nest more difficult than locating a nest from only a few solitary nesting females. A greater percentage of nests should therefore be discovered for solitary nesting females than if nesting is synchronized. Though the smell of eggs would be much stronger during an arribada, thus attracting more predators to the area, the success of those predators in locating nests would be lower due to the massive numbers of turtles nesting on the beach at one time (Eckrich and Owens 1995). This correlates to a greater survival rate for eggs laid in an arribada than by solitary nesting females (Eckrich and Owens 1995).

The arribada behavior in the Kemp's ridley could be affected by a variety of factors including social facilitation. For example, *Lepidochelys* is the only genus of marine turtle to possess inframarginal pores, called "Rathke glands" that secrete substances (e.g. pheromones) that potentially aid in the coordination of arribadas (Pritchard 1969, Ackerman 1977, Pritchard and Trebbau 1984, Marquez 1990, Bernardo and Plotkin 2007). Further, the use of a single primary nesting beach could contribute to the arribada behavior, enhancing the ability of Kemp's ridleys to congregate for the mass nesting event.

Though solitary female Kemp's ridleys have nested on a variety of locations along the Gulf of Mexico and Atlantic coast of the U.S., there is no historical indication of any other major arribada nesting beaches for the Kemp's ridley other than the beaches near Rancho Nuevo (Marquez 1994). This unique characteristic of the Kemp's ridley makes this species ideally suited for studying the effects of long-term environmental changes on nearly an entire species, yet also increases its vulnerability to the impacts of climate change. All sea turtles return to approximately their natal coastal region as adults to reproduce (Lutz et al. 2002). For the Kemp's ridley, the vast majority of the species will continue to return to their natal nesting beaches even if these beaches become unsuitable for successful hatchling production in the near future as beach temperatures rise to potentially lethal levels and nesting habitat throughout the Gulf of Mexico is lost due to sea level rise and increased rates of erosion (Fuentes and Hawkes 2011).

The Kemp’s ridley is the only sea turtle that habitually nests during the daytime (Pritchard and Marquez 1973, Marquez 1994). Spending only 50-60 minutes on the nesting process, Kemp’s ridleys lay the shallowest (35-40 cm deep) and the smallest nests of all marine turtles. Unique to the Kemp’s ridley, they use lateral blows of their characteristically round and depressed bodies to compact sand over freshly-laid nests (Marquez 1994). Every 1.8 (Rostal and Plotkin 2007) to 2.0 years (TEWG 2000) females migrate back to the nesting beach to lay their nests. The clutch frequency for female Kemp’s ridleys has been estimated by several previous studies and results range from a minimum of approximately 1.88 nests per female (Marquez 1994) from tagging studies, to a maximum frequency of 3.075 nests per female from physiological and ultrasound studies (Rostal et al. 1990, 1997). Each nest has an average of 94-95 eggs that incubate for approximately 45-58 days before hatching (Marquez 1994, Rostal and Plotkin 2007).

Temperature-Dependent Sex Determination (TSD)

Secondary sexual characteristics in sea turtles are not exhibited until reaching the subadult or adult stage, by which point the males have generally developed long muscular tails and more pronounced claws on their pectoral flippers in comparison to females (Carr 1952). Without these secondary sex characteristics, the sex of immature turtles can be determined by viewing internal features using laparoscopy on live individuals or dissection in the case of dead turtles (Wibbels et al. 2000). The endangered status of sea turtles prevents the sacrifice of large sample sizes for sex ratio estimations for most sea turtle populations. Other, non-invasive methods have also been used to distinguish between males and females, such as measuring blood hormone levels. Several studies have effectively used circulating serum testosterone levels to determine the sex of immature sea turtles (Owens et al. 1978, Wibbels et al. 2000). In adults, testosterone affects the reproductive physiology of both sexes (Wibbels et al. 1991), but serum testosterone levels increase in males before females in preparation for seasonal breeding and courtship (Wibbels et al. 2000, Geis et al. 2003).

Sea turtles are one of many reptiles to exhibit temperature-dependent sex determination (TSD) where the sex of the embryo is determined by the incubation temperature of the nest. Thus, environmental temperatures can have a profound impact on the reproductive output and success of temperature-dependent species. In sea turtles, cooler nest temperatures produce males while warmer temperatures result in females. The range over which 100% male hatchling production shifts to 100% female is termed the "transitional range of temperatures" (TRT), with the temperature resulting in a 1:1 ratio known as the "pivotal temperature" (Yntema and Mrosovsky 1979). These parameters are determined by incubating groups of eggs at different temperatures, then verifying the sex ratio of each group through histological examination of hatchling gonads. However, a major drawback to this method is the required killing of hatchlings of an endangered species and non-lethal methods of sex ratio determination are preferred. If the pivotal temperature and transitional range for a sea turtle population is known, this information can be used to predict the sex ratio of hatchlings from individual nests (Hanson et al. 1998, Wibbels et al. 1998, Valenzuela 2001). Previous data suggest that the TRT for sea turtles is rather narrow (1-3˚C), indicating that a change of only a few degrees could significantly shift the sex ratios of nests if ambient temperatures are close to pivotal (Wibbels 2003). Given that IPCC models project an approximate 0.3 to 4.8°C increase in global temperatures by 2100 (Pachauri et al. 2014), sea turtles are particularly vulnerable to the impacts of environmental changes on their population sex ratios and hatchling survival. Shaver et al. (1988) studied the effects of temperature on sex ratios for nests between 1982 and 1987 from Kemp's ridleys nesting at Padre Island National Seashore (PAIS) in Texas, and determined the pivotal temperature for the Kemp's ridley population to be approximately 30.2˚C. Data from 2006 - 2008 from PAIS was analyzed using curve fitting models and indicated a pivotal temperature of approximately 30.0˚C and a transitional range of temperatures from approximately 29.0 to 32.5˚C (LeBlanc et al. 2012).

From an evolutionary perspective, a 1:1 sex ratio would be predicted for a population in which parental investment in both sexes is equal (Fisher 1930). However, given the capacity of TSD to result in a wide range of sex ratios, studies on this aspect of sea turtle biology may have profound implications on conservation management and our understanding of the species. A population's sex ratio is an important aspect of sea turtle ecology since it can have a significant influence on the reproductive success of a population. Hatchling sex ratios often do not adhere to the expected 1:1 value, including many produced on the Kemp's ridley nesting beach at Rancho Nuevo (Wibbels 2003, Shaver and Wibbels 2007). A female bias has been reported for many marine turtle populations and for these endangered species a greater percentage of female hatchlings should facilitate the population's recovery through greater egg production in the future (Wibbels 2003). From an evolutionary viewpoint, a variety of hypotheses have been proposed to explain why a biased sex ratio might be selected for in nature (Shine 1999). TSD could therefore be a potentially advantageous mechanism for enhancing the recovery of endangered populations (Wibbels 2003, Witzell et al. 2005, Coyne et al. 2007). Alternatively, TSD could also offer a mechanism by which to mitigate the impacts of long-term increases in environmental temperatures (Fuentes and Hawkes 2011).

Several issues are confronted when attempting to analyze the sex ratio of a sea turtle population. One must decide which life history stage of a population to analyze (e.g. adult, immature, or hatchling). Ideally, all life history stages should be studied to evaluate the temporal dynamics in the population sex ratio. However, some life history stages can be influenced by certain factors that can confound sex ratio analyses. For example, hatchling sex ratios can vary considerably depending on the location and timing of nesting since they possess TSD. Adult sex ratios are susceptible to sampling error since they exhibit sex-specific migratory behavior (Ackerman and Prange 1972, LeBlanc et al. 2012). Alternatively, the immature portion of a population is not affected by sex-specific migrations and represents a collection of many years of hatchling production. Thus, analyzing the immature portion of a population presents several advantages in evaluating sex ratios within a sea turtle population.

Considering that most nests at Rancho Nuevo have been moved to egg corrals, studies since 1998 have shown that egg corrals are typically warmer than natural beach temperatures (Geis et al. 2001, Geis 2004, Park 2006, Eich 2009, Bevan 2013). This trend can serve a critical role in evaluating the impact of recovery programs on the sex ratios of a species, especially as the goal of a recovery program should be to leave more nests to incubate *in situ* as the population recovers. A shift in the management strategy for the Kemp's ridley, from using egg hatcheries to leaving nests on the natural nesting beach, could potentially alter the recovery rate of this population, yet a lower female percentage may reflect a more natural sex ratio for this species (Eich 2009, Bevan 2013).

Sex ratios predicted for the majority of nests moved to the egg hatchery at Rancho Nuevo for the 2007 - 2013 nesting seasons ranged from approximately 75.6 to 80.6% female (Eich 2009, Bevan 2013). Hypothetically, had these nests been left *in situ* on the natural nesting beach, the predicted sex ratios would range from 50.9 to 56.1% female. Collectively, these data suggest that significantly female-biased sex ratios are produced from the Rancho Nuevo hatcheries (Geis et al. 2001, Eich 2009, Bevan 2013). Previous data suggest nests moved to egg hatcheries in the Kemp's Ridley Recovery Program could produce more female hatchlings than nests that remain on the nesting beach. However, those left on the nesting beach may still produce a female bias (Eich 2009, Bevan 2013).

A Model Organism for Evaluating Climate Change

Many aspects of the biology and ecology of sea turtles are thermally sensitive. In addition to the sex determination of hatchlings, other aspects of sea turtle life history, such as reproductive timing (e.g. the timing of reproductive migrations, mating and nesting) are also temperature sensitive (Weishampel et al. 2004, Weishampel et al. 2010). However, several factors contribute to the greater vulnerability of the Kemp's ridley to thermal changes in its critical habitat than for other species of sea turtle. In contrast to all other sea turtles, the distribution of this species is primarily restricted to the Gulf of Mexico with a single primary nesting beach in the western Gulf of Mexico. Hence, Kemp's ridleys of all life stages, including incubating nests, are exposed to a more limited variation in thermal environment across critical habitats than other species of sea turtle. The topography of the primary nesting beach exhibits relatively limited variation in beach and consequently temperature profile. Another factor restricting the variation in temperatures experienced by Kemp's ridley nests is the arribada (mass nesting) nesting behavior of this species, which can temporally and spatially concentrate the distribution of and further reduce any variation in the thermal environment of nests. Therefore, the entire species is exposed to a limited range of temperatures that may influence life history factors such as growth rates, foraging, and seasonal and reproductive migrations. Lastly, in addition to affecting hatchling sex ratios, the incubation temperature in nests has also been shown to affect the fitness of hatchling sea turtles (Mickelson and Downie 2010). Collectively, these factors result in a more thermally-sensitive physiology and ecology for the Kemp's ridley relative to other sea turtles and make this species an important indicator by which to monitor the impacts of climate change on the Gulf of Mexico ecosystem.

Even conservative IPCC end-of-century projections in global surface temperatures (e.g. an increase of ~1°C) could potentially result in significant impacts on a variety of aspects of the biology of the Kemp's ridley including sex ratios, hatchling fitness, and reproductive timing (Poloczanska et al. 2009). Thus, this species can serve as an important model by which to develop plans for mitigating the impacts of climate change on other sea turtle species.

Unmanned Aerial Systems (UAS) for Conservation

Evaluating the impacts of large-scale environmental changes emphasizes the necessity for and value of long-term data. The recent availability of unmanned aerial technology, or “drones”, has introduced a novel tool for enhancing the collection of long-term data (such as population abundance surveys) that can enhance our assessment of environmental changes. The use of drones has become a widespread methodology used in a variety of wildlife studies (Jones et al. 2006, Hodgson 2007, Hodgson and Marsh 2007, Hodgson et al. 2013). Drones can offer an unprecedented opportunity to address many fundamental aspects of the biology and ecology of terrestrial, marine and aquatic species. They can provide a methodology for surveying habitats that are too remote or logistically challenging to access (Bevan et al. 2015, Bevan et al. 2016), provide more accurate species and population counts (Hodgson et al. 2016, Hodgson et al. 2017), increase survey efficiency (Chabot and Bird 2015, Rees et al. 2018), and minimize or eliminate the influence of observer presence on behavioral studies (Acevedo-Whitehouse et al. 2010, Bevan et al. 2015, Vas et al. 2015). Despite the rapid advances in the field of unmanned technology, there is limited information regarding the impact that drones have on wildlife and at what distances a given species can be approached by a drone without being disturbed (Smith et al. 2016). Factors that determine the level of disturbance introduced by a drone include the ability of a given species to detect the auditory and visual disturbance of a drone, the specific sound signature emitted by the drone, and the level of background noise of a particular habitat. Seeking to understand these factors can help elucidate the impact of drones on wildlife and provide critical information for governing the use of drones in research activities.

Drones have been used to study a variety of marine species, including sea turtles at both nesting beach and in-water environments. These studies have demonstrated that drones can provide a stable platform for recording high-quality video of sea turtles in their natural habitat to study behavior, quantify turtle abundance and movements, and all from an advantageous aerial perspective (Bevan et al. 2016, Schofield et al. 2017a, Schofield et al. 2017b). Recent studies at the primary nesting beach of the Kemp's ridley at Rancho Nuevo have specifically demonstrated the use of drones for enhancing sea turtle conservation efforts (Bevan et al. 2015). These studies can provide insight into sea turtle behaviors and their evolutionary significance. Collectively, the rapidly advancing field of unmanned aerial technology can provide new avenues for research that can enhance and expand our understanding of the ecology and evolution of these endangered species in light of a changing environment, while enhancing the definition and designation of their critical habitats for optimal conservation management.

ESTIMATING THE HISTORIC SIZE AND CURRENT STATUS OF THE KEMP’S RIDLEY SEA TURTLE (LEPIDOCHELYS KEMPII) POPULATION

by

E. BEVAN, T. WIBBELS, B.M.Z. NAJERA, L. SARTI, F.I. MARTINEZ, J.M. CUEVAS, B.J. GALLAWAY, L.J. PEÑA, and P.M. BURCHFIELD

Ecosphere 7(3):e01244. 10.1002/ecs2.1244

Format adapted and errata corrected for dissertation

CHAPTER 1

ESTIMATING THE HISTORIC SIZE AND CURRENT STATUS OF THE KEMP'S RIDLEY SEA TURTLE (LEPIDOCHELYS KEMPII) POPULATION

ABSTRACT

This study is a quantitative evaluation of historic nesting levels of the Kemp's ridley sea turtle (*Lepidochelys kempii*) in 1947 based on (1) the Herrera film of a 1947 arribada, (2) Hildebrand's 1963 report regarding the 1947 arribada shown in the Herrera film, (3) historic documentation regarding the Herrera film, and (4) current nesting characteristics related to arribada size relative to total nests for a season. Using this information in a quantitative approach, we estimate a total of approximately 26,916 nests during the 1947 arribada recorded by Herrera. Based on current nesting trends, we also predict that this would equate to approximately 121,517 total nests for the 1947 season (range of 82,514–209,953), which would represent approximately 48,607 nesting females (range of 33 006–83 981). This suggests that during and prior to the 1947 nesting season a relatively robust population of Kemp's ridleys existed, which could support arribadas consisting of at least 26,916 females. The results of the current study indicate that from 1947 through 1985 (the lowest point in the decline of Kemp's ridley nesting) the Kemp's ridley population underwent a 99.4% decline (range of 99.2–99.7%) from an estimated 121,517 nests per season in 1947 to 702 nests per season in 1985. Although the Kemp's ridley population has been recovering since the 1985 season, it has deviated from its

exponential recovery rate and has declined in recent years. The current levels of nesting (12,053 nests in 2014) are still relatively low at 9.9% (range of 5.7–14.6%) of the total estimated nests that occurred in 1947. It is currently not clear whether this population will recover to historic levels considering recent nesting trends and due to a variety of threats that may hinder its recovery.

INTRODUCTION

A common problem encountered when trying to assess the survival status of an endangered sea turtle population is the estimation of historic numbers of nests that occurred prior to a population's decline. Benchmarks estimating historic population sizes are usually not available. Nesting beach surveys often do not occur until after a population's survival becomes tenuous. A classic example of this is the Kemp's ridley, in which the first organized beach surveys were conducted in 1966 by the Mexican federal fisheries amid concern that the population had significantly declined and its future survival was in jeopardy (Chavez et al. 1968). The 1966 survey of the nesting beach at Rancho Nuevo, Mexico, recorded nesting between 3 May and 25 June, with four arribadas of approximately 200 turtles or more, the largest of which occurred on 31 May with 1,317 nests. It was subsequently reported that during the 1970 and 1971 nesting seasons, the largest arribadas were composed of approximately 2,000–2,500 turtles (Pritchard and Marquez 1973). Marquez (1994) provides a summary of data from 1966 through the early 1990s indicating a maximum number of approximately 5,000 recorded nests during the 1966 nesting season, with the number of nests continually decreasing to approximately 900 per nesting season by the late 1970s. Several factors contributed to the precipitous decline of the Kemp’s ridley between 1966 and the early 1990s. Local exploitation of eggs at Rancho Nuevo had grown exponentially during the 1950s and early 1960s due to commercialized harvesting (Hildebrand 1963, Adams 1966, Chavez et al. 1968, Marquez 1994). This was occurring at the same time that the shrimping industry was expanding in the Gulf of Mexico (Nance 1992), resulting in the increased incidental capture of juvenile and adult Kemp’s ridleys (Magnuson et al. 1990). Combined with natural sources of mortality, such as predation of eggs and hatchlings, these factors led to the near extinction of this species. Although more than a decade of initial surveys documented that the Kemp’s ridley population was declining, the historic levels of nesting prior to 1966 were unknown, and the magnitude of decline could have remained a mystery. Fortunately, a nesting event at Rancho Nuevo was filmed by Andres Herrera in 1947. In the classic publication from 1963, Hildebrand described the massive arribada that Herrera recorded on 18 June 1947 and estimated that it consisted of approximately 40,000 turtles (Hildebrand 1963). Subsequently, Carr (1963) supported Hildebrand’s estimation of 40,000 turtles in the arribada after reviewing the Herrera film.

The Herrera film is clearly informative in regard to documenting a historic arribada, but it can also be used for estimating the historic population size during the 1947 nesting season at Rancho Nuevo prior to the near collapse of the species. In contrast to the situation for most endangered species, the Herrera film provides a benchmark for estimating the size of the historic Kemp’s ridley population. However, using the Herrera film for such an estimate requires an accurate estimation of the number of nests in that historic 1947 arribada and how that arribada size relates to the total number of nests for that season. To address the first aspect of this prediction requires an accurate assessment of the number of turtles in that 1947 arribada. Hildebrand (1963) indicates that based on the numbers of turtles in the film and discussions with Herrera, he estimated that at least 10,000 turtles were on the beach at a given time, and that approximately 40,000 turtles nested on that day in 1947. However, Hildebrand did not include the methodology by which he derived his estimate for the size of that arribada. Therefore, part of the current study is to provide an independent evaluation of the number of turtles in the 1947 arribada based on the Herrera film and historic documentation regarding that event.

The second part of this study is to provide a prediction of the total number of nests for the 1947 nesting season based on that arribada to provide insight on the historic population size. In 1963 it was not possible to address this question because little was known about the Kemp's ridley or its nesting biology. Fortunately, the Kemp's ridley has recovered to some extent, and its current nesting biology provides clues to the historic level of nesting back in 1947.

The ability to estimate the historic population size of an endangered species has significant implications for evaluating its current status. For example, one of the listing criteria used by the International Union for the Conservation of Nature (IUCN) in their Red List Assessment takes into account the percent decline of a species over multiple generations. In the case of the Kemp's ridley, the species came close to extinction in the mid-1980s. Due to intense, binational (Mexico and Unites States) conservation efforts, the species began to rebound in the 1990s and acquired an exponential recovery rate. This recovery rate was anticipated to continue, but since 2009, the annual number of nests has declined, with a low of approximately 13,000 nests in 2014, but the causal basis for the decline is unclear (Burchfield 2014, Caillouet 2014; Wibbels and Bevan 2016).

Therefore, understanding the historic population size is critical for evaluating the current conservation status and recent decline of the Kemp’s ridley.

METHODS

Herrera Film and Quantification of Turtle Density

Three digitized copies of the Herrera film were obtained for analysis. During June 2014, the original Herrera film, as well as a DVD copy of the original film, were obtained from the Herrera family. A second digitized copy was then commercially produced from the original Herrera film. Additionally, a third digital copy was made from a U-m atic copy that was dubbed from the original Herrera film by KUHT public television during the 1981 production of the Heartbreak Turtle (Heartbreak Turtle Documentary, 1981, KUHT Public Television, Houston, TX, USA). All three copies of the Herrera film were initially evaluated and the film with the greatest clarity (i.e., the DVD copy obtained from the Herrera family) was used for quantitative analysis of turtle density.

The film was viewed in its entirety, and all aspects of the film were initially evaluated based on their relevance for quantification. Of the entire film, two panoramic views of the beach were the most informative. Each panoramic view was digitally stitched together into a single composite image for quantification. The first image was a wide pan of the beach starting at the northernmost extent of the field of view and extending to the southernmost field of view which included Herrera’s plane (Figure 1).

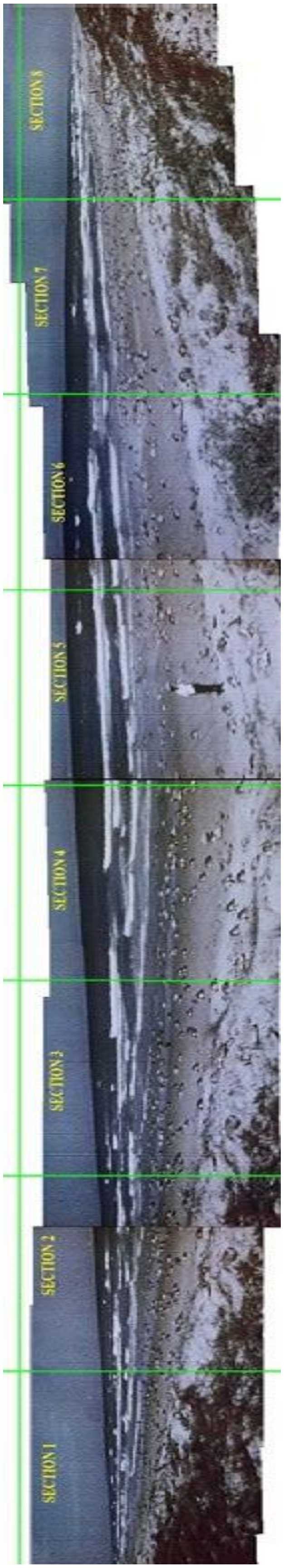
SECTION 8
SECTION 7
SECTION 6
SECTION 5
SECTION 4
SECTION 3
SECTION 2
SECTION 1

Figure 1. A composite image from a wide panoramic view of the June 18, 1947 arribada at Rancho Nuevo, Mexico filmed by Andres Herrera. This represents the widest panoramic view of the arribada shown in the film. The analysis of nesting density is shown in Table 1. Note: From "Estimating the historic size and current status of the Kemp's ridley sea turtle (*Lepidochelys kempii*) population" by Bevan, E., T. Wibbels, B.M.Z. Najera, L. Sarti, F.I. Martinez, J.M. Cuevas, B.J. Gallaway, L.J. Peña, and P.M. Burchfield, 2016, *Ecosphere,* 7(3): e01244. Copyright 2016 by Bevan et al. Reprinted with permission.

This figure was used to evaluate variability in nesting density over a wide section of beach. This was the same view that was previously evaluated by Dickerson and Dickerson (2006). The second image was a scene in which Herrera was standing approximately midway between the surf and the dune, and panned the camera from the surf to the dune with his airplane positioned at the southern boundary of the arribada (Figure 2).

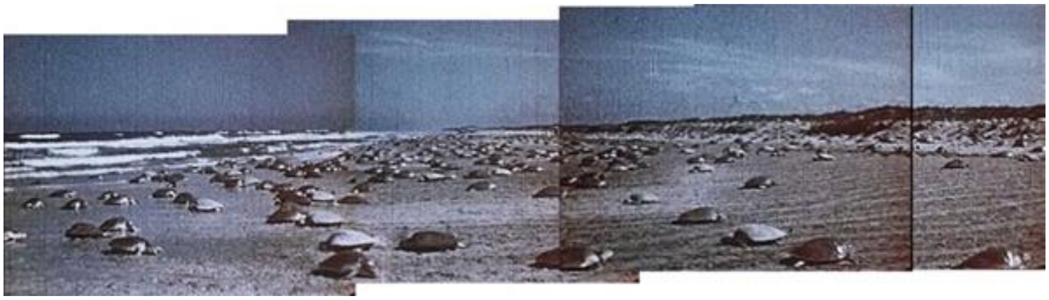

Figure 2. A composite image from the June 18, 1947 arribada at Rancho Nuevo, Mexico filmed by Andres Herrera. This image represents the best panoramic view from the film that includes all sections of the beach, ranging from the surf up through the dune. The analysis of nesting density is shown in Table 1. Note: From "Estimating the historic size and current status of the Kemp's ridley sea turtle (*Lepidochelys kempii*) population" by Bevan, E., T. Wibbels, B.M.Z. Najera, L. Sarti, F.I. Martinez, J.M. Cuevas, B.J. Gallaway, L.J. Peña, and P.M. Burchfield, 2016, *Ecosphere*, 7(3): e01244. Copyright 2016 by Bevan et al. Reprinted with permission.

This composite photo was used to quantify the total number of turtles on the beach, including those on the dune where the majority of nesting is known to occur.

Since turtles were abundant throughout each of the composite photos, the relative lengths of the turtles were used as a metric for estimating the distance of beach analyzed in each of the photos. Adult female Kemp's ridleys have a relatively narrow range of carapace lengths, and a carapace length to width ratio of nearly 1:1, thus the carapace is nearly as wide as it is long in comparison to most other sea turtles (Pritchard and Marquez 1973, Marquez 1994, Epperly and Teas 1999). These two factors enhanced the accuracy of using the turtles in the photos as a metric for estimating distances in the photos.

We adopted two novel methods for estimating relative distances on the beach using carapace sizes of the turtles. In the first approach the relative carapace lengths of the turtles in the photos were directly used to estimate distances. This method was optimal for Figure 1 since it included relatively large numbers of turtles spread over a wide expanse of beach that included various camera angles. The panoramic view was divided into eight equal segments and turtle lengths were analyzed throughout each segment on the beach flat adjacent to the tidal interface. The segment length was then divided by the average turtle carapace length for each segment, which converted the lengths of each segment into a specific number of "turtle carapace equivalents" (TCEs). Considering the turtles were oriented in a variety of directions in Figure 1, we used a general estimate of 65 cm for a single TCE, based on the average carapace lengths and widths reported for nesting females (Pritchard and Marquez 1973, Marquez 1994).

In the second method, turtle carapace lengths were used to generate relative carapace length ratios (CLRs) at various distances from an observation point (i.e., camera). Sixty-five-centimeter pieces of one-half-inch PVC pipe were used to represent the straight carapace length of nesting ridleys. Segments were placed at 10-m intervals from 5 to 360 m and photographs were taken. Relative lengths of the pipes at various distances in the photographs were measured using ImageJ software. A series of ratios were generated by comparing those lengths at various distances. In similar fashion, ImageJ software was used to determine the relative lengths of the turtle carapaces at various distances from the camera in the composite images. Those lengths were then used to generate ratios that were then compared to the experimental ratios to estimate distances. The second method was optimal for estimating distances in Figure 2 due to the camera perspective from the middle of the beach pointed directly south towards Herrera’s airplane and with most turtles oriented perpendicular to the camera. In the case of Figure 2, the carapace lengths of the three closest turtles were compared to the carapace lengths of six turtles near the southern border of the arribada immediately in front of Herrera’s airplane. The ratio of those carapace lengths were then compared to those in the experiment to estimate the distance from the camera to the airplane. As an independent validation, the TCE method was also applied to Figure 2 with similar results. Further, the CLR method described above was also applied to Figure 1 with similar estimates to those produced by the TCE method.

Beach Topography

The nesting beach at Rancho Nuevo is a relatively broad sand beach, bordered by a well- defined and vegetated dune area, as described by Pritchard and Marquez (1973), which often includes two berms separated by a trough (Marquez 1994). Marquez (1994)

further partitions the beach into zones defined as, (1) beach flat, (2) the front (base) of the primary dune, (3) the seaward face of the primary dune, and
(4) the top of the primary dune.

Quantification and Location of Nesting

Figure 2 was optimal for quantifying the total number of turtles on a portion of the beach since it included all areas that were occupied by turtles ranging from the water up through the top of the primary dune. The number of turtles in the image was independently estimated by 26 individuals using photo editing software (e.g., Paint, etc.) that allowed for enlarging the image and marking the turtles. We partitioned these estimates into the number of turtles on the beach flat (zone one, as indicated by Marquez (1994)) vs. the number of turtles located in the area at the base of the dune and up through the top of the primary dune. In contrast to Figure 2, the camera perspective in Figure 1 does not facilitate the accurate quantification of turtles at the base of the dune and on the dune. Therefore, the percentage of turtles at the base of the dune and on the dune in Figure 2, was used to estimate the number of turtles at the base of the dune and on the dune in Figure 1 based on the number of turtles quantified on the beach flat in Figure 1. For the purposes of the current study, we defined the base of the dune as the area within approximately 3 m directly in front of the primary dune, up to the seaward facing slope of the primary dune, which corresponds to zone two as described in Marquez (1994). Marquez (1994) reported that 47.64% of Kemp’s ridley nesting occurred in zone three (i.e., the seaward facing slope of the primary dune), followed by 24.11% of nesting in zone two, and 17.77% of nesting in zone four. The value we obtained for zones 2 and 3 from Figure 2 (35.8%) may be conservative, since we also calculated this value hypothetically based on previously reported data on the timing of nesting events on the beach (e.g., emerging from the surf, crawling up the beach, nesting, and return to the water). Previously reported data indicate that Kemp’s ridleys spend approximately 15 min moving onto the beach and selecting a nesting area, approximately 30 min for the nesting process, and approximately 5 min or less to return (Pritchard 1969, Pritchard and Marquez 1973, Marquez 1994). Although the dynamics of arribada nesting have not been well quantified, if the main portion of an arribada represents a steady state in which the same number of turtles are moving onto as well as off of the beach, then we could predict that during this portion of the arribada, approximately 60% would be engaged in the nesting process and 30% would be in transit moving up the beach preparing to nest or returning to the sea. Based on current nesting trends, the majority of nesting at Rancho Nuevo occurs in the area at the base of the dune or on the dune, with 10% or less of nesting occurring on the beach flat (J. Peña, personal communication). The turtle density in Figure 2 was calculated for the entire portion of beach shown by dividing the total number of turtles quantified by the length of beach estimated using the CLR method. For comparison, we performed a similar analysis on an image from a recent arribada from a similar camera perspective in June of 2011 (Figure 3).

Figure 3. An example of a recent, relatively large Kemp's ridley arribada on June 5, 2011 at Rancho Nuevo, Mexico. In this image of the arribada, an estimated 313 turtles were quantified on approximately 50 m of beach for a turtle density of 6.3 turtles/meter. It is estimated that a total of 7000 turtles nested over approximately 200 m of beach or less from approximately 3 pm until 9 pm. (Photo Credit: Toni Torres, Gladys Porter Zoo). Note: From "Estimating the historic size and current status of the Kemp's ridley sea turtle (*Lepidochelys kempii*) population" by Bevan, E., T. Wibbels, B.M.Z. Najera, L. Sarti, F.I. Martinez, J.M. Cuevas, B.J. Gallaway, L.J. Peña, and P.M. Burchfield, 2016, *Ecosphere,* 7(3): e01244. Copyright 2016 by Bevan et al. Reprinted with permission.

The camera perspective (i.e., from the top of the dune) used in Figure 1 did not provide a full view of all sections that were occupied by turtles and therefore a complete count of turtles was not possible. Specifically, due to the camera perspective, the seaward portion of the dune along with any turtles nesting in that region were not visible towards the northern and southern portions of the image. Additionally, due to the relatively large distance shown in the image, it becomes increasingly difficult to quantify turtles near the northern and southern extremes of the composite image. Therefore, we focused on quantifying turtles on the beach flat, which were more accurately distinguishable throughout this image, and used those data to evaluate variation in turtle density. The number of turtles in Figure 1 was independently estimated by eight individuals using photo editing software (e.g., Paint, etc.) that allowed for enlarging the image and marking the turtles.

Figure 1 was arbitrarily divided into eight equal segments to calculate turtle density. As indicated above, only turtles on the beach flat area were counted (i.e., turtles on the dune were excluded). The turtle density for each segment was calculated by dividing the total number of turtles on the beach flat in each segment by the estimated length of each segment (length calculations are described above). In Figure 2, all turtles were counted and the density was calculated by dividing the total number of turtles by the estimated distance from the camera to the turtles directly in front of Herrera's plane.

Historic Information and Documentation Regarding the Herrera Film

In addition to reviewing Hildebrand's 1963 publication, research was conducted to compile pertinent information regarding the 1947 arribada recorded by Herrera. This included (1) information and personal correspondence from Andres Herrera that was obtained from the Herrera family, (2) correspondence and information compiled by Henry Hildebrand that was obtained from USFWS/NPS, (3) video interviews from the Heartbreak Turtle recorded by KUHT public television (Heartbreak Turtle Documentary, 1981, KUHT Public Television, Houston, TX, USA), (4) video discussions with the family of Andres Herrera including his wife, Evelina Herrera and long-t ime residents of Rancho Nuevo, and (5) relevant information from other publications that address the 1947 arribada (e.g., Carr 1963, 1967, Phillips 1989, etc.). This information was reviewed with the intention of refining the 1947 arribada, including (1) the duration of the arribada,

(2) the length of beach over which the arribada occurred, and (3) the density of nesting. Each of these parameters is discussed in more detail below.

Percentage of Total Seasonal Nesting Represented by Large Arribadas

Considering the only historic data we have from 1947 is the Herrera film, we propose a novel method for estimating the total number of nests for the 1947 nesting season based on recent nesting trends and the relative size of arribadas. For more than two decades, the Binational Kemp's Ridley Recovery Program has conducted multiple surveys daily of the beach at Rancho Nuevo over the nesting season. Multiple personnel are mobilized to monitor and translocate the nests to the egg corrals during an arribada, and the beach is monitored after an arribada to evaluate predation and emergence of any nests that were not moved to the egg corrals. This has provided a robust database for evaluating total nests per season as well as relative arribada size. It is plausible that during an arribada some nests may be undetected, and as such, the arribada nest counts should be considered a minimum. Specifically, we have evaluated the percentage of the total nests per season that are represented in the largest arribada for each year during eight recent nesting seasons (2006–2013). These years were chosen since each nesting season included a relatively large arribada of approximately 1,000–7,000 nests. We then used this information to predict the total the number of nests during the 1947 nesting season based on the arribada recorded in the Herrera film.

RESULTS

Nesting Density Estimates

A total of 26 individuals counted the number of turtles in Figure 2 from the 1947 Herrera film to yield an average of 286.0 and 43.5 SD turtles (Table 1).

Table 1. Quantification of turtles on the beach in Figure 2 from the June 18, 1947 arribada filmed by Andres Herrera at Rancho Nuevo, Mexico.

Individual	Turtles on the Beach Flat	Turtles Counted on the Dune†	Total Number of Turtles Counted in Fig. 2	Percent of Turtles in Dune†
1	189	121	310	39.0
2	203	82	285	28.8
3	212	137	349	39.3
4	181	104	285	36.5
5	271	161	432	37.3
6	174	101	275	36.7
7	180	95	275	34.5
8	175	89	264	33.7
9	177	108	285	37.9
10	176	133	309	43.0
11	149	76	225	33.8
12	186	91	277	32.9
13	228	93	321	29.0
14	169	72	241	29.9
15	215	93	308	30.2
16	159	92	251	36.7
17	183	117	300	39.0
18	160	104	264	39.4
19	156	132	288	45.8
20	152	84	236	35.6
21	185	80	265	30.2
22	127	107	234	45.7
23	246	90	336	26.8
24	163	95	258	36.8
25	155	97	252	38.5
26	202	109	311	35.0
Average	184	102	286	35.8
Standard Deviation	31	21	44	4.9

† Dune represents beach zones two (i.e., the base of the primary dune), three (i.e., the seaward facing slope of the dune), and four (i.e., on top of the primary dune), as described in Marquez (1994).

Note: From "Estimating the historic size and current status of the Kemp's ridley sea turtle (*Lepidochelys kempii*) population" by Bevan, E., T. Wibbels, B.M.Z. Najera, L. Sarti, F.I. Martinez, J.M. Cuevas, B.J. Gallaway, L.J. Peña, and P.M. Burchfield, 2016, *Ecosphere*, 7(3): e01244. Copyright 2016 by Bevan et al. Reprinted with permission.

Results indicated that approximately 35.8% and 4.9% SD of turtles occurred in the dunes. Based on the CLR method using the relative carapace lengths of the closest vs. the farthest turtles in Figure 2, it was estimated that the turtles in the composite image were on approximately 60 m of beach, yielding a density of 4.8 turtles per meter of beach (Table 2).

Table 2. Evaluation of nesting density in Figs. 1 and 2 from the June 18, 1947 arribada filmed by Andres Herrera at Rancho Nuevo, Mexico.

Beach Section Analyzed	Estimated Length of Beach Section (meters)	Turtles Counted on Beach Flat	Turtle Density on Beach Flat†	Turtles in Dune	Total Number of Turtles	Total Turtle Density†	Predicted Number of Turtles for 2 km of Beach	Predicted Number of Turtles Over 4 h‡
Fig. 1- Section 1	72.0	74.0	1.0	41.3§	115.3	1.6	3204.9	15383.7
Fig. 1- Section 2	36.0	99.0	2.7	55.2§	154.2	4.3	8512.9	40861.9
Fig. 1- Section 3	31.0	80.0	2.5	44.6§	124.6	4.0	7928.1	38054.7
Fig. 1- Section 4	22.0	58.0	2.6	32.3§	90.3	4.1	8152.9	39134.0
Fig. 1- Section 5	22.0	44.0	2.0	24.5§	68.5	3.1	6153.0	29534.4
Fig. 1- Section 6	29.0	54.0	1.9	30.1§	84.1	2.9	5889.8	28271.2
Fig. 1- Section 7	36.0	89.0	2.5	49.6§	138.6	3.9	7742.5	37164.1
Fig. 1- Section 8	73.0	79.0	1.1	44.1§	123.1	1.7	3385.4	16249.7
Entire Fig. 1	321.0	578.0	1.8	322.3§	900.3	2.8	5607.6	26916.7
Entire Fig. 2	60.0	183.6	3.1	102.4¶	286.0	4.8	9533.3	45760.0

† Represents one meter of beach length extending from the surf through the dune.
‡ Based on 4 h of high- density nesting over 2 km of beach with an average time spent on the beach of 50 min per turtle.
§ Hypothetical based on 35.8% of total turtles located in the dune, as per analysis of Figure 2.
¶ Actual number counted in dune.

Note: From "Estimating the historic size and current status of the Kemp's ridley sea turtle (*Lepidochelys kempii*) population" by Bevan, E., T. Wibbels, B.M.Z. Najera, L. Sarti, F.I. Martinez, J.M. Cuevas, B.J. Gallaway, L.J. Peña, and P.M. Burchfield, 2016, *Ecosphere*, 7(3): e01244. Copyright 2016 by Bevan et al. Reprinted with permission.

The lengths for each of the eight segments in Figure 1 were calculated using the TCE method and the results are shown in Table 2. The number of turtles on the beach flat and the resulting turtle density for the beach flat is shown for each segment in Table 2. Additionally, the hypothetical number of turtles in the dune is also shown in Table 2 for each segment based on intrinsic data from Figure 2, as described in Methods. The data from Figure 2 indicated that 35.8% and 4.9% SD of the total turtles on the beach were located on the dune, and 64.2% were located on the beach flat. The total length of the beach in Figure 1, calculated by the TCE method, was estimated to be 321 m with a total of 578 turtles counted on the beach flat and an estimated 322 turtles in the dune, for a total of 900 turtles and a density of 2.8 turtles per meter.

Duration of the Arribada

Hildebrand (1963) estimated that, based on reports provided by Herrera, the duration of the 1947 arribada was approximately 4 h lasting from nine am until about one pm. Hildebrand therefore used a duration of 4 h in his calculations for the total number of turtles in the 1947 arribada. This was supported in a letter from Andres Herrera to Hildebrand in which Herrera states that arribadas occur from 9 in the morning to 12 or 1 in the afternoon. In addition to discussions with Herrera, Hildebrand also interviewed local residents of Rancho Nuevo, who corroborated that 4 h is a reasonable estimate for the duration of an arribada. Using this information, our initial estimates are based on a 4-h duration for the arribada. However, there are several lines of evidence that suggest the arribada could have been longer than 4 h and these points are addressed below in the discussion.

Temporal and Spatial Dynamics in Arribada Nesting Density

The temporal dynamics of nesting density for arribadas is not well documented in any study of arribada nesting in ridleys. The time required to reach high-density nesting and subsequently the time required for nesting to decrease at the end of the arribada has also not been quantified. Data from studies from olive ridleys as well as recent data from Kemp's ridleys indicate that high nesting density during arribadas can last for multiple hours. There is anecdotal evidence that heavy nesting density can be reached relatively quickly. As an example, Cornelius (1986) indicates that the transition from low level nesting to high density nesting in olive ridleys can occur rapidly "in less than an hour", followed by many hours of high- density nesting. In the case of the 1947 Herrera arribada, Hildebrand (1963) indicates that high- density nesting occurred over at least a 4-h period, based on discussions with Herrera and local residents of Rancho Nuevo. Further, Herrera indicated that high density nesting was occurring at the time when he left the beach after recording the film. Therefore, as a conservative estimate, we are only using the 4-h value that represents the period of high-d ensity nesting as indicated by Hildebrand and Herrera and does not reflect the time periods prior to and after the high-density nesting levels.

During the period of high-density nesting in the arribada, there appears to be both spatial and temporal variation in nesting density, as evident in Figures 1 and 2, and listed in Table 2. The highest density of turtles recorded is shown in Figure 2 with five turtles per meter. Interestingly, this same area appears to show a lower density of turtles in Figure 2, which suggests temporal diversity in turtle density during the arribada and Table 2 exemplifies the spatial diversity in turtle density during the arribada. These factors are taken into consideration in the estimates below in the calculations for predicting the total number of turtles in the arribada.

Length of Beach Over Which Nesting Occurred

The Herrera film does not appear to document the entire length of beach occupied by the arribada. The widest pan of the camera in the Herrera film shows several hundred meters of beach with relatively high-density nesting. The high- density nesting extends to, and potentially beyond, the northernmost field of view that was recorded in the pan of the beach and to the south, the high- density nesting extends to Herrera's airplane. However, the southern border of the arribada may have expanded while Herrera was on the beach, since he noted that he had to push his airplane to the south to take off because turtles were moving under it ("to the degree that when I came back to my plane I could not take off because they were passing below it", stated in Hildebrand (1963), and stated in a letter from Herrera to Hildebrand dated 20 May 1961). Although the entire length of beach was not documented in the film, Herrera is quoted on the subject. Hildebrand (1963) quotes Herrera who indicated that more than 1 mile of beach was totally covered with turtles ("tenia una extension de mas de una milla totalmente llena de tortugas"). The observation of "more than a mile of beach" was also specifically stated in two of Herrera's letters to Hildebrand (letters dated February 10, 1961 and May 20, 1961). In a video interview of Herrera in the 1981 documentary "The Heartbreak Turtle", Herrera states "possiblemente dos milos", possibly 2 miles of beach covered with turtles (Heartbreak Turtle Documentary, 1981, KUHT Public Television, Houston, Texas, USA). Hildebrand (1963) reports that he verified these observations with Juan Gonzales

Galvan, a local resident of Rancho Nuevo who had been observing arribadas for 25 years, and who had learned details of previous arribadas by word of mouth from local residents and indicated that the observations reported by Herrera are certainly not exaggerated. Hildebrand also states that based on his discussions with Herrera and local residents, arribadas usually cover approximately 2 km or less of beach. Based on this information, we chose 2 km as the length of beach used in the calculations below. Two kilometers was also the estimate used by Dickerson and Dickerson (2006) in their evaluation of the 18 June arribada.

Average Time Spent on the Beach by a Nesting Turtle

No comprehensive studies have directly addressed the average time required by a Kemp’s ridley to complete the nesting process, yet a variety of anecdotal information does exist and suggests approximately 45 min to 1 h. Pritchard (1969) meticulously documented the entire nesting process from emergence to return to the water and reported approximately 50 min. Marquez (1994) reported that the nesting process takes approximately 50–60 min. Based on direct observations, Pritchard and Marquez (1973) reports that the total time from emergence to return to the sea was approximately 50 min, which was confirmed in discussions with local residents of Rancho Nuevo. Biologists currently conducting the conservation project at Rancho Nuevo indicate that 50 min appears to be a reasonable estimate for the time spent by a Kemp’s ridley on the nesting beach. Based on these anecdotes, we used 50 min as the value for the average time spent on the entire nesting process.

Predicting Total Number of Turtles in the 18 June 1947 Arribada

Based on the material reviewed above, we chose the following values for our initial estimate of the total number of nests in the 1947 arribada: (1) Duration of high density nesting was 4 h, (2) Average time spent on the beach by a nesting turtle was 50 min, (3) Length of the beach occupied by the arribada was 2 km. Considering the spatial and temporal diversity in turtle density observed in the Herrera film, we used two methods of estimating the total number of turtles in the arribada. Based on Figure 1, an estimate of 578 turtles were counted on the beach flat, which represents 64.2% of the estimated total number of turtles on the beach. Combining this number with the predicted 35.8% of turtles on the dune would result in an estimate of 900 turtles on the beach over the 321 m. Using this density in the equation below results in an estimate of 26,916 turtles for the 4 h of high density nesting during the 1947 arribada.

Estimated total number of nests in Figure 1 = [density (900 turtles per 321 m of beach) X length of beach (2,000 m/321 m)] × [duration of the arribada (4 h)/amount of time needed for nesting (50 min)] = 26,916 turtles.

Based on Figure 2, which represented the highest nesting density zone evaluated, a total of 286 turtles were estimated over 60 m of beach, including both the beach flat and dune area. Using this nesting density in the equation above results in a total of 45,760 turtles during 4 h of high- density nesting in the 1947 arribada.

We provide a detailed discussion below of underlying assumptions and potential sources of error that could confound this prediction.

Estimating Total Seasonal Nesting Represented by Large Arribadas

The largest Kemp's ridley arribada each year for the 2006–2013 nesting seasons at Rancho Nuevo is shown in Table 3. The 2006–2013 nesting seasons included two to four relatively large arribadas (greater than approximately 750 nests or more per arribada). The number of nests in the largest arribada of each nesting season ranged from a minimum of 1797 nests out of 14,018 total recorded nests in 2010, to a maximum of 7,000 nests of 21,462 total recorded nests in 2011. The largest arribada of each nesting season accounted for a minimum of 12.82% in 2010, to a maximum of 32.62% in 2011 (mean 22.15%) of the total number of nests recorded during each respective nesting season. We have attempted to be conservative in our approach to prevent overestimating the total number of nests in the 1947 nesting season by (1) only using the largest arribada each year and (2) by providing a range of predictions that reflect the variability seen in arribadas from recent nesting seasons. Further, we provide a detailed discussion below of underlying assumptions and potential sources of error that could confound these predictions. If these percentages are applied to our estimates of 26,916 total nests in the 1947 Herrera arribada (as described above), it results in a predicted range of total nests for the season of approximately 82,514–209,953 total nests (using recently observed large arribadas that range from 12.82% to 32.62% of total nesting for the season). If the June 18, 1947 arribada represented the mean percentage of total nesting for the season (22.15%), then the estimate for the total number of nests in the 1947 nesting season becomes approximately 121,517 nests.

Table 3. Largest Kemp’s ridley arribada each year from 2006 to 2014. The total number of seasonal nests reflects those reported from the entire state of Tamaulipas, including Rancho Nuevo, Texas, and Tecolutla, Veracruz.

Year	Total Number of Recorded Nests For Nesting Season	Largest Arribada of the Nesting Season (Date)	Largest Arribada of the Nesting Season Approximate Number of Nests	Percent of Total Seasonal Nests Represented by Largest Arribada
2014	12053	4/30/2014	2000	16.6
2013	17359	6/6/2013	3100	17.9
2012	22818	5/16/2012	6600	28.9
2011	21462	6/5/2011	7000	32.6
2010	14018	6/3/2010	1797	12.8
2009	22012	5/17/2009	5023	22.8
2008	18867	4/12/2008	2558	13.6
2007	15567	5/20–24/2007	5000	32.1
2006	12629	5/11/2006	2085	16.5

Note: From “Estimating the historic size and current status of the Kemp’s ridley sea turtle (*Lepidochelys kempii*) population” by Bevan, E., T. Wibbels, B.M.Z. Najera, L. Sarti, F.I. Martinez, J.M. Cuevas, B.J. Gallaway, L.J. Peña, and P.M. Burchfield, 2016, *Ecosphere*, 7(3): e01244. Copyright 2016 by Bevan et al. Reprinted with permission.

Based on a value of 2.5 clutches per nesting female per season (TEWG 2000), our predictions suggest a range of 33,006–83,981 (mean 48 607) females nested during the 1947 nesting season.

It is important to note that our analysis of Figures 1 and 2 indicates that nesting density was higher on the same approximate portion of the beach during the time when Figure 2 was taken. This suggests that the overall nesting density could have been greater over the area of beach shown in Figure 1 during some portions of the arribada.

Estimating Total Nesting in 1947 Using Hildebrand’s Estimate for the 18 June Arribada and Current Nesting Trends

We can also apply the percentage of total nesting represented by the largest arribadas in recent years to the Hildebrand (1963) estimate of 40,000 turtles for the 18 June arribada to estimate total nesting for 1947 as a comparison to our estimate for total nesting derived from the analysis of Figures 1 and 2. Assuming that Hildebrand’s estimate (1963) of 40,000 turtles represented an average of 22.15% (range of 12.82 and 32.62%) of total nesting in 1947, then the predicted total nests for the season would be an average of 180,587 (range of 122,624– 312,013) (Figure 4).

DISCUSSION

This study is an independent evaluation of historic nesting levels of the Kemp’s ridley sea turtle (*Lepidochelys kempii*) in 1947 based on (1) the Herrera film of a 1947 arribada, (2) Hildebrand’s 1963 report regarding the 1947 arribada shown in the Herrera film, (3) historic documentation regarding the Herrera film, and (4) current nesting characteristics related to arribada size relative to total nests for a season. Using this information, we estimate a total of approximately 26,916 nests during the 1947 arribada recorded by Herrera. Based on current nesting trends, we also predict that this would equate to approximately 121,517 total nests during the 1947 season (range of 82,514–209,953), which would represent approximately 48,607 nesting females (range of 33,006–83,981).

In the initial scientific evaluation of the Herrera film, Hildebrand (1963) estimates that the arribada filmed on June 18, 1947 had approximately 40,000 turtles on the beach. Based on the 1947 film and discussions with Herrera, Hildebrand estimated that “there were at least 10,000 turtles on the beach at a given time and that probably 40,000 individuals nested on that day”. In the 1963 publication, he did not clearly indicate the methodology by which he estimated the 10,000 turtles on the beach. However, it appears that Hildebrand used a 4- h duration and 1- h time period spent by each turtle on the beach in his calculations of the arribada size, and 1.6–2 km as the length of beach occupied by the arribada, based on discussions with Herrera and information gathered from local residents from Rancho Nuevo. In evaluating Hildebrand’s office documents, it appears that he counted turtles on a section of beach and extrapolated this value over the entire length of beach occupied by the arribada. However, the exact portion of the film and Hildebrand’s specific method of calculation was not clearly indicated. In the current study, we used quantitative methodology and estimate 26,916 turtles for the June 18, 1947 arribada, but as discussed below, the nesting densities varied (see Table 1) and some could extrapolate to values that equate or exceed the estimate by Hildebrand (1963). During the current evaluation, we have also identified potential sources of error that could be associated with this estimate (see discussion below).

In a separate evaluation of the 1947 Herrera film, Dickerson and Dickerson (2006) estimated an average of 6,000 turtles for the 4-h duration of the 18 June arribada. That study was pivotal in addressing the need for quantitative methodology to assess the size of the 1947 Herrera arribada. They adopted a logical approach of quantifying turtles in a wide pan of the beach and extrapolated that number to include a total of 2 km of beach over a 4- h arribada. They generated a composite image of the widest pan in the Herrera film, based on a VHS copy of a film that was dubbed from a Umatic dub of the original film made by KUHT Public Television (Houston, TX) for the Heartbreak Turtle documentary (1981) (VHS copy obtained by Dena Dickerson from Dave Owens, D. Dickerson, personal communication). The total number of turtles in that composite image was independently estimated by 39 individuals and the length of the beach surveyed was subjectively estimated by the volunteers to be 650 m, with an average number of 475 turtles counted on that stretch of beach. This was then extrapolated out to 2 km for the length of the beach over which the arribada occurred and was multiplied by four to account for the 4-h duration of the arribada. In keeping with Hildebrand’s methodology, Dickerson and Dickerson (2006) used a 1-h duration for the average time spent on the beach by a nesting turtle.

The estimate by Dickerson and Dickerson (2006) clearly differs from those in the current study. However, there are several factors that account for these differences. Of particular interest, the current study uses recent information and resources that were not available during the previous study. First, we were able to obtain a high resolution DVD copy of the film from the Herrera family which enhanced our ability to quantify turtles on the beach. Although the composite image used by Dickerson and Dickerson (2006) and Figure 1 in the current study are from the same portion of the film, we included a wider pan of the beach in our composite image. We only counted turtles on the beach flat and obtained an average of 578 turtles, whereas volunteers in the Dickerson and Dickerson (2006) study obtained an average of 475 turtles for both beach flat and any dune areas that were visible. Additionally, we used a novel approach to estimate the length of the beach in the composite image based on turtle carapace lengths throughout the image. The results indicated an approximate 321- m stretch of beach, in contrast to the 650 m of beach from the subjective volunteer estimates in the Dickerson and Dickerson (2006) study. Further, based on information from recent arribadas at Rancho Nuevo, a large proportion of the turtles on the beach during an arribada are located at the base of the dune, or on the dune. Due to the camera perspective in the composite image used by Dickerson and Dickerson (2006) as well as Figure 1 in the current study, a large portion of the dune is not visible towards the northern and southern extremes of the image. Therefore, in the current study we objectively evaluated the percentage of turtles in the dune area vs. turtles on the beach flat using the full beach perspective in Figure 2, resulting in an estimate of 35.8% of the turtles occurring in the dune. As indicated in the results, considering the chronology of events during the nesting process, this may represent a conservative estimate. We then used this value to estimate the total number of turtles on the beach in Figure 1 based on the number that we counted on the beach flat alone, resulting in a total value of 900 turtles over the 321 m of beach. Finally, based on historic and current nesting data we estimated that a turtle spends approximately 50 min on the beach during the nesting process in contrast to the 1 h that Dickerson and Dickerson (2006) used to stay consistent with the Hildebrand methodology. Collectively, these factors account for the difference in the estimate obtained in the current study vs. the estimate from the Dickerson and Dickerson (2006) study.

As indicated above, our analysis estimates a total of 26,916 turtles in the 1947 Herrera arribada. However, there are a variety of factors that could represent sources of error in such an estimate. An obvious factor that could affect the predicted total number of nests in the arribada is the spatial and temporal variation in nesting density. This is exemplified by the nesting densities that were quantified in Figure 1 and 2 and, depending on the portion of the beach would extrapolate out to a range of 15,384–45,760 total turtles for the entire arribada (see Table 2).

Although Hildebrand (1963) suggests that the arribada occurred over approximately 2 km, our largest and most informative pan in the Herrera film (shown in Figure 1) only represents 23% of the full length of beach occupied by the arribada (i.e., 321 m of beach). However, information from Herrera that was reported by Hildebrand in 1963, personal correspondence from Herrera to Hildebrand (letters dated 10 February and 20 May 1961), and Herrera's interviews in the Heartbreak Turtle documentary and the Great Ridley Rescue book (Phillips 1989), suggest that nesting densities observed on the area of beach in the Herrera film were consistent throughout the entire range of the arribada. It is not clear why Herrera chose the portion of the arribada shown in the film, but it is plausible the area of the arribada filmed related to the logistics of where he could land the plane (i.e., at the southern border of the arribada in an area of low-density nesting). For example, Hildebrand (1963) clearly indicated that based on discussions with Herrera and local residents, nesting density was relatively high for at least 4 h over more than a mile of beach, resulting in a beach that was inundated with turtles to the extent that turtles were crawling over one other and frequently dug up the nests that other individuals had deposited, leaving the beach completely saturated with nests. Similar comments were made by Herrera in the 1981 documentary, the Heartbreak Turtle. His comments indicated that he observed the arribada from the air and flew the length of the arribada before landing and only landed once the arribada was underway. When he landed, the arribada had already reached a high level of nesting density that extended for over a mile of beach. It is important to note that Herrera's estimate of more than a mile of high-density nesting was not simply a ground- based estimation, but was also based on his aerial surveys of the arribada.

Based on Hildebrand's discussion with Herrera and with local residents, several generalizations regarding characteristics of historic arribadas are suggested in his 1963 publication; (1) the typical duration of arribadas is approximately 4 h, and (2) covers approximately 2 km of beach or less. Additionally, Hildebrand indicated that a typical nesting season includes three large arribadas per year. It is possible that these generalizations influenced the Hildebrand (1963) estimate of 40,000 turtles in the 1947 arribada. Of particular interest is the length of the 1947 arribada, for which 4 h has been used in all of the estimates, yet it has clearly been stated that when Herrera landed, the arribada was already underway and it is assumed that he determined the time when the arribada started from the locals on the beach. When Herrera left the beach, the arribada had expanded to the south and he had to push his plane further south past the turtles to take off. This suggests that the arribada could have lasted for longer than 4 h, which would suggest that all of the previous estimates may represent conservative values.

Arribadas during recent years can also provide insight on predictions regarding the 1947 arribada in regard to nesting density, duration, and total number of turtles. As an example, an arribada during June 2011 (Figure 3) occurred over approximately 200 m of beach or less, lasting from approximately three pm until nine pm. Based on a photo from that arribada, we quantified approximately 313 turtles on 50 m of beach, similar to the density of nesting on portions of the beach shown in the Herrera film (see Figure 2) and the nesting density in the 2011 arribada remained high for over 4 h. Data from recent years indicate that some arribadas can include high-density nesting for longer than 4 h periods. It was estimated that there was a total of 7000 turtles over approximately 200 m of beach or less in the 2011 arribada. Extrapolating that level of high- density nesting out to the 2 km of beach estimated for the 1947 arribada would have resulted in a total number of nests consistent with the Hildebrand (1963) estimate as well as the estimate from the high- density nesting areas in the current study.

Estimating the Total Number of Nests for the 1947 Nesting Season

The population estimates in this study are based on comprehensive surveys being collected by the Binational Kemp's Ridley Recovery Program. However, the accuracy of the predictions is also dependent upon a number of assumptions which could represent potential sources of error. As indicated above, the predictions are based upon the assumption that the percentage of total nests per season represented in large arribadas in recent years is similar to that from 1947. It is currently unknown if or how this value might change relative to population size and the decline and recovery of this species. However, the reappearance of relatively large arribadas in recent years attests to the instinctive nature of arribada nesting behavior in the Kemp's ridley. Further, recent nesting seasons typically include two to three large arribadas, similar to the historic, seasonal occurrence of arribadas described by Hildebrand based on conversations with locals of Rancho Nuevo and information that had been passed on through multiple generations. Although anecdotal, this suggests that recent nesting behavior is consistent with historic nesting behavior prior to the collapse of the population. To be conservative we have used a range of values reflecting the variability in the size of the largest arribadas in recent years. Furthermore, our estimates are based upon the assumption that the arribada in the Herrera film was one of the largest arribadas of the 1947 season. If not, then our predictions could represent underestimates. Hildebrand indicated that Herrera witnessed two other arribadas, one earlier that season on 26 April, and one the following year on 30 April, but there was no indication or comparison of the relative size of the arribadas. Hildebrand's interview with people from Rancho Nuevo in the early

1960s indicated that arribadas could occur from April through June or even into July. In recent years it is not uncommon to have two or three relatively large arribadas, and some large arribadas have occurred during early June. However, evaluation of nesting in recent years suggests that the largest arribadas of the season are typically observed in April and May. Therefore, it is plausible that the arribada witnessed by Herrera on June 18, 1947 may not have been the largest arribada of the season.

The results from this study predict that approximately 48,607 females nested during the 1947 nesting season with a total of 121,517 predicted nests for the season. A previous study using an independent method (back- calculation of seasonal nesting numbers using linear regression) estimated 177,478 total nests for the season (Caillouet 2006). However, as Caillouet (2006) indicates, back-calculating static rates of decline for 1947–1966 based on the rates of decline from 1966 to 1977, cannot be tested. Regardless, the estimate from Caillouet (2006) is of the same order of magnitude as in the current study. The results of this study indicate that from 1947 through 1985 (the lowest point in the decline of Kemp's ridley nesting) the Kemp's ridley population underwent a 99.4% decline (range of 99.2–99.7%) from an estimated 121,517 nests per season in 1947 to 702 nests per season in 1985. Although the Kemp's ridley population has been recovering since the 1985 season, current levels of nesting (12,053 nests in 2014) (Burchfield 2014) are still relatively low at 9.9% (range of 5.7–14.6%) of the total estimated nests that occurred in 1947 based on the current analysis of Figures. 1 and 2 (see Figure 4). As a comparison, if we use the same methodology with the Hildebrand (1963) estimate of 40,000 turtles in the June 18, 1947 arribada, a total of 180,587 total nests would be predicted for the 1947 season. Using this estimate, the 12,053 nests in 2014 would represent 6.7% (range of 3.9–9.8%) of the total nesting in 1947. Thus, our current estimate as well as that by Hildebrand (1963) suggest that the size of the current population is a relatively small percentage of the historic population.

Collectively, the results of this study suggest that during and prior to the 1947 nesting season a relatively robust population of Kemp's ridleys existed, which could support arribadas of at least 26,916 females. The Kemp's ridley population has shown a strong recovery over the past several decades following its collapse, however, the current status of the population appears to be a small percentage (approximately 9.9%) of the historic 1947 population based on the Herrera arribada and current nesting trends. Further, in the last 5 yr, the Kemp's ridley has deviated from the previous exponential recovery rate and has declined. It is currently not clear whether this population will recover to the point of historic levels. As indicated in the most recent recovery plan, the Kemp's ridley faces a variety of threats that could hinder its recovery, such as impacts from fisheries, pollution, climate change, and predation (NMFS et al. 2011). It is plausible that these as well as other factors could be impacting the Kemp's ridley and its habitat (Gallaway et al. 2016 a, b), thus limiting the species' ability to recover to historic levels.

ACKNOWLEDGMENTS

This study was conducted in collaboration with the Binational Kemp's Ridley Recovery Program and the Kemp's Ridley Working Group. This Program is coordinated in Mexico by the General Directorate for Wildlife of the Secretariat of the Environment and Natural Resources (SEMARNAT), the National Commission of Natural Protected

Areas (CONANP), and the Tamaulipas State Wildlife Agency (SEDUMA). The Binational Recovery Program includes the U.S. agencies U.S. Fish and Wildlife Service, NOAA Fisheries, National Park Service, and Texas Parks and Wildlife. We would like to acknowledge the Herrera family for graciously providing a variety of support materials, including the original film of the 1947 arribada filmed by Andres Herrera. We thank Tom Shearer of U.S. Fish and Wildlife Service for providing access to the office files of Henry Hildebrand. Bryan Wallace provided comments and suggestions regarding this manuscript. We would like to acknowledge the volunteers who helped quantify the number of turtles in the composite photos from the Herrera film. We also acknowledge the support of NOAA Fisheries and the U.S. Fish and Wildlife Service via the Marine Turtle Conservation Fund for their continued support of ongoing research in the Kemp's Ridley Recovery Program.

LITERATURE CITED

Adams, D. E. 1966. More about the ridley operation: Padre Island egg transplanting. International Turtle and Tortoise Society Journal 1:18–45.

Burchfield, P. M. 2014. Report on the Mexico/United States of America population restoration project for the Kemp's ridley sea turtle, Lepidochelys kempii, on the coast of Tamaulipas. Mexico, Gladys Porter Zoo, Brownsville, Texas, USA.

Caillouet, C. W. Jr. 2006. Review of the Kemp's ridley recovery plan. Marine Turtle Newsletter 114:2–5.

Caillouet, C. W. Jr. 2014. Interruption of the Kemp's ridley population's pre-2 010 exponential growth in the Gulf of Mexico and its aftermath: one hypothesis. Marine Turtle Newsletter 143:1–7.

Carr, A. 1963. Panspecific reproductive convergence in *Lepidochelys kempi*. Ergebnisse der Biologie 26:298–303.

Carr, A. F. 1967. So excellent a fishe; a natural history of sea turtles. Natural History Press, Garden City, New York, USA.

Chavez, H., M. Contreras-G, and T. Hernandez-D. 1968. On the coast of Tamaulipas. International Turtle and Tortoise Society Journal 2:20–29.

Cornelius, S. E. 1986. The sea turtles of Santa Rosa National Park. Fundación de Parques Nacionales, San José, Costa Rica.

Dickerson, V. L. and D. D. Dickerson. 2006. Analysis of arribada in 1947 film at Rancho Nuevo, Mexico. Pages 290–291in Frick M., A. Panagopoulou, A. F. Rees, and K. Williams, compilers. Proceedings of the 26th Annual Symposium on Sea Turtle Biology and Conservation, Athens, Greece, April 3-8, 2006. International Sea Turtle Society.

Epperly, S. P. and W. G. Teas. 1999. Evaluation of TED opening dimensions relative to size of turtles stranding in the western north Atlantic. SEFSC contribution PRD-98/99/08. U.S. Department of Commerce, National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, Florida, USA.

Gallaway, B. J., et al. 2016 a. Development of a Kemp's ridley sea turtle stock assessment model. Gulf of Mexico Science, in press.

Gallaway, B. J., W. J. Gazey, D. Shaver, T. Wibbels and E. Bevan. 2016 b. Evaluation of the status of the Kemp's ridley sea turtle following the 2010 Deepwater Horizon oil spill. Gulf of Mexico Science, in press.

Hildebrand, H. H. 1963. Hallazgo del area de anidacion de la tortuga marina "lora", Lepidochelys kempi (Garman), en la costa occidental del Golfo de Mexico. Ciencia (Mexico) 22:105–112.

Magnuson, J. J., K. A. Bjorndal, W. D. DuPaul, G. L. Graham, D. W. Owens, C. H. Peterson, P. C. H. Pritchard, J. I. Richardson, G. E. Sual, and C. W. West. 1990. Decline of the sea turtles: causes and prevention. National Academy Press, Washington, D. C., USA.

Marquez, M. R. 1994. Synopsis of biological data on the Kemp's ridley sea turtle, Lepidochelys kempi (Garman, 1880). NOAA Technical Memorandum,

NMFS-SEFC-343. U. S. Department of Commerce, National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, Florida, USA.

Nance, J. M. 1992. Estimation of effort for the Gulf of Mexico shrimp fishery. NMFS-SEFSC-300:12. NOAA Technical Memorandum. U.S. Department of Commerce, National Marine Fisheries Service, Southeast Fisheries Science Center, Galveston, Texas, USA.

Phillips, P. 1989. The great ridley rescue. Mountain Press Publishing Company, Missoula, Montana, USA.

Pritchard, P. C. H. 1969. Studies of the systematics and reproductive cycles of the genus Lepidochelys. Dissertation. The University of Florida, Gainsville, Florida, USA.

Pritchard, P. C. H. and R. Marquez 1973. Kemp's ridley turtle or Atlantic ridley. IUCN Monograph No. 2. International Union for the Conservation of Nature and Natural Resources, Morges, Switzerland.

TEWG. 2000. Assessment update for the Kemp's ridley and loggerhead sea turtle populations in the western north Atlantic. NMFS-SEFSC-444:115. NOAA Technical Memorandum, U.S. Department of Commerce, National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, Florida, USA.

Wibbels, T. and E. Bevan. 2016. A historical perspective of the biology and conservation of the Kemp's ridley sea turtle. Gulf of Mexico Science Supporting Video. Andres Herrera Film of a Kemp's Ridley Arribada in 1947. Historic film of a mass nesting event ("arribada") near Rancho Nuevo, Tamaulipas, Mexico, recorded on 18 June 1947 by Andres Herrera. This film was obtained and included here with permission from the Herrera family. Gulf of Mexico Science 2:129-137.

USING UNMANNED AERIAL VEHICLE (UAV) TECHNOLOGY FOR LOCATING, IDENTIFYING, AND MONITORING COURTSHIP AND MATING BEHAVIOR IN THE GREEN TURTLE (*CHELONIA MYDAS*)

by

E. BEVAN, T. WIBBELS, E. NAVARRO, M. ROSAS, B.M.Z. NAJERA, L. SARTI,
F.I. MARTINEZ, J.M. CUEVAS, L.J. PEÑA, and P.M. BURCHFIELD

Herpetological Review 47(1), 27-32

Format adapted and errata corrected for dissertation

CHAPTER 2

USING UNMANNED AERIAL VEHICLE (UAV) TECHNOLOGY FOR LOCATING, IDENTIFYING, AND MONITORING COURTSHIP AND MATING BEHAVIOR IN THE GREEN TURTLE (*CHELONIA MYDAS*)

The rapidly advancing field of unmanned aerial vehicle (UAV) technology is currently being used to address a wide variety of subjects regarding wildlife biology and conservation (Jones et al. 2006; Koh and Wich 2012; Hodgson et al. 2013). This technology is a highly applicable platform for identifying and monitoring sea turtles in their in-water habitat (Bevan et al. 2015) and is particularly useful for studying courtship and mating activities in sea turtles. These behaviors are often observed in nearshore areas adjacent to nesting beaches, near or at the water's surface, and can occur over prolonged periods of time (e.g., mating behavior in Green Turtles can last over multiple hours; Wood and Wood 1980). Additionally, surveys using UAV technology can be used for identifying critical habitat and areas used for courtship and mating activities in endangered sea turtles, while reducing the overall time, effort, and cost that has traditionally been required to conduct manned boat- and airplane-based surveys. A variety of both fixed-wing and rotorcraft UAV designs are currently available and each offers distinct capabilities that should be considered when deciding on which aircraft to use in a specific project. As an example, fixed-wing aircraft typically have longer flight durations, but do not have the ability to stop and hover above an area of interest. In contrast to traditional airplane and boat-based surveys, as well as fixed-wing UAVs, a rotorcraft UAV provides a stable, stationary video platform that can hover directly above the behavior of interest. Therefore, upon locating sea turtles, a rotorcraft UAV can be used to hover, follow, and record video footage of their behaviors. The current study provides an evaluation of the applicability of UAVs for studying sea turtle courting and mating behavior in nearshore waters.

In the current study, we evaluated the use of the DJI Inspire 1™ (DJI, Shenzhen, China) rotorcraft quadcopter (Figure 1) for studying sea turtle courtship and mating behavior off a major sea turtle rookery in the Gulf of Mexico near Rancho Nuevo, Tamaulipas, Mexico (Figure 2). The DJI Inspire 1™ is a relatively small, relatively low-cost, and commercially available UAV capable of traveling at least 2 km away from the handheld controller. The aircraft is controlled through the GO app from DJI™ that runs on a tablet; we used the NVIDIA Shield ™ (NVIDIA Corporation, Santa Clara, California) that displays a live high-definition video feed from the aircraft as well as real-time readings for altitude, vertical and horizontal speed, and distance from the controller. Each UAV battery allows for approximately 20 minutes of total flight time (using the DJI TB48 battery which provides the longest flight time). This UAV model includes a camera capable of recording up to 4K quality video. In the current study, all surveys were recorded in 1080p video quality at 30 frames per second. The camera is attached to a three-axis gimbal system that stabilizes the video in flight and allows the operator to remotely control multiple aspects of the camera angle. The aircraft has a GPS stabilized flight control system and is stable in relatively windy conditions (e.g., 5–7 m/sec).

Figure 1. In the current study, we used the DJI Inspire 1™ rotorcraft UAV platform for monitoring sea turtles in nearshore waters at Rancho Nuevo, Mexico. This UAV is equipped with a camera capable of up to 4K quality video. It provides a live, high-definition video feed up to 2 km from the operator. The controller interfaces with a tablet (NVIDIA Shield™ shown in the inset) running the DJI GO App™ to operate the aircraft. Note: From "Using unmanned aerial vehicle (UAV) technology for locating, identifying, and monitoring courtship and mating behavior in the green turtle (C*helonia mydas*)" by E. Bevan, T. Wibbels, E. Navarro, M. Rosas, B.M.Z. Najera, L. Sarti, F.I. Martinez, J.M. Cuevas, L.J. Peña, and P.M. Burchfield, 2016, *Herpetological Review,* 47(1), p. 27-32. Copyright 2016 by the Society for the Study of Amphibians and Reptiles. Reprinted with permission.

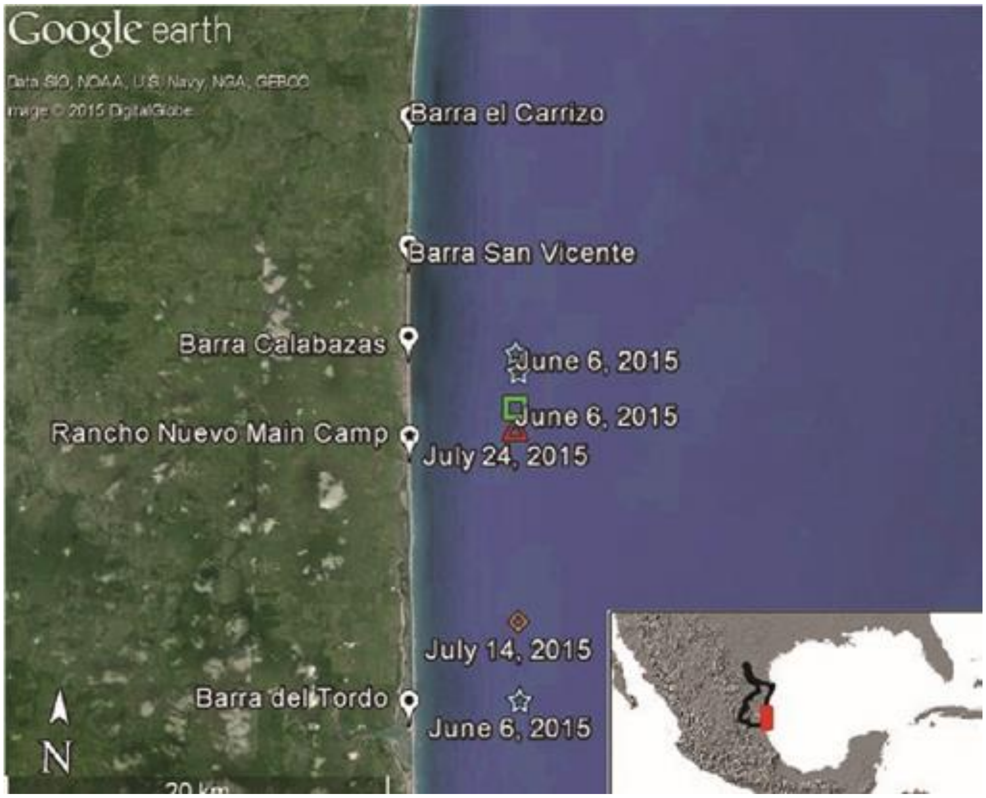

Figure 2. UAV surveys were conducted in the western Gulf of Mexico, in the State of Tamaulipas, Mexico (study area indicated by the red rectangle on inset map). The landmarks shown in the figure represent mouths of seasonal rivers (barras) and are represented as white markers. Surveys were conducted at approximately 5-km intervals between Barra del Tordo and Barra el Carrizo. Reproductive behaviors between individual Green Turtles were observed on multiple occasions as shown in the figure. Shapes indicate the location and date when reproductive behaviors were observed. Blue stars represent instances when a mating pair was observed. Blue stars represent instances when a mating pair was observed, the orange diamond represents courtship behavior, the green square represents a mated pair that was accompanied by an escort male, and the red triangle indicates an observed interaction between two male turtles. Note: From “Using unmanned aerial vehicle (UAV) technology for locating, identifying, and monitoring courtship and mating behavior in the green turtle (C*helonia mydas*)” by E. Bevan, T. Wibbels, E. Navarro, M. Rosas, B.M.Z. Najera, L. Sarti, F.I. Martinez, J.M. Cuevas, L.J. Peña, and P.M. Burchfield, 2016, *Herpetological Review*, 47(1), p. 27-32. Copyright 2016 by the Society for the Study of Amphibians and Reptiles. Reprinted with permission.

The nearshore waters adjacent to the Rancho Nuevo nesting beach were surveyed over an approximate four-month period at 2–3-week intervals. A typical set of surveys was conducted over a two-day period and over the entire nesting season a total of nine sets of surveys were conducted. A set of surveys consisted of seven surveys over an approximate 30-km stretch of nearshore water at approximately 5-km intervals, ranging from Barra del Tordo to Barra el Carrizo (Figure 2). At each survey location, transects of approximately 2 km in length, parallel to the shore, were run at 0.5 and 1.0 km offshore (Figure 3). Thus, each survey included 4 km of transects parallel to shore, but also included an additional 4 km perpendicular to shore as the aircraft was flying to and from transect lines (see Figure 3). An entire survey at each location typically required approximately 30–40 minutes of flight time. Therefore, each survey was conducted as two separate flights, each with a fully-charged battery, one flight surveying to the north and one to the south of the operator. The order in which the north and south segments were flown was randomized or selected based on local weather conditions (i.e., the aircraft was not flown in the direction of impending rain). All surveys were conducted between 0800 and 1800 h and we were able to identify turtles in videos throughout this range of sampling times. Collectively, the surveys over the entire study period generated approximately 40–50 h of video footage, all of which was directly viewed during analysis. The ability to identify turtles in the video feed and recording was affected by water clarity, sea conditions, wind, sun glare, and combinations of these factors. We attempted to address sun glare by using a polarizing filter and adjusting the angle of the camera between straight down (i.e. 90°) and 45° forward. Typically, we experienced less glare when the sun was near or at its zenith.

Figure 3. Example of a typical survey using the UAV during the current study. Each location surveyed included 2 transects that were 2 km in length and parallel to shore. These transects were conducted at 0.5 and 1.0 km from shore. The operator's location is indicated by the "H". Two flights were required to complete the transects at each location, one to the north of the operator and one to the south of the operator as indicated by the arrows in the figure. These surveys were conducted at approximately 5-km intervals over a 30-km stretch of beach at Rancho Nuevo, Mexico. Note: From "Using unmanned aerial vehicle (UAV) technology for locating, identifying, and monitoring courtship and mating behavior in the green turtle (C*helonia mydas*)" by E. Bevan, T. Wibbels, E. Navarro, M. Rosas, B.M.Z. Najera, L. Sarti, F.I. Martinez, J.M. Cuevas, L.J. Peña, and P.M. Burchfield, 2016, *Herpetological Review*, 47(1), p. 27-32. Copyright 2016 by the Society for the Study of Amphibians and Reptiles. Reprinted with permission.

As part of an ongoing study, we were surveying the pre-nesting and internesting locations of Kemp's Ridleys (*Lepidochelys kempii*) during their nesting season at their primary nesting beach at Rancho Nuevo, Mexico. An unanticipated addition to our regular surveys for Kemp’s Ridleys was the observation of Green Turtles (*Chelonia mydas*), including turtles engaged in various reproductive behaviors. In addition to being the primary nesting beach for the Kemp’s Ridley, Rancho Nuevo also provides nesting habitat for Green Turtles. The Green Turtle nesting season typically extends from June through September with several thousand nests laid annually at Rancho Nuevo. This provided the unique opportunity to evaluate UAV technology for recording and studying this critical life-history stage in Green Turtles (i.e., courtship and mating). During these encounters, the utility of the rotorcraft UAV used in the current study (in contrast to a fixed-wing UAV) was demonstrated by its ability to hover and provide a stable video platform during our observations of a wide variety of reproductive behaviors.

The logistical difficulties in observing sea turtle courtship and mating behaviors have limited the information generated on this subject. Initial observations of courtship and mating behavior were reported for wild Green Turtles by Booth and Peters (1972) and Bustard (1972) and for captive Green Turtles at the Cayman Turtle Farm (Comuzzie and Owens 1990). The last study led to the development of an ethogram that identified 11 specific behaviors associated with courtship and mating (Table 1) in captive Green Turtles (Comuzzie and Owens 1990). The high-resolution video from the UAV surveys in the current study allowed us to identify many of these behaviors in the wild (Table 1) as well as previously undescribed behaviors associated with courtship and mating. Further, the mobility and relatively wide observation window provided by UAVs significantly increases the probability of chance encounters with sea turtles in contrast to traditional boat-based observations. Although it was not possible to identify the sex of all individual turtles observed during surveys, males were frequently identified based on tail length (Figure 4) and were observed on at least seven occasions. The ability to identify the sex of turtles using UAVs could provide insight on when male turtles potentially move into mating areas. Our observation of courting and mating behaviors and the presence of male sea turtles in the current study also indicate that this region in the western Gulf of Mexico is not only an important nesting ground, but a critical mating habitat as well. Collectively, these attributes demonstrate the potential of UAV technology to advance and enhance field-based studies of courtship and mating behavior of sea turtles, as well as the identification of critical habitat.

Table 1. Courtship and mating behaviors that were observed in the current study that had been previously reported for captive and wild Green Turtles.

Behavior	Observed	Possibly observed
Nuzzling[1]	X	
Biting neck and rear flippers[2,3]		X
Male chasing fleeing female[1,2,3]	X	
Female circling and biting male[2]		
Male circling and biting female[2,3]	X	
Female refusal position[2]		
Gular rub[3]	X	
Cloacal check[1,3]	X	
Attempted mount[1,2,3]	X	
Successful mount[1,2,3]		
Copulation interference/escorting[1,2,3]	X	

[1] Bustard 1972

[2] Booth and Peters 1972

[3] Comuzzie and Owens 1990

Note: From "Using unmanned aerial vehicle (UAV) technology for locating, identifying, and monitoring courtship and mating behavior in the green turtle (C*helonia mydas*)" by E. Bevan, T. Wibbels, E. Navarro, M. Rosas, B.M.Z. Najera, L. Sarti, F.I. Martinez, J.M. Cuevas, L.J. Peña, and P.M. Burchfield, 2016, *Herpetological Review,* 47(1), p. 27-32. Copyright 2016 by the Society for the Study of Amphibians and Reptiles. Reprinted with permission.

Figure 4. Example of a male green sea turtle observed during the nesting season in nearshore waters off the nesting beach at Rancho Nuevo, Mexico. Arrow shows the distinct tail extending beyond the carapace. Note: From "Using unmanned aerial vehicle (UAV) technology for locating, identifying, and monitoring courtship and mating behavior in the green turtle (C*helonia mydas*)" by E. Bevan, T. Wibbels, E. Navarro, M. Rosas, B.M.Z. Najera, L. Sarti, F.I. Martinez, J.M. Cuevas, L.J. Peña, and P.M. Burchfield, 2016, *Herpetological Review*, 47(1), p. 27-32. Copyright 2016 by the Society for the Study of Amphibians and Reptiles. Reprinted with permission.

Among the various behaviors that were documented in the current study, courtship behaviors between a male and female Green Turtle were observed, as shown in Figure 5 (A–F). These behaviors included A) circling of the female by the male, B) cloacal checks, C) gular (throat region) rubbing, D) possible biting, D) fleeing of the female from the male, and F) attempted mounting. During circling behavior, a male approached the female from behind and the female then turned to face the male, thereby forcing the male to circle in an apparent effort to mount the female from behind (Figure 5A). Circling behavior has been previously described for Green Turtles in the wild (Booth and Peters 1972) and in captivity (Comuzzie and Owens 1990). In all of the courtship interactions observed in the current study, the male approached the female from behind and placed his head in the vicinity of the female’s tail and cloaca (Figure 5B). Cloacal checks and subsequent “gular rubbing” by both male and female captive Green Turtles have been described by Comuzzie and Owens (1990). That study also suggested that cloacal checks could represent a method of chemosensory investigation of the approximate readiness of a female for mating (Comuzzie and Owens 1990) and the release of a pheromone from the cloaca of the freshwater turtle, *Trachemys scripta*, has previously been hypothesized (Jackson and Davis 1972). Male turtles were also observed biting the neck and both front and rear flipper areas of females and males (Figure 5D). Bustard (1972) reported males biting the rear flippers of females in wild Green Turtles, while Comuzzie and Owens (1990) reported biting of the front and rear flippers by both male and female captive Green Turtles. Males were also observed positioning their gular regions on top of the females’ heads (Figure 5C). Periodically during the courting process, the female would quickly swim a relatively long distance away from the male, then slow her pace and partially turn towards the male, causing the male to pursue her (Figure 5E). Fleeing behavior by females, followed by pursuit behavior by males, has been reported for Green Turtles in the wild (Booth and Peters 1972; Bustard 1972) and in captivity (Comuzzie and Owens 1990). On several occasions, the male approached the female from behind and attempted to position himself for mounting but was unsuccessful and slid off the side of her carapace (Figure 5F). Unsuccessful mounting has previously been observed for both wild (Booth and Peters 1972; Bustard 1972) and captive Green Turtles (Comuzzie and Owens 1990).

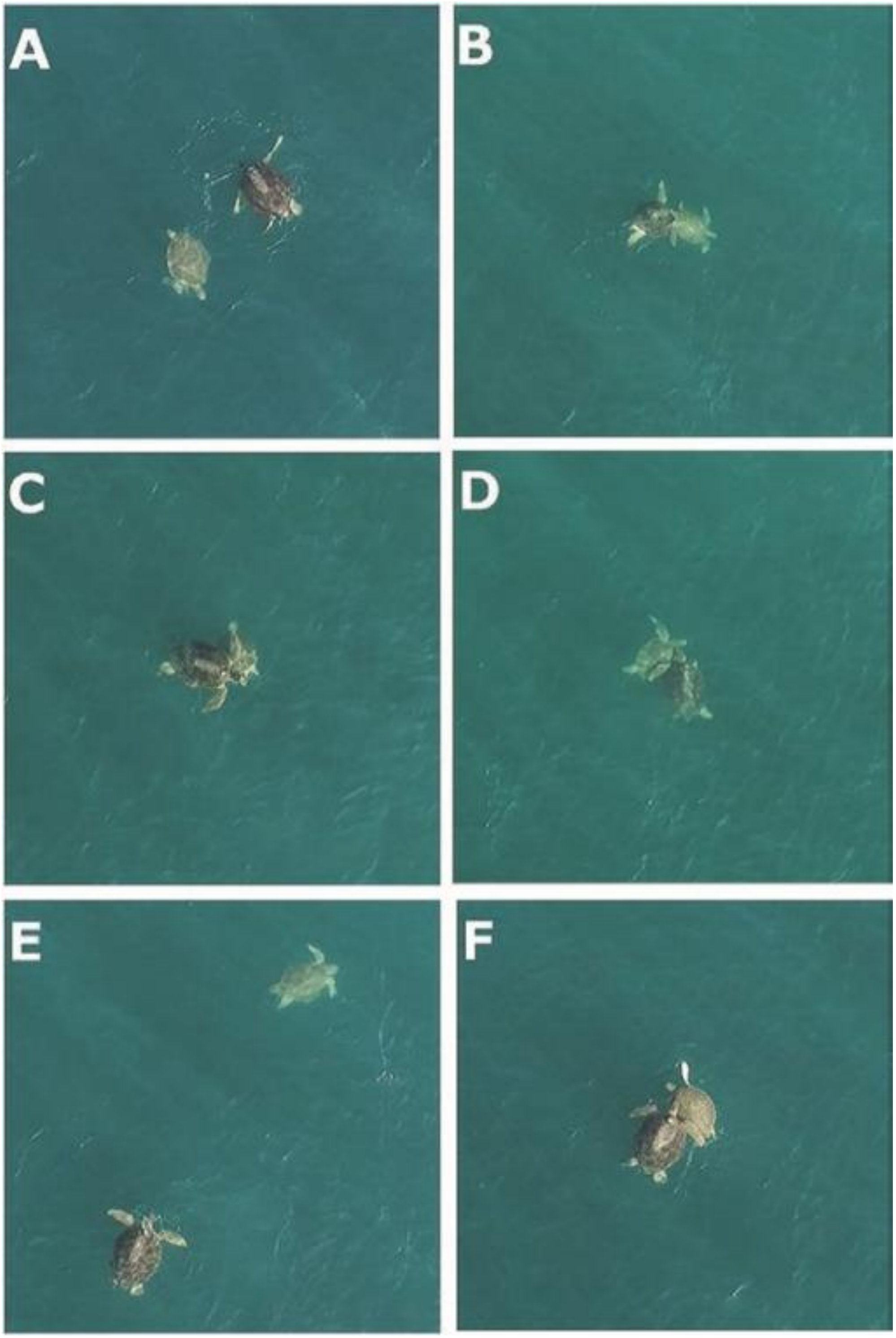

Figure 5. Courtship behavior between a male and female Green turtle was recorded for approximately 10 minutes by an UAV off Rancho Nuevo, Mexico from an altitude of approximately 20 m. The courtship behavior involved A) circling of the female by the male, B) cloacal checks, C) gular rubbing, D) possible biting, D) fleeing of the female from the male, and F) attempted mounting. Note: From "Using unmanned aerial vehicle

(UAV) technology for locating, identifying, and monitoring courtship and mating behavior in the green turtle (C*helonia mydas*)" by E. Bevan, T. Wibbels, E. Navarro, M. Rosas, B.M.Z. Najera, L. Sarti, F.I. Martinez, J.M. Cuevas, L.J. Peña, and P.M. Burchfield, 2016, *Herpetological Review*, 47(1), p. 27-32. Copyright 2016 by the Society for the Study of Amphibians and Reptiles. Reprinted with permission.

In addition to courtship behavior, mounted pairs of copulating Green Turtles were observed on seven occasions. A mounted pair of Green Turtles that was recorded for an approximate 10-minute period (due to limited battery life), initially at an altitude of 30 m (Figure 6A) and later at an altitude as low as 6.2 m (Figure 6B). This observation was typical of many of our encounters: once a mating pair was spotted from the standard 30-m survey altitude, the remaining flight time based on battery life was used to hover and observe the behavior. We often reduced the altitude of the aircraft to approximately 20 m to enhance observations and on the occasion noted above, the aircraft was lowered to an altitude of 6.2 m above the mating pair. We did not detect changes in turtle behavior that appeared to result from the presence of the UAV during any of our observations. Although seven mounted pairs were encountered, the initial mounting of the male onto the female was not observed. In the case of mounted pairs, the males were observed to use front and rear flippers as well as the tail to stay securely attached to the female throughout the period observed. Due to limited flight time per battery (20 min or less), we were unable to determine the full duration of mating, but in all of our encounters of mating pairs, mating continued for the entire length of the observation (i.e., approximately 5–10 min). Observations in captivity and in the wild indicate that mating can occur over prolonged periods of time, up to 119 h (Wood and Wood 1980).

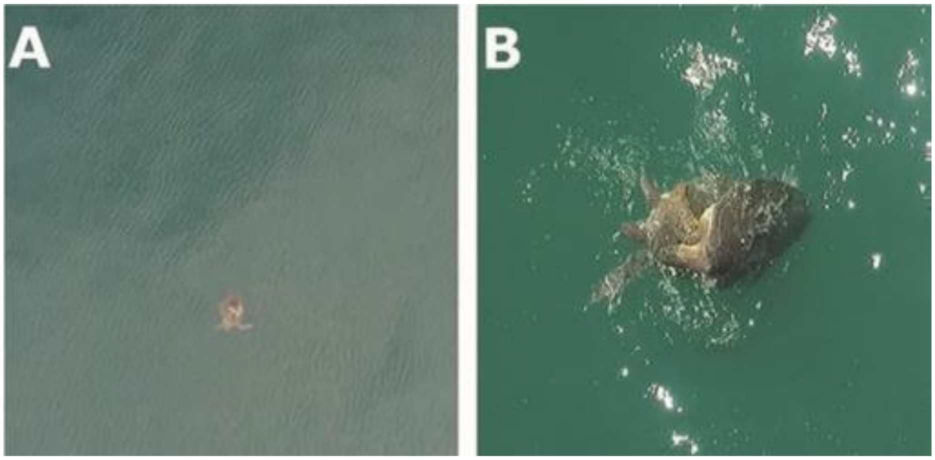

Figure 6. Examples of screen shots from an approximate 10-minute video of mounted green sea turtles (*Chelonia mydas*) off the nesting beach at Rancho Nuevo, Mexico, observed at altitudes of A) 30 m and B) 6.2 m. Note: From “Using unmanned aerial vehicle (UAV) technology for locating, identifying, and monitoring courtship and mating behavior in the green turtle (C*helonia mydas*)” by E. Bevan, T. Wibbels, E. Navarro, M. Rosas, B.M.Z. Najera, L. Sarti, F.I. Martinez, J.M. Cuevas, L.J. Peña, and P.M. Burchfield, 2016, *Herpetological Review,* 47(1), p. 27-32. Copyright 2016 by the Society for the Study of Amphibians and Reptiles. Reprinted with permission.

We observed a copulating pair of Green Turtles with an “escort” male (Figure 7A). The occurrence of escort males with a mated pair has previously been reported for Green Turtles in several studies (Booth and Peters 1972; Hendrickson 1958; Hirth 1971). In the current study, the escort male appeared to exhibit interference behavior that included attempting to disrupt the forward swimming of the female and positioning his head along the sides of the mated pair to potentially dislodge the copulating male. This group of turtles was recorded for approximately 10 min from an initial altitude of 30 m and then at 20 m as shown in the panel of photos in Figure 7. During the time period observed, the escort male was unsuccessful at separating the mated pair. In Figure 7 (B–D), the escort male can be seen B) circling, C) attempting to interfere with the copulating pair, and D) potentially engaging in cloacal checks and/or biting. In addition to the behaviors described in the current study, Comuzzie and Owens (1990) also described an additional interference behavior during which the escort male bit the tail and rear flippers of the copulating male.

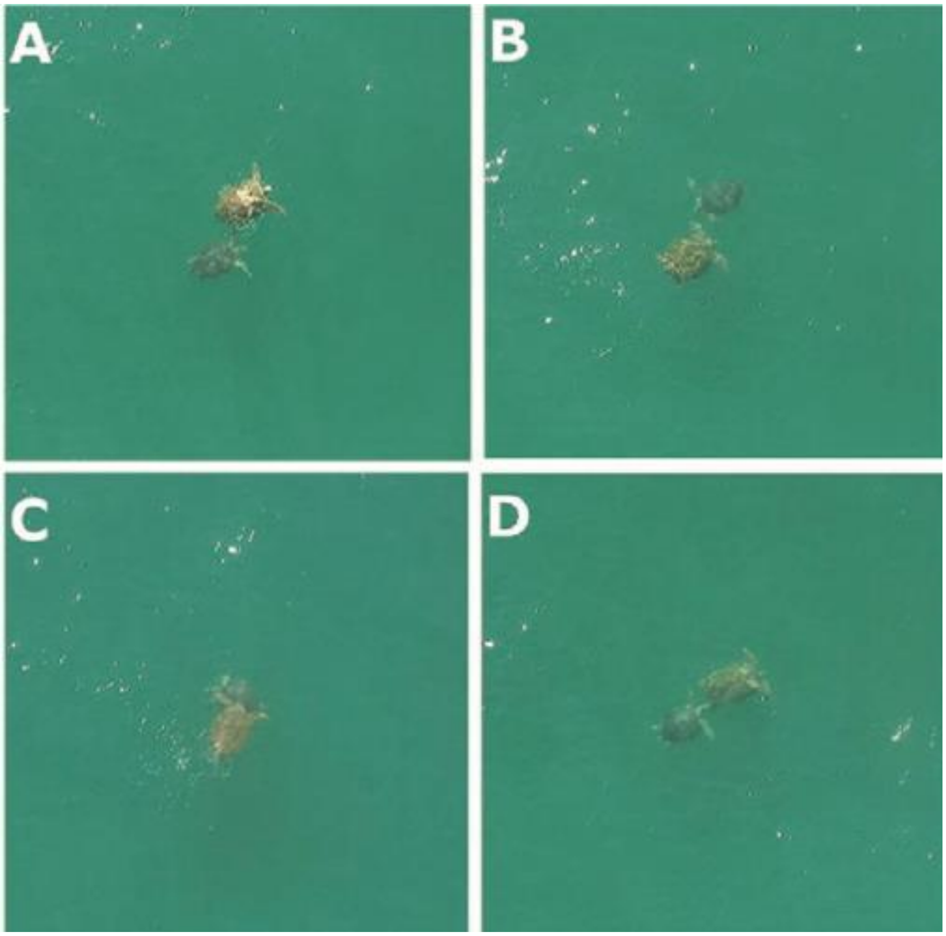

Figure 7. A copulating pair of Green turtles accompanied by an escort male was recorded by UAV off Rancho Nuevo, Mexico from an altitude of 20 m for approximately 10 min. In this panel, the escort male can be seen A) accompanying the mated pair, B) circling the pair, C) attempting to interfere with the pair, and D) potentially engaging in cloacal checks and/or biting. Note: From "Using unmanned aerial vehicle (UAV) technology for locating, identifying, and monitoring courtship and mating behavior in the green turtle (C*helonia mydas*)" by E. Bevan, T. Wibbels, E. Navarro, M. Rosas, B.M.Z. Najera, L. Sarti, F.I. Martinez, J.M. Cuevas, L.J. Peña, and P.M. Burchfield, 2016, *Herpetological Review*, 47(1), p. 27-32. Copyright 2016 by the Society for the Study of Amphibians and Reptiles. Reprinted with permission.

In addition to courtship and mating interactions between male and female turtles, an interaction between two males was observed on 24 July 2015, with no female turtle visible in the camera's field of view. When initially encountered during the survey, the two males were engaged in circling behavior and their interaction was observed for approximately 8 min prior to the males departing from each other (Figure 8). During this interaction, the males engaged in what appeared to be A) circling, B) cloacal checks, C) possible biting, and D) attempted mounting, before E) the two turtles departed from one another and left the vicinity. Based on these observations, this could represent mate-recognition behavior. Alternatively, it is possible that this interaction could represent a display of dominance between two males, as has been commonly documented in many other reptilian taxa (Brattstrom 1974). Although the specific behaviors of circling, biting, cloacal checks, and attempted mounting have been described for Green Turtles, the interaction of two males followed by departure represents a new observation.

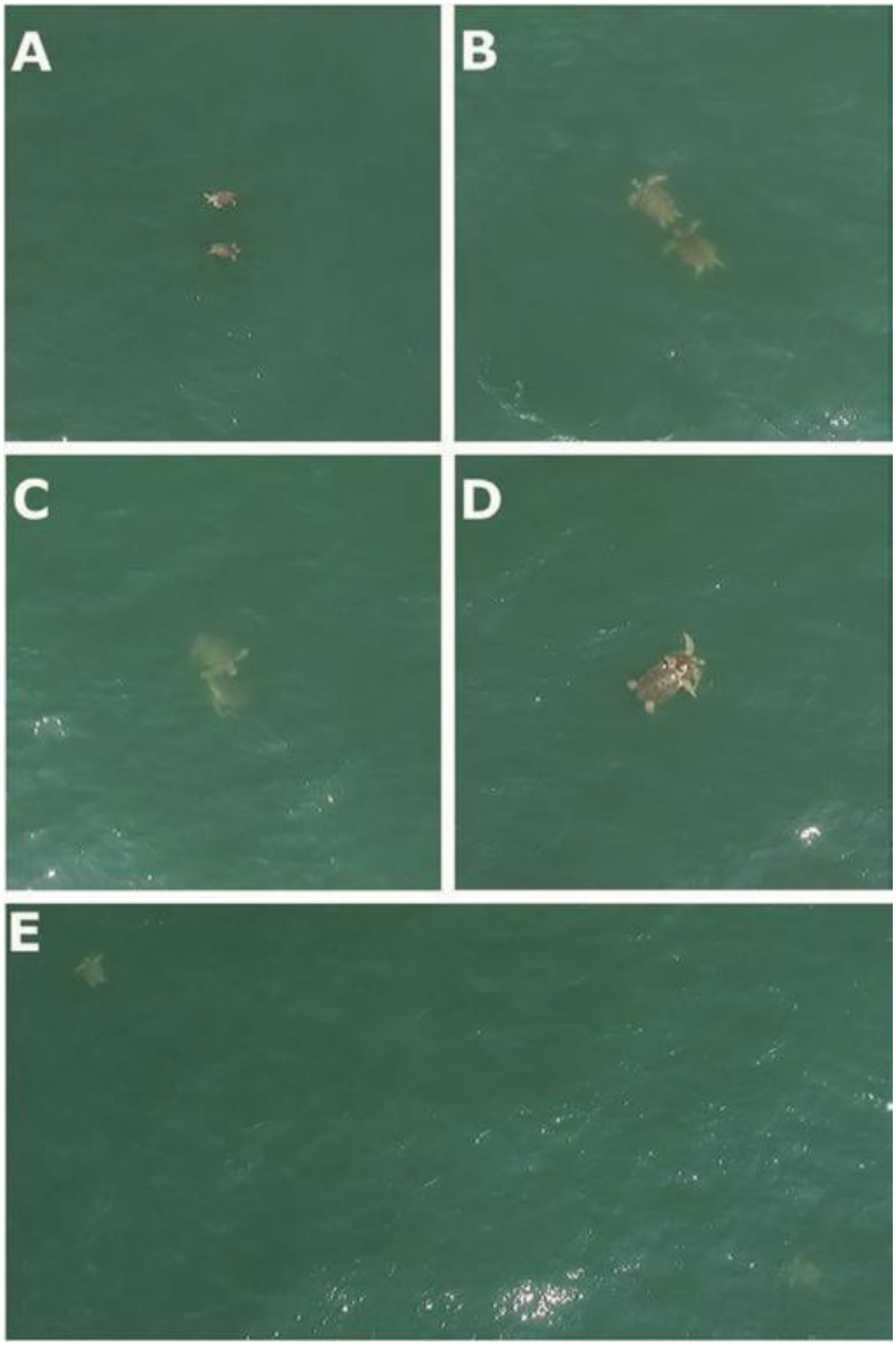

Figure 8. Interaction observed between two male Green Turtles observed on 24 July 2015. This interaction involved A) circling, B) cloacal checks, C) possible biting, D) attempted mounting, and E) final departure from one another. Note: From “Using unmanned aerial vehicle (UAV) technology for locating, identifying, and monitoring courtship and mating behavior in the green turtle (C*helonia mydas*)” by E. Bevan, T.

Wibbels, E. Navarro, M. Rosas, B.M.Z. Najera, L. Sarti, F.I. Martinez, J.M. Cuevas, L.J. Peña, and P.M. Burchfield, 2016, *Herpetological Review,* 47(1), p. 27-32. Copyright 2016 by the Society for the Study of Amphibians and Reptiles. Reprinted with permission.

The results of the current study document a variety of courtship and mating behaviors in Green Turtles in the wild and indicate that the nearshore waters off the nesting beach near Rancho Nuevo in the western Gulf of Mexico potentially represents critical habitat for mating in Green Turtles. In addition, the observations from the current study reveal the utility and applicability of UAV technology for documenting and studying courtship and mating behaviors in sea turtles. The advantages of this technology include a stable, high-resolution video platform located at an optimal angle of observation, as well as the ability to maintain this viewpoint as turtles move in their environment. However, the effectiveness of using UAVs for in-water sea turtle studies will depend upon multiple factors, including water clarity and the depth of the turtles in the water. Thus, the applicability of this technology may vary by location, species of interest, and specific sea turtle population. Currently, the primary weakness inherent to this type of UAV platform is limited flying time due to battery life. This is of particular importance to studies of courtship and mating behavior in sea turtles since chance encounters of mating in the wild may require a significant amount of time searching for turtles. Additionally, these behaviors can occur over many hours (Comuzzie and Owens 1990), which limits the use of UAVs for determining total mating duration. However, although each flight in the current study was limited to approximately 20 min, the GO app from DJI™ made it possible to return to specific locations where turtles were initially recorded after returning to the operator for battery replacement. The results from the current study indicate that the rapidly evolving UAV technology can significantly advance our ability to study sea turtle behavior in the natural environment. We detected very few weaknesses using the rotorcraft UAV platform for this application. The primary limitations were the flight time per battery (approximately 20 min or less) and the maximum distance from the controller. However, even with these limitations, UAV technology is useful for not only enhancing our understanding of sea turtle behaviors in the natural environment, but also in identifying the location of critical habitat for important life-history events, such as courtship and mating.

ACKNOWLEDGMENTS

This research was conducted as part of the Binational Kemp’s Ridley Recovery Program which is coordinated in Mexico by the General Directorate for Wildlife of the Secretariat of the Environment and Natural Resources (SEMARNAT), the National Commission of Natural Protected Areas (CONANP), and the Tamaulipas State Wildlife Agency (SEDUMA). The Binational Recovery Program includes the U.S. agencies U.S. Fish and Wildlife Service, NOAA Fisheries, National Park Service, and Texas Parks and Wildlife. Funding was provided, in part, by the UAB Department of Biology and the NOAA Fisheries and the U.S. Fish and Wildlife Service through the Marine Turtle Conservation Fund. We thank Diana Crowell Comuzzie for her help and insight.

LITERATURE CITED

Bevan, E., T. Wibbels, B. M. Z. Najera, M. A. C. Martine, L. A. M. Sarti, F. I. Martinez, J. M. Cuevas, T. Anderson, A. Bonka, M. H. Hernandez, L. J. Peña, and P. M. Burchfield. 2015. Unmanned aerial vehicles (UAVs) for monitoring sea turtles in near-shore waters. Mar. Turtle Newsl. 145:19–22.

Booth, J., and J. A. Peters. 1972. Behavioural studies on the green turtle (Chelonia mydas) in the sea. Anim. Behav. 20:808–812.

Brattstrom, B. H. 1974. The evolution of reptilian social behavior. Am. Zool. 14:35–49.

Bustard, H. R. 1972. Sea Turtles: Natural History and Conservation. Taplinger, New York. 220 pp.

Comuzzie, D. K. C., and D. W. Owens. 1990. A quantitative analysis of courtship behavior in captive green sea turtles (Chelonia mydas). Herpetologica 46:195–202.

Hendrickson, J. R. 1958. The green sea turtle, Chelonia mydas, in Malaya and Sarawak. Proc. Zool. Soc. London 130:455–535.

Hirth, H. F. 1971. Synopsis of biological data on the green turtle, Chelonia mydas (Linnaeus) 1758. Food and Agricultural Organization of the United Nations Fisheries Synopsis 85.

Hodgson, A., N. Kelly, and D. Peel. 2013. Unmanned aerial vehicles (UAVs) for surveying marine fauna: a dugong case study. PLOS ONE 8:e79556.

Jackson, C. G., Jr., and J. D. Davis. 1972. A quantitative study of the courtship display of the red-eared turtle, Chrysemys scripta elegans. Herpetologica 28:58–64.

Jones, G. P. IV, L. G. Pearlstine, and H. F. Percival. 2006. An assessment of small unmanned aerial vehicles for wildlife research. Wildl. Soc. Bull. 34:750–758.

Koh, L. P., and S. A. Wich. 2012. Dawn of drone ecology: low-cost autonomous aerial vehicles for conservation. Trop. Conserv. Sci. 5:121–132.

Wood, J. R., and F. E. Wood. 1980. Reproductive biology of captive green sea turtles Chelonia mydas. Am. Zool. 20:499–505.

MEASURING BEHAVIORAL RESPONSES OF SEA TURTLES, SALTWATER CROCODILES, AND CRESTED TERNS TO DRONE DISTURBANCE TO DEFINE ETHICAL OPERATING THRESHOLDS

by

E. BEVAN, S. WHITING, T. TUCKER, M. GUINEA, A. RAITH, AND R. DOUGLAS

PLoS ONE 13(3): e0194460. https://doi.org/10.1371/journal.pone.0194460

Format adapted and errata corrected for dissertation

CHAPTER 3

MEASURING BEHAVIORAL RESPONSES OF SEA TURTLES, SALTWATER CROCODILES, AND CRESTED TERNS TO DRONE DISTURBANCE TO DEFINE ETHICAL OPERATING THRESHOLDS

ABSTRACT

Drones are being increasingly used in innovative ways to enhance environmental research and conservation. Despite their widespread use for wildlife studies, there are few scientifically justified guidelines that provide minimum distances at which wildlife can be approached to minimize visual and auditory disturbance. These distances are essential to ensure that behavioral and survey data have no observer bias and form the basis of requirements for animal ethics and scientific permit approvals. In the present study, we documented the behaviors of three species of sea turtle (green turtles, *Chelonia mydas,* flatback turtles, *Natator depressus*, hawksbill turtles, *Eretmochelys imbricata*), saltwater crocodiles (*Crocodylus porosus)*, and crested terns (*Thalasseus bergii*) in response to a small commercially available (1.4 kg) multirotor drone flown in Northern Territory and Western Australia. Sea turtles in nearshore waters off nesting beaches or in foraging habitats exhibited no evasive behaviors (e.g. rapid diving) in response to the drone at or above 20-30 m altitude, and at or above 10 m altitude for juvenile green and hawksbill turtles foraging on shallow, algae-covered reefs. Adult female flatback sea turtles were not deterred by drones flying forward or stationary at 10 m altitude when crawling up the beach to nest or digging a body pit or egg chamber. In contrast, flyovers elicited a range of behaviors from crocodiles, including minor, lateral head movements, fleeing, or complete submergence when a drone was present below 50 m altitude. Similarly, a colony of crested terns resting on a sand-bank displayed disturbance behaviors (e.g. flight response) when a drone was flown below 60 m altitude. The current study demonstrates a variety of behavioral disturbance thresholds for diverse species and should be considered when establishing operating conditions for drones in behavioral and conservation studies.

INTRODUCTION

Unmanned aerial vehicles (i.e. UAVs or drones) have become widely-used as a cost-effective tool in wildlife conservation, management, and research. Drones are an efficient method for evaluating animal behavior, abundance and distribution [1-3]; enhancing animal photo ID and photogrammetry [1, 4-6]; and increasing the accuracy of data collection relative to traditional methods (e.g. surveys conducted on foot, by boat, or by terrestrial vehicle) [6-8]. Additionally, a growing network of drone operators, hobbyists, and commercial users is broadening access to an array of open source image processing and operating platforms. A key benefit of using drones in wildlife studies is to minimize the potential influence of observer presence. Many applications (e.g. identifying the species, sex, and conducting population censuses, measuring abiotic and biotic factors, and observing the behavior of one or a small group of distinct subjects or densely aggregated individuals [9-12]) require the operation of drones (typically multirotor) in close proximity to target species (e.g. <30 meters) to achieve sufficient resolution. However, studies focusing on the effects of drones near wildlife are limited

[4]. To evaluate the impact of drones on target species requires knowledge of: 1) the capabilities of a target species to detect the drone, 2) the nature of disturbance introduced by a specific model drone, and 3) background conditions of the habitat in which the study is conducted (e.g. ambient noise levels). Only then can an attempt be made to understand the broader implications of applying drone technology to behavioral and ecological studies that enhance wildlife conservation, research, and management.

Drones have been used to study a suite of terrestrial [1, 12-17] and marine species [3, 5, 8, 18, 19], including elephants [20, 21], cetaceans [18, 22, 23], and sea turtles [9, 10, 24, 25]. Despite the increasing applications for drones in wildlife biology [11, 26-30], relatively few studies specifically focus on assessing the behavioral responses of taxa to drones at low altitudes. Some key exceptions [5, 12, 15, 31, 32] highlight the complexity of this endeavor.

A critical component for evaluating the level of behavioral disturbance imposed by drones is to understand the spectrum of responses displayed by each species. Sea turtles in shallow habitats (i.e. <1 m water depth) can detect and respond to a threatening stimulus (e.g. humans walking towards them in shallow water) by swimming at high speed towards deeper water, often generating a “bow wave” in front of the turtle (E. Bevan, *pers. obs*.). In deeper water habitats (i.e. >1 m water depth) acoustic disturbances to sea turtles (e.g. high-pressure air gun pulses and nearby vessels or objects) can elicit a range of behavioral responses from head retraction, flipper movement, and changes in swimming patterns and orientation [33], to diving [34-36]. A range of behavioral responses to auditory disturbance have been reported in birds, including crested terns (*Thalasseus bergii)*, ranging from minor head-scanning to flushing [7, 37, 38]. Pomeroy et al. [5] examined two species of pinnipeds and found that behavioral responses (varying from increased alertness to fleeing towards the water) varied depending on the type of drone used, and age, sex, and in some cases, reproductive status of individuals. Such studies suggest that future research using drones should consider these variables, in addition to altitude when assessing threshold levels for behavioral responses to drones.

Evaluating drone detectability at different altitudes is multifaceted and involves assessing the sensory abilities of target species to discern the drone or its shadow (visual component) and detect the unique noise emission characteristics of each drone (auditory component). Although limited, there are some data available on the auditory capabilities of sea turtles, crocodilians, and shorebirds that provide a basis for understanding whether these species can detect the sound emitted by drones and at what specific threshold. In sea turtles (loggerhead (*Caretta caretta*) and *C. mydas*), peak auditory sensitivity in air occurs between 300 and 400 Hz, and in water between 50 and 400 Hz [39, 40]. The American alligator (*Alligator mississipiensis*) exhibits a range of auditory sensitivity in water from 100 Hz to 2 kHz, and in air 100 Hz to 8 kHz, with peak sensitivities in water at 800 Hz and in air at 1000 Hz [41]. Audiograms from 49 species of birds suggest that birds generally exhibit an optimal auditory frequency range of 2-3 kHz [38]. By comparison, the noise emitted by small, multirotor drones (sound levels reported at 57.8-81 dB, and frequencies of 60 and 150 Hz [31, 32, 42]) is likely to be audible to many taxa at low altitudes (between 5 and 10 m). However, the influence of altitude and ambient noise levels on the detectability of drones for different species remains generally understudied.

In the current study, we tested a small, commercial drone (DJI Phantom 4 Pro®) in wildlife surveys at field sites in tropical Australia: Bare Sand Island, Northern Territory (NT), Cape Domett in Western Australia (WA), and at multiple reefs across Camden Sound, WA. Collectively, these locations provide prime nesting and/or foraging habitat for sea turtles [43, 44], seabirds [45, 46], and saltwater crocodiles [47]. Yet ecological studies in these habitats are often logistically challenging, and an overall paucity of data exists regarding species in remote tropical locations of WA and the NT. Thus, the focus of the current study was to provide preliminary information that can guide the integration of drone-based studies into studies of wildlife and effective conservation resource management.

MATERIALS AND METHODS

Field sites for the current study are presented in Table 1 to illustrate the types of habitats and target species encounter during drone flight trials. A 1.4-kg DJI Phantom 4 Pro® (www.dji.com) drone was used for the current study. The drone can travel up to 5 km, and each high capacity battery (5870 mAh) provides a maximum of 30 min flight time. The drone was operated using a tablet-based app (Litchi™, VC Technology Ltd.) that displayed real-time drone telemetry information (e.g. drone altitude, speed, distance, etc.). Flight records were automatically uploaded to Airdata.com. All flights were compliant with CASA regulations and conducted as part of permitted research activities by AusTurtle (NT) and Department of Biodiversity, Conservation and Attractions (WA).

Table 1. Study locations, habitat type, and target species observed during drone flight trials in Australia.

Study Site	**Location (Lat, Long)**	**Habitat Type**	**Cb**	**Cs**	**Tb**	**Ts**	**BC**
BSI	-12.536173 130.420038	Beach, Reef	X		X		X
CD	-14.802778 128.413889	Beach, Nearshore	X	X	X	X	
SC	-15.540833 124.410556	Nearshore				X	
MR	-15.948923 124.204102	Reef				X	
TR	-16.272721 123.892815	Reef				X	

BSI, Bare Sand Island, NT, Australia; CD, Cape Domett in WA; SC, Sampson Cove in Camden Sound, WA; MR, Montgomery Reef (Yawajaba Island) in Camden Sound, WA; TR, Turtle Reef in Camden Sound, WA; Cb, crocodile basking on the beach or in the surf; Cs, crocodile swimming in nearshore waters; Tb, turtle on the beach; Ts, turtle swimming in nearshore waters; BC, bird colony. Note: From "Measuring behavioral responses of sea turtles, saltwater crocodiles, and crested terns to drone disturbance to define ethical operating thresholds" by Bevan E, Whiting S, Tucker T, Guinea M, Raith A, Douglas R, 2018, *PLoS ONE*, 13(3): e0194460. https://doi.org/10.1371/journal.pone.0194460. Copyright 2018 by Bevan et al. Reprinted with permission.

Sea Turtles

The focus of surveys off CD, in the nearshore waters of SC, and over reef habitat was to evaluate potential behavioral responses to the presence of a drone at various altitudes between 15 and 30 m. All surveys were conducted at an initial altitude of 30 m and a constant speed of approximately 6-8 m/s. If a turtle was encountered during a survey, the behavioral response of the turtle was documented during this initial flyover at 30 m, and the drone was flown such that the aircraft did not stop and continued along the original trajectory of the survey away from the turtle. Once the drone was approximately 100 m away from where the turtle was originally observed, the aircraft was stopped, the altitude was reduced to 20 m, and the drone was flown back to where the turtle was first observed to conduct a second flyover at 20 m. If the turtle was still visible, this process was conducted again for a third flyover at 15 m. If possible, a flyover at 30, 20, and 15 m altitude was conducted for each turtle encountered, while documenting the behavioral response of the turtle during each flyover, constituting a “flight trial”. After completing a flyover at 15 m, or if the turtle was no longer visible during a flyover, the flight trial was ended, and the aircraft resumed the standard survey. Since control data (sea turtle behaviors documented when the drone was not present) was not available, behavioral responses documented in the present study of sea turtles in nearshore and reef habitats were evaluated relative to known startle responses documented in previous studies [33-36].

Nearshore Habitat

Nine nearshore surveys were conducted off CD beach between 0730 and 1600 hrs from 5-11 August 2017. Each drone survey consisted of two straight-line transects parallel to the nesting beach, one 500 m, the other 1 km offshore. Additionally, a straight-line transect was conducted perpendicular to the nesting beach out to 2 km offshore. Nearshore surveys throughout SC were conducted on 15 August 2017, at approximately 1330 hr. Unlike surveys at CD, flights at SC were flown an altitude of 50-60 m to provide a wider field of view from the drone to locate and avoid overflying humpback whales (*Megaptera novaeangliae*) that are known to frequent the area during Austral winter. Civil Aviation Safety Authority (CASA) regulations restrict the maximum altitude of recreational drones to 120 m that conflicts with the required 500 m exclusion zone when flying near whales [48]. The flight paths at SC paralleled the coastline at approximately 300-500 m offshore.

Reef Habitat

An interconnected network of shallow, algae-covered rocky reefs extends between the islands of Fog Bay in the NT, approximately 50 km west of Darwin [49]. Similar habitats comprise MR and TR. In the NT, two sites were surveyed between 26 June and 24 July, one south of BSI, and the other north of BSI. Thirteen surveys following the edge of the reef were conducted between 1100 and 1500 hrs.

A total of 7 surveys were conducted on MR and TR on 16-17 August, and 18 August, respectively, including one survey of MR conducted at 15 m altitude to compare the behavioral responses of sea turtles to a drone at 15 and 30 m altitude. Surveys involved two types of transect paths, one that followed the edge of the reef between exposed shallow portions of the reef and the slope, and the other traversing the region from the slope of the reef into its interior.

Nesting Beaches

BSI and CD are important rookeries for the flatback sea turtle [43, 44, 50, 51]. Drone flights over turtles that emerged to nest during daylight were conducted at altitudes between 10 and 30 m during stages of the nesting process at which Witherington [52] and Guinea (*unpub. data*) indicate sea turtles are particularly susceptible to being deterred from nesting: 1) initial emergence from the sea and progression towards the dune, 2) digging a body pit, and 3) constructing an egg chamber. When a turtle was observed in any stage of the nesting process, the drone was launched from behind the primary dune and at least 500 m away from the turtle. The drone was raised to an initial altitude of 30 m, and the aircraft was flown at regular survey speed (6-8 m/s) perpendicular to the orientation of the turtle and out in front of its head to best achieve maximum visibility of the drone to each turtle. Any change in behavior or visual signs of disturbance (i.e. increased crawl speed, abrupt change in direction, abandonment of the excavated body pit or egg chamber, or return to the sea) were documented following each flyover. Drone flyovers were conducted according to the same protocols described for nearshore surveys and flyovers of least 2 consecutive stages of the nesting process were conducted for each turtle.

Saltwater Crocodiles

All survey transects were conducted according to the methods described for sea turtle surveys, from an initial altitude of 30 m and a speed of approximately 6-8 m/s. If a crocodile was encountered during a survey, the behavioral response of the crocodile to the initial flyover at 30 m was documented. The previously described protocol for conducting a flight trial during a nearshore survey was used to conduct a flight trial for each crocodile, with flyovers at 30, 20, and if possible, 10 m, to evaluate potential behavioral responses at each altitude. An additional flyover at 40 m altitude was conducted following the initial flyover at 30 m during each flight trial to refine the upper threshold drone altitude above which behavioral responses are not elicited.

Nearshore Habitat

The abundance of saltwater crocodiles in nearshore waters was documented during 8 drone-based surveys off CD between 0730 and 1600 hrs. Surveys occurred from 5-11 August, 2017. There is a lack of control data (behaviors of crocodiles in the absence of the drone) for crocodiles in nearshore habitats and these data were therefore not available in the current study.

Surf Zone

Drone transect surveys were conducted on BSI and on CD over saltwater crocodiles that were resting on the beach or in the surf zone. On BSI, two drone flyovers of a 2.4-meter crocodile (length measured using imagery from the drone) were conducted on 26 and 28 June 2017 at 30 and 40 m altitude, as the crocodile was resting out of the water on a sand spit. Eight transect surveys were flown parallel to the beach and over the surf zone to document crocodiles at CD between 4 and 11 August 2017. Most drone surveys were flown between 0530 and 0630 hrs when daylight was sufficient for optimal visibility of beach tracks. On 4 August 2017 a survey was conducted at 1330 hrs. Binoculars were used to observe crocodiles in the surf zone or on the beach immediately prior to each drone flight and these observations were used to evaluate the behaviors observed during each drone flight.

Nesting Birds

A sand-bank approximately 1 km in length is located southwest of BSI provided a resting location for a colony of crested terns. Eight drone surveys were conducted between 27 June and 24 July 2017, from 1200 to 1700 hrs, and at altitudes between 30 and 70 m. Flyovers were limited to 2 per day to avoid the possibility of habituation to the potential disturbance due to the drone. A flight trial began at the highest altitude being tested (e.g. 70 m) and progressed lower (e.g. 60 m) if no flushing response was elicited. If the colony took flight during flyovers, the trial was stopped. The drone was launched approximately 1 km from the resting colony of crested terns. Once the drone was within 500 m of the sand island, the drone was flown at a speed of 3-5 m/s. Although the colony of crested terns was observed using binoculars immediately prior to each drone flight from the southwestern tip of BSI, the angle of observation was not sufficient to record a quantitative description of the number of birds taking flight before the drone flight.

RESULTS

Sea Turtles

Nearshore Habitat

Two flatback (1 male and 1 female), 1 female green, and 1 sea turtle of unknown species and sex, were observed during drone flights over nearshore waters off CD. At SC, 2 flatback sea turtles were observed by drone in nearshore waters. Although the turtles encountered during flights spent relatively little time at the surface of the water (3-60 sec at CD, 10-30 sec at SC), the turtles did not exhibit avoidance behaviors (i.e. rapid diving or change in direction) in response to the presence of the drone or its shadow at or above 20 m altitude. Both sea turtles at SC submerged before drone flight trials could be conducted (Fig 1).

Figure 1. Male sea turtle observed from a drone off a nesting beach. Male flatback turtle sea turtle (*Natator depressus*) observed from a drone at an altitude of 18.6 m approximately 2 km off the nesting beach at Cape Domett, Western Australia on 6 August, 2017. Note: From "Measuring behavioral responses of sea turtles, saltwater crocodiles, and crested terns to drone disturbance to define ethical operating thresholds" by Bevan E, Whiting S, Tucker T, Guinea M, Raith A, Douglas R, 2018, *PLoS ONE,* 13(3): e0194460. https://doi.org/10.1371/journal.pone.0194460. Copyright 2018 by Bevan et al. Reprinted with permission.

Reef Habitat

We surveyed the behavioral responses of multiple green and hawksbill sea turtles (>10 turtles/survey) to the drone while foraging on algae-covered rocky reef habitat at BSI, MR, and TR (Fig 2). The turtles did not exhibit avoidance behaviors (e.g. a bow wave generated by the rapid flight response) in response to the presence of the drone or its shadow at either 15 or 30 m. Individuals were completely submerged, at the surface of the water, or partially exposed while feeding (<1m water depth). The submerged sea turtles were either stationary, potentially foraging on the reef, or slowly swimming along the bottom at approximately 2 m depth or less. Turtles at the surface were encountered floating over the reef slope, or over deeper channels along the reef.

Figure 2. Sea turtles observed from a drone on shallow reef foraging habitat.
Sea turtles observed foraging on algae-covered reef habitat from a drone altitude of 30 m at Turtle Reef, Camden Sound, Western Australia. Note: From “Measuring behavioral responses of sea turtles, saltwater crocodiles, and crested terns to drone disturbance to define ethical operating thresholds” by Bevan E, Whiting S, Tucker T, Guinea M, Raith A, Douglas R, 2018, *PLoS ONE*, 13(3): e0194460. https://doi.org/10.1371/journal.pone.0194460. Copyright 2018 by Bevan et al. Reprinted with permission.

At TR and MR, the drone altitude for two flights was reduced from 30 m to 9 m and 5 m, respectively. In both instances, sea turtles were foraging in less than 2 m of water. At MR, the green sea turtle was in less than 0.5 m depth of water and displayed no response to the presence of the drone, despite a shadow cast in front of the turtle (Fig 3). At TR, a hawksbill sea turtle was observed slowly swimming over the reef in 1-2 m depth of water. In the presence of the drone at 9 m altitude, the individual increased the force of flipper strokes, potentially to accelerate to deeper water before slowing and turning around. This behavior could be classified as a minor behavioral response to a drone flying at low altitude. However, rapid avoidance or major evasive responses were not observed during this trial.

Figure 3. Sea turtle observed foraging on a shallow reef from a drone at low altitude. Examples of a drone being lowered to approximately 5 m over a foraging green turtle (*Chelonia mydas*) on Montgomery Reef, Camden Sound, Western Australia. Note: From “Measuring behavioral responses of sea turtles, saltwater crocodiles, and crested terns to drone disturbance to define ethical operating thresholds” by Bevan E, Whiting S, Tucker T, Guinea M, Raith A, Douglas R, 2018, *PLoS ONE*, 13(3): e0194460. https://doi.org/10.1371/journal.pone.0194460. Copyright 2018 by Bevan et al. Reprinted with permission.

Nesting Beach

At BSI, a female flatback sea turtle emerged to nest on 25 July at 1900 hr. At CD, 5 female flatback sea turtles emerged to nest from 5 to 9 August between 1600 and 1700 hrs. No disruption or abandonment of the nesting attempt was observed for any of the turtles encountered at any altitude. Collectively, the stages of nesting during which a female turtle is likely to be disturbed, (i.e. emerging from the sea, and digging a body pit and egg chamber) were examined for signs of drone disturbance at altitudes between 10 and 40 m (Fig 4).

Figure 4. Behavioral response of a sea turtle during the nesting process observed from a drone at low altitude. Testing the behavioral response of a flatback turtle (*Natator depressus*) to the presence of a drone at 10 m altitude during the nesting process at Cape Domett, Western Australia. Note: From "Measuring behavioral responses of sea turtles, saltwater crocodiles, and crested terns to drone disturbance to define ethical operating thresholds" by Bevan E, Whiting S, Tucker T, Guinea M, Raith A, Douglas R, 2018, *PLoS ONE*, 13(3): e0194460. https://doi.org/10.1371/journal.pone.0194460. Copyright 2018 by Bevan et al. Reprinted with permission.

Saltwater Crocodiles

Eleven drone surveys were conducted at BSI and CD, resulting in 31 crocodile sightings. It is possible that the same individuals were observed on multiple surveys over the study period, given the tendency of crocodiles to return to established core activity areas [47]. However, individual identity could not be verified in the present study and each crocodile observed was treated as a new sighting.

Nearshore Habitat

Eighteen of the 31 crocodile sightings in the present study were observed swimming in nearshore habitat at CD. The crocodiles did not exhibit avoidance behaviors (e.g. movement of the head or body) in response to the presence of the drone or its shadow at 30 m or above. Initial signs of disturbance were observed at a maximum drone altitude of 30 m and involved one or more lateral movements of the head. Drone flight trials conducted at 20 m altitude elicited more pronounced lateral head movements, and flight trials conducted at 10 m altitude resulted in crocodile submergence.

Surf Zone

At BSI, one crocodile was observed basking on the sand during each survey. One to 4 crocodiles were observed during each drone survey at CD. Signs of crocodile disturbance from the drone when basking on the sand included minor to substantial lateral head movements and/or retreat to deeper water. However, in contrast to BSI, crocodiles at CD were only observed basking on the sand on the initial day of surveys (4 August), after which all crocodiles were observed resting in the surf or swimming in nearshore waters. Crocodiles were observed basking motionless on the sand or in the surf zone immediately prior to each drone flight.

Collectively, drone surveys of crocodiles at BSI and CD suggest that adult and sub-adult crocodiles basking on the sand or swimming in nearshore waters are disturbed by drones when flying below approximately 50 m in altitude (Figs 5 and 6). All trials conducted at 10 m altitude caused rapid head movements, after which crocodiles either submerged or retreated to deeper water.

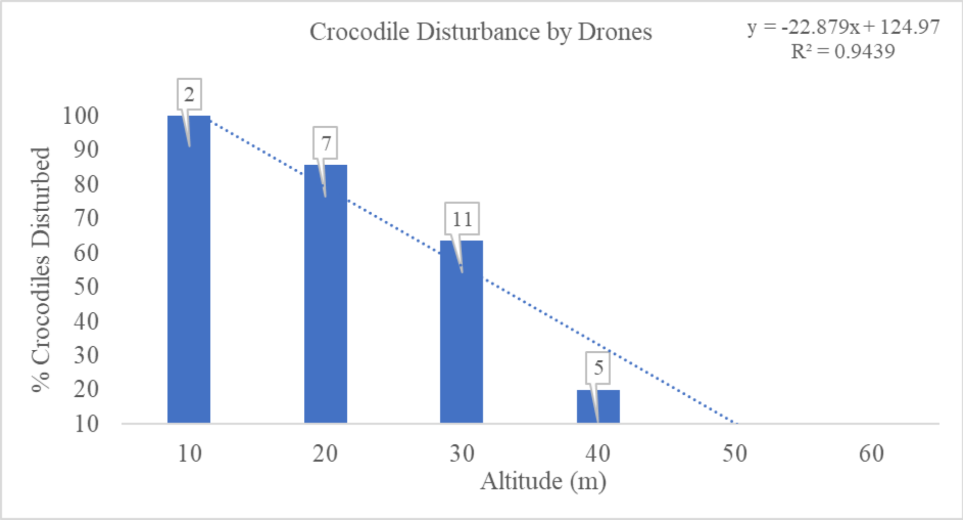

Figure 5. Crocodiles disturbed by a drone at various altitudes. Percentage of crocodiles (*Crocodylus posorus*) observed during drone-based surveys Bare Sand Island, Northern Territory, and Cape Domett, Western Australia, that were disturbed by the presence of a drone at various altitudes. Results are based on a total of 31 crocodile sightings over 10 surveys observed either resting on the beach, in the surf, or actively swimming on the surface of nearshore waters between the surf and approximately 300 m off the nesting beach. The numbers of total crocodiles sampled for each altitude are show in boxes above the bars. Note: From “Measuring behavioral responses of sea turtles, saltwater crocodiles, and crested terns to drone disturbance to define ethical operating thresholds” by Bevan E, Whiting S, Tucker T, Guinea M, Raith A, Douglas R, 2018, *PLoS ONE*, 13(3): e0194460. https://doi.org/10.1371/journal.pone.0194460. Copyright 2018 by Bevan et al. Reprinted with permission.

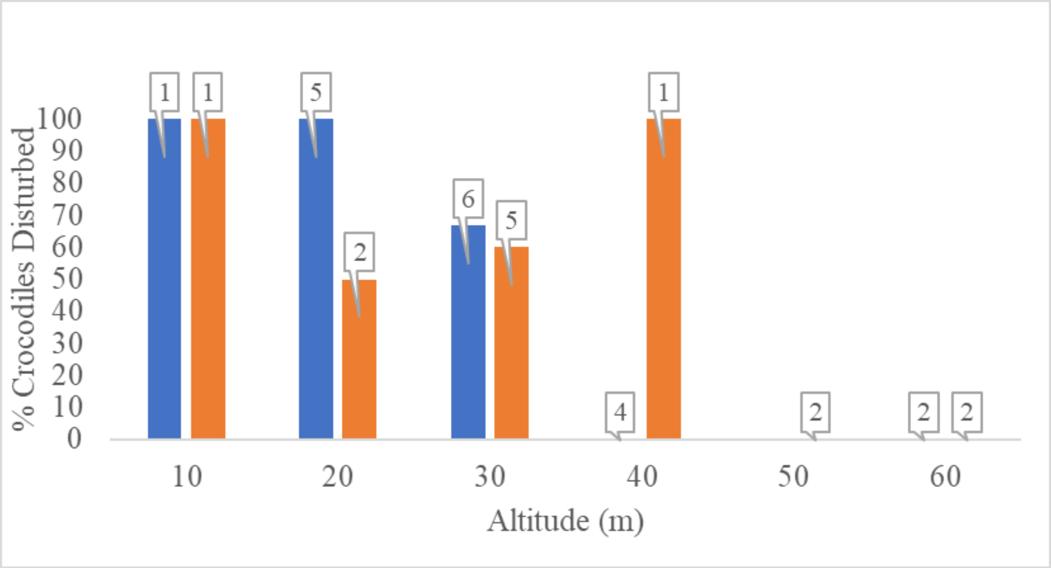

Figure 6. Drone disturbance to crocodiles by habitat. The percentage of crocodiles (*Crocodylus posorus*) that were disturbed by the presence of a drone while resting on the beach or in the surf (orange bars), or actively swimming in nearshore waters (blue bars) at Bare Sand Island, Northern Territory, and Cape Domett, Western Australia. The numbers of total crocodiles sampled for each altitude are show in boxes above the bars. Note: From "Measuring behavioral responses of sea turtles, saltwater crocodiles, and crested terns to drone disturbance to define ethical operating thresholds" by Bevan E, Whiting S, Tucker T, Guinea M, Raith A, Douglas R, 2018, *PLoS ONE*, 13(3): e0194460. https://doi.org/10.1371/journal.pone.0194460. Copyright 2018 by Bevan et al. Reprinted with permission.

Nesting Birds

The mean size of the crested tern colony on the sand-bank throughout the 8 drone surveys was 153 birds (range = 19 - 334 birds) (Table 2). Flight trials indicated that the crested tern colony was generally disturbed by a drone flying below 60 m altitude (Fig 7). Observed disturbance behaviors consisted of increased vigilance (i.e. raised wings and multiple, lateral head movements) and flushing of one to many birds in the colony.

Table 2. Drone flight trials over a colony of crested terns on a sand-bank southwest of BSI from 27 June to 24 July, 2017.

Date	Time	Altitude	Tide	# Birds that took flight	Total # of birds	% Disturbed
3-Jul	1700	70	Falling	4	121	3.3%
27-Jun	1328	60	Falling	1	334	0.3%
28-Jun	1430	50	Falling	246	246	100.0%
4-Jul	1215	50	Rising	9	128	7.0%
6-Jul	1430	50	High	1	172	0.6%
9-Jul	1432	45	Rising	0	112	0.0%
24-Jul	1515	45	Rising	4	38	10.5%
6-Jul	1430	40	High	16	211	7.6%
24-Jul	1515	40	Rising	9	19	47.4%

Note: From “Measuring behavioral responses of sea turtles, saltwater crocodiles, and crested terns to drone disturbance to define ethical operating thresholds” by Bevan E, Whiting S, Tucker T, Guinea M, Raith A, Douglas R, 2018, *PLoS ONE*, 13(3): e0194460. https://doi.org/10.1371/journal.pone.0194460. Copyright 2018 by Bevan et al. Reprinted with permission.

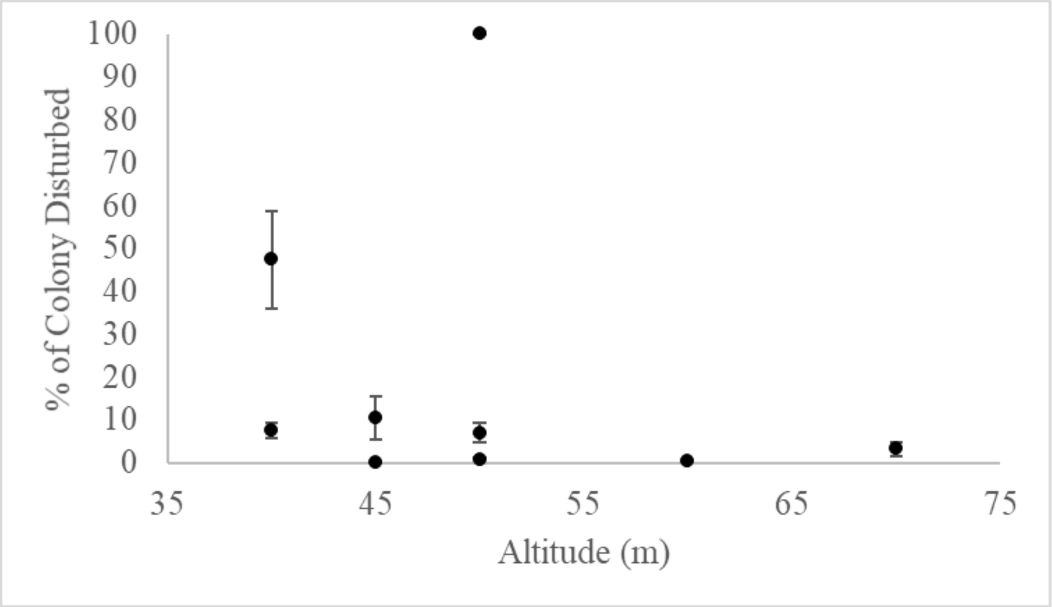

Figure 7. Crested terns disturbed by a drone at various altitudes. The percentage of crested terns (*Thalasseus bergii*) observed on the sand-bank to the southwest of Bare Sand Island, NT that took flight as a drone passed overhead at various altitudes. Although trials at altitudes lower than 40 m were possible ethical considerations and research permits prevented flyovers at lower altitudes. Note: From “Measuring behavioral responses of sea turtles, saltwater crocodiles, and crested terns to drone disturbance to define ethical operating thresholds” by Bevan E, Whiting S, Tucker T, Guinea M, Raith A, Douglas R, 2018, *PLoS ONE,* 13(3): e0194460. https://doi.org/10.1371/journal.pone.0194460. Copyright 2018 by Bevan et al. Reprinted with permission.

DISCUSSION

Collectively, the present approach threshold study demonstrates that the altitude for eliciting disturbance when using a drone varies by taxa. Factors that contribute to the specific disturbance threshold for a given species include the ability of a species to detect the visual disturbance of drones and the unique sound signature of a particular drone, the degree to which drone disturbance is associated with a threatening stimulus (a predator), and the ambient noise level of a given habitat. Although sound levels emitted by the DJI Phantom 4 Pro® used in the current study have not been quantified, it is likely similar to noise levels reported for other drones of the same size class used in previous studies (57.8-81 dB, and frequencies of 60 and 150 Hz) [12, 31, 42]. Characterizing the noise emitted by multirotor drones is challenging since sounds emitted by the aircraft change in response to wind gusts while hovering, and to operator controls during flight [42]. At 30 m altitude, these sound levels may be lost against background noise, such as in a penguin colony [32], or may be undetectable at 1 m below the surface of the water when the drone is at approximately 10 m altitude [53]. Coupling these findings with known auditory capabilities of several species of cetaceans, penguins and pinnipeds, it is likely these marine species would be unable to detect small drones [31, 32]. Each unique sound profile presents a distinct auditory stimulus to target species and can elicit different types and intensities of animal behaviors in response.

Based on previous studies of sea turtles, the maximum range of auditory sensitivity for *C. mydas* and *C. caretta* is from 100 to 1000 Hz in water, and although this range can vary with taxa and age class, other species of sea turtle are likely to exhibit similar capabilities [39, 40, 54]. Thus, it is possible sea turtles can detect the noise levels reported in previous studies for small, commercial drones at altitudes between 5 and 10 m (50 – 200 Hz, 57.8-80 dB; [12, 31, 32, 42]). This is especially likely without higher levels of background noise, such as water rushing off the reef flat, to mask the sound from the drone. One note of caution in our study is that 4 of the 6 sea turtles encountered in nearshore waters exhibited relatively short surface intervals (3-60 seconds), which could be interpreted as a potential behavioral response to drone disturbance. However, the degree to which sound levels emitted by commercial drones are influenced by higher flight altitudes (e.g. 15 m or higher) and background noise remains largely undetermined [31, 32].

The auditory capabilities of crocodiles are concentrated at low frequencies and coupled to a diverse array of vocalizations that aid in group coordination, mating, territorial defense, and maternal care [41, 55, 56]. Based on previously reported sound levels for small, commercial drones at altitudes between 5 and 10 m, and our results from the current study, it is possible crocodiles can visually detect and/or hear small drones at low altitudes. Further, our preliminary findings suggest that specific activities (i.e. basking on the beach, in the surf, or actively swimming in nearshore waters) may influence the threshold altitude above which a drone can be used without eliciting behavioral changes from crocodiles (Fig 6).

The results from the present study suggest that using drones to study colonies of *T. bergii* requires a higher altitude approach (> 60 m) than the other species we investigated to avoid disturbance. The auditory capabilities reported for birds (optimal frequencies between 2-3 kHz), paired with the sound levels emitted by small commercial drones (50 – 200 Hz, 57.8-80 dB), suggests that the noise emitted by drones may not be audible to colonies of *T. bergii,* but that the disturbance may be due to other factors (e.g. visual disturbance). A previous study supports our conclusion that this species is not disturbed by the presence of a drone above 60 m altitude [6]. Nevertheless, studies are needed that decouple the auditory and visual components of drone disturbance to evaluate behavioral disturbance thresholds for birds.

An additional concern when evaluating the potential for drone disturbance is whether a given species is startled by visual detection of the drone and/or its shadow. If sea turtles could visually detect and were disturbed by the drone at 15-30 m altitude, we would have expected to see rapid avoidance behavior (e.g. submergence behavior, swimming towards deeper water). For adult sea turtles at nearshore habitat and juveniles foraging on reefs, our drone approached many of the individuals from either the front or within the peripheral field of view of the sea turtle and cast a shadow that was potentially visible to these individuals. However, no sea turtles exhibited evasive behaviors, suggesting that individuals either are unable to visually detect a drone at 15-30 m altitude, or did not perceive the drone/its shadow as a threat. Thus, it is possible that drone shadows are not impacting the behavior of sea turtles. These results suggest that altitudes above 15 m are adequate for providing high resolution imagery of sea turtles in nearshore waters and shallow reef habitat and documenting natural sea turtle behaviors. Further investigation is needed to characterize the behaviors of different sea turtle species in response to the potential visual disturbance of a drone at low altitudes and/or its shadow.

The current study supports the use of drone technology in studies of marine species in a variety of habitats. Our findings indicate that operating a drone at or above 20 m altitude is a non-invasive protocol for studying sea turtles in nearshore waters off nesting beaches. Likewise, operating a drone at or above 15 m altitude in shallow reef habitats may be an optimal method for use in behavioral studies of sea turtles. At sea turtle nesting habitats, the results from the current study were consistent across multiple locations and populations and suggest that the nesting processes of flatback sea turtles are not disrupted by drones at or above 10 m altitude. If sea turtles can detect the noise emitted from small drones at low altitudes (5-10m), the drone did not provide a perceived threatening stimulus sufficient to change nesting behavior or cause abandonment of a nesting attempt. Collectively, our findings suggest that drones can be used to study sea turtles at low altitudes (from 10-30 m) without disturbing individuals, but that the threshold for disturbance for each species depends on habitat and environmental conditions. Drone technology may therefore be an optimal tool for eliminating human observer presence, a known factor in sea turtle disturbance [52], while studying nesting processes or monitoring nesting activity on beaches.

Drone surveys of saltwater crocodiles resting on sea turtle nesting beaches and resting or swimming in nearshore waters suggests that operating a small drone at lower altitudes (10-30 m) to study crocodile behaviors can cause behavioral disturbance. Previous studies have used a variety of drones at altitudes of 100 to 300 m to study crocodilians with no indication of disturbance to individuals [57-59]. However, these altitudes may be insufficient for mapping or behavioral studies that require imagery in greater detail and higher resolution, and therefore necessitate lower altitude surveys. Collectively, video imagery from the current study suggests crocodiles can detect visual and/or auditory disturbance from a small drone. However, studies evaluating the visual and auditory capabilities of crocodilians, and quantifying the disturbance caused by commonly-used drones are areas of need in conservation management research.

At Raine Island National Park (RINP), Queensland, preliminary data suggests that other avian species are even more sensitive to drone disturbance than *T. bergii* [60]. Official guidance for drone use within RINP indicates that drone altitudes of 80 and 120 m, respectively, are required to avoid disturbing brown booby (*Sula leucogaster*) and common noddy (*Anous stolidus*) birds. These requirements suggest that drone disturbance may be species-specific, and that different avian taxa exhibit different behavioral disturbance threshold altitudes. Such thresholds for target species should be determined prior to initiating drone-based biological studies. Future studies of *T. bergii* should incorporate other factors, such as environmental conditions, time of day, and reproductive status, to determine how these factors may influence behavioral reactions of *T. bergii* to drones. Previous studies of crested tern flight patterns indicate that non-breeding individuals regularly take flight while breeding individuals typically remained grounded during the breeding season (March – July) [45, 61]. The flight trials in the current study were conducted between June and July 2017, which falls within the known breeding season for *T. bergii* in the NT [45]. Thus, despite the lack of control data (number of individuals that take flight prior to a drone flight) for comparison in the current study, flights when a large portion of individuals took flight could represent a startle response due to the presence of the drone rather than normal flight movements. However, breeding colonies in this region have been reported to number in the thousands to hundreds of thousands, and the average colony size reported in the current study was a few hundred individuals. It is possible that the group of *T. bergii* observed by drone on the sand bank represents a relatively small portion of individuals from a nearby larger breeding colony. A comparison of the behavioral disturbance thresholds of non-breeding with breeding colonies could provide insights on whether reproductive status influences behavioral responses to drones.

An important consideration for the current study is that the results for species observed in the water are representative of individuals located within the depth of detection from the drone, which is directly influenced by water clarity. Therefore, it is possible that some individuals could have been obscured by reduced water clarity at some study sites. Additional studies and larger sample sizes are necessary to account for individual variation in behavioral responses to drone disturbance, as well as the influence of environmental factors such as water clarity and habitat type on results. A simple power analysis suggests a larger sample size (>52 individual sightings) would provide the ability to detect a medium effect of drone disturbance on the behavioral responses of a given species as a factor of drone altitude. Future studies should also aim to obtain behavioral control data for each species (behaviors displayed in the absence of a potentially disturbing stimulus, such as the presence of a drone or human observer). Collectively, future drone-based behavioral studies should incorporate these considerations as factors in their experimental design.

We used the same drone coupled with consistent protocols to evaluate behavioral responses of multiple species to drones throughout a range of habitats across northwestern, tropical Australia. It is likely that different drones and flight patterns may elicit different behavioral responses for the species evaluated. However, with drone type and flight pattern held relatively constant, the differences in threshold altitude that elicits disturbance behaviors are indicative of fundamental differences between the species. Of note, these differences in behavioral responses to drones may be founded in the basic ecology of each species and the level of response to drones may relate to the degree to which each species associates drone disturbance with the threat of a predator [12].

Regardless, the findings characterize important threshold altitudes above which the behaviors of target species do not appear to change.

CONCLUSIONS

Drones are rapidly revolutionizing the observational and monitoring capabilities of scientists working in remote habitats where survey locations are often logistically challenging or dangerous to access. However, without first quantifying the impact of drones on wildlife, the benefit of minimizing observer presence may be diminished. We have demonstrated that a variety of disturbance thresholds exist for the suite of species that may occur within a single habitat. In establishing optimal drone-use protocols, resource managers are challenged with balancing the quality and type of data needed, with the level of disturbance inflicted upon a variety of species. The current study provides preliminary information to address these concerns and highlights promising directions for future research in this advancing field.

ACKNOWLEDGMENTS

All flights were conducted by FAA-sUAS pilot, Elizabeth Bevan, and were consistent with CASA regulations. Logistical support and access to study locations for the current study were provided by AusTurtle, Inc. and the Kenbi Land Council in the NT, and the Western Australian Department of Biodiversity, Conservation and Attractions (DBCA), Lalang-garram Land Council, and Dambimangari Aboriginal Corporation in WA. Ben Corey (DBCA) for arranging travel to CD; Danny Barrow, Adrian Lane and the crew of the DBCA research vessel, *Worndoom* while in CS. Special thanks to Dean Wright and Scott McDonald (AusTurtle, Inc.) for providing valuable insight on this study; Jessica Hoffman, Jim McClintock, Ken Marion (UAB), and Corrine Douglas (DBCA) for editing this manuscript.

REFERENCES

1. Jones GP, Pearlstine LG, Percival HF. An assessment of small unmanned aerial vehicles for wildlife research. Wildlife Society Bulletin. 2006;34(3):750-8.

2. Smith KW. The Use of Drones in Environmental Management. World Environmental and Water Resources Congress 20152015. p. 10.

3. Kiszka JJ, Mourier J, Gastrich K, Heithaus MR. Using unmanned aerial vehicles (UAVs) to investigate shark and ray densities in a shallow coral lagoon. Marine Ecology Progress Series. 2016;560:237-42.

4. Smith CE, Sykora-Bodie ST, Bloodworth B, Pack SM, Spradlin TR, LeBoeuf NR. Assessment of known impacts of unmanned aerial systems (UAS) on marine mammals: data gaps and recommendations for researchers in the United States. Journal of Unmanned Vehicle Systems. 2016;4(1):31-44.

5. Pomeroy P, O'connor L, Davies P. Assessing use of and reaction to unmanned aerial systems in gray and harbor seals during breeding and molt in the UK. Journal of Unmanned Vehicle Systems. 2015;3(3):102-13.

6. Hodgson JC, Mott R, Baylis SM, Pham TT, Wotherspoon S, Kilpatrick AD, et al. Drones count wildlife more accurately and precisely than humans. bioRxiv. 2017:165019.

7. Hodgson JC, Baylis SM, Mott R, Herrod A, Clarke RH. Precision wildlife monitoring using unmanned aerial vehicles. 2016;6:22574. doi: 10.1038/srep22574. https://www.nature.com/articles/srep22574#supplementary-information.

8. Martin J, Edwards HH, Burgess MA, Percival HF, Fagan DE, Gardner BE, et al. Estimating distribution of hidden objects with drones: From tennis balls to manatees. PLoS One. 2012;7(6):e38882.

9. Bevan E, Wibbels T, Navarro E, Rosas M, Najera BM, Sarti L, et al. Using unmanned aerial vehicle (UAV) technology for locating, identifying, and monitoring courtship and mating behaviour in the green turtle (Chelonia mydas). Herpetol Rev 2016b. 2016;47(1):27-32.

10. Bevan E, Wibbels T, Najera BMZ, Martine MAC, Sarti LAM, Martinez FI, et al. Unmanned Aerial Vehicles (UAVs) for monitoring sea turtles in near-shore waters. Marine Turtle Newsletter. 2015;(145):19-22.

11. Chabot D, Bird DM. Wildlife research and management methods in the 21st century: Where do unmanned aircraft fit in? Journal of Unmanned Vehicle Systems. 2015;3(4):137-55.

12. Vas E, Lescroël A, Duriez O, Boguszewski G, Grémillet D. Approaching birds with drones: first experiments and ethical guidelines. Biology letters. 2015;11(2):20140754.

13. Mulero-Pázmány M, Stolper R, van Essen LD, Negro JJ, Sassen T. Remotely Piloted Aircraft Systems as a Rhinoceros Anti-Poaching Tool in Africa. PLOS ONE. 2014;9(1):e83873. doi: 10.1371/journal.pone.0083873.

14. Israel M. A UAV-based roe deer fawn detection system. International Archives of Photogrammetry and Remote Sensing. 2011;38:1-5.

15. Ditmer Mark A, Vincent John B, Werden Leland K, Tanner Jessie C, Laske Timothy G, Iaizzo Paul A, et al. Bears Show a Physiological but Limited Behavioral Response to Unmanned Aerial Vehicles. Current Biology. 2015;25(17):2278-83. doi: https://doi.org/10.1016/j.cub.2015.07.024.

16. Chabot D, Carignan V, Bird DM. Measuring habitat quality for least bitterns in a created wetland with use of a small unmanned aircraft. Wetlands. 2014;34(3):527-33.

17. Chabot D, Bird DM. Evaluation of an off-the-shelf unmanned aircraft system for surveying flocks of geese. Waterbirds. 2012;35(1):170-4.

18. Koski WR, Allen T, Ireland D, Buck G, Smith PR, Macrander AM, et al. Evaluation of an unmanned airborne system for monitoring marine mammals. Aquatic Mammals. 2009;35(3):347.

19. Hodgson A, Kelly N, Peel D. Unmanned aerial vehicles (UAVs) for surveying marine fauna: a dugong case study. PloS one. 2013;8(11):e79556.

20. Linchant J, Vermeulen C, Lisein J, Lejeune P, Bouche P. Using drones to count the elephants: a new approach of wildlife inventories. 2013.

21. Vermeulen C, Lejeune P, Lisein J, Sawadogo P, Bouché P. Unmanned aerial survey of elephants. PloS one. 2013;8(2):e54700.

22. Hodgson A, Peel D, Kelly N. Unmanned Aerial Vehicles (UAVs) for surveying marine fauna: assessing detection probability. Ecological Applications. 2017:n/a-n/a. doi: 10.1002/eap.1519.

23. Acevedo-Whitehouse K, Rocha-Gosselin A, Gendron D. A novel non-invasive tool for disease surveillance of free-ranging whales and its relevance to conservation programs. Animal conservation. 2010;13(2):217-25.

24. Schofield G, Katselidis KA, Lilley MKS, Reina RD, Hays GC. Detecting elusive aspects of wildlife ecology using drones: New insights on the mating dynamics and operational sex ratios of sea turtles. Functional Ecology. 2017. doi: 10.1111/1365-2435.12930.

25. Schofield G, Papafitsoros K, Haughey R, Katselidis K. Aerial and underwater surveys reveal temporal variation in cleaning-station use by sea turtles at a temperate breeding area. Marine Ecology Progress Series. 2017;575:153-64.

26. Linchant J, Lisein J, Semeki J, Lejeune P, Vermeulen C. Are unmanned aircraft systems (UASs) the future of wildlife monitoring? A review of accomplishments and challenges. Mammal Review. 2015;45(4):239-52.

27. Colomina I, Molina P. Unmanned aerial systems for photogrammetry and remote sensing: A review. ISPRS Journal of Photogrammetry and Remote Sensing. 2014;92(Supplement C):79-97. doi: https://doi.org/10.1016/j.isprsjprs.2014.02.013.

28. Watts AC, Perry JH, Smith SE, Burgess MA, Wilkinson BE, Szantoi Z, et al. Small unmanned aircraft systems for low-altitude aerial surveys. Journal of Wildlife Management. 2010;74(7):1614-9.

29. Anderson K, Gaston KJ. Lightweight unmanned aerial vehicles will revolutionize spatial ecology. Frontiers in Ecology and the Environment. 2013;11(3):138-46.

30. Rees AF, Avens L, Ballorain K, Bevan E, Broderick AC, Carthy RR, et al. The potential of unmanned aerial systems for sea turtle research and conservation: a review and future directions. Endangered Species Research. 2018. doi: 10.3354/esr00877.

31. Christiansen F, Rojano-Doñate L, Madsen PT, Bejder L. Noise Levels of Multi-Rotor Unmanned Aerial Vehicles with Implications for Potential Underwater Impacts on Marine Mammals. Frontiers in Marine Science. 2016;3(277). doi: 10.3389/fmars.2016.00277.

32. Goebel ME, Perryman WL, Hinke JT, Krause DJ, Hann NA, Gardner S, et al. A small unmanned aerial system for estimating abundance and size of Antarctic predators. Polar Biology. 2015;38(5):619-30. doi: 10.1007/s00300-014-1625-4.

33. Samuel Y, Morreale S, Clark C, Greene C, Richmond M. Underwater, low-frequency noise in a coastal sea turtle habitat. The Journal of the Acoustical Society of America. 2005;117(3):1465-72.

34. DeRuiter SL, Doukara KL. Loggerhead turtles dive in response to airgun sound exposure. Endangered Species Research. 2012;16(1):55-63.

35. Lenhardt M. Sea turtle auditory behavior. The Journal of the Acoustical Society of America. 2002;112(5):2314.

36. Weir CR. Observations of marine turtles in relation to seismic airgun sound off Angola. Marine Turtle Newsletter. 2007;116:17-20.
37. Brown A. Measuring the effect of aircraft noise on sea birds. Environment International. 1990;16(4-6):587-92.

38. Dooling RJ, Popper AN. The effects of highway noise on birds. Sacramento, CA: The California Department of Transportation Division of Environmental Analysis. 2007;74.

39. Martin KJ, Alessi SC, Gaspard JC, Tucker AD, Bauer GB, Mann DA. Underwater hearing in the loggerhead turtle (*Caretta caretta*): a comparison of behavioral and auditory evoked potential audiograms. Journal of experimental Biology. 2012;215(17):3001-9.

40. Piniak WED, Mann DA, Eckert SA, Harms CA. Amphibious hearing in sea turtles. The effects of noise on aquatic life: Springer; 2012. p. 83-7.

41. Higgs D, Brittan-Powell E, Soares D, Souza M, Carr C, Dooling R, et al. Amphibious auditory responses of the American alligator (*Alligator mississipiensis*). Journal of Comparative Physiology A. 2002;188(3):217-23. doi: 10.1007/s00359-002-0296-8.

42. Cabell R, Grosveld F, McSwain R, editors. Measured Noise from Small Unmanned Aerial Vehicles. INTER-NOISE and NOISE-CON Congress and Conference Proceedings; 2016: Institute of Noise Control Engineering.

43. Whiting SD, Guinea ML, editors. The nesting biology of flatback turtles in the tropics: seven years of surveys on Bare Sand Island, Darwin, Northern Territory, Australia. Proceedings of the twenty-third annual symposium on sea turtle biology and conservation; 2006.

44. Whiting AU, Thomson A, Chaloupka M, Limpus CJ. Seasonality, abundance and breeding biology of one of the largest populations of nesting flatback turtles, Natator depressus: Cape Domett, Western Australia. Australian Journal of Zoology. 2009;56(5):297-303.

45. Chatto R. The distribution and status of colonial breeding seabirds in the Northern Territory. Palmerston, N.T. : Parks and Wildlife Commission of the Northern Territory, 2001, 2001 Contract No.: 70.

46. Masini RJ, Sim CB, Simpson CJ, McKenzie NL, Start AN, Burbidge AA, et al. Kimberley. 2009;(May 2009).

47. Kay WR. Movements and home ranges of radio-tracked *Crocodylus porosus* in the Cambridge Gulf region of Western Australia. Wildlife Research. 2005;31(5):495-508.

48. CASA 96/17-Direction - operation of certain unmanned aircraft, F2017L01370 (2017).

49. Whiting SD. Rocky reefs provide foraging habitat for dugongs in the Darwin region of northern Australia. Australian Mammalogy. 2002;24(1):147-50.

50. Limpus CJ, Fien L. A biological review of Australian marine turtles: Environmental Protection Agency; 2009.

51. Guinea ML, Ryan PG, Umback L, Hills L. Nesting seasonality of the Flatback Turtle at Bare Sand Island, Northern Territory, Australia. Mar Turtle Newsl. 1991;52:4-5.

52. Witherington BE. Behavioral Responses of Nesting Sea Turtles to Artificial Lighting. Herpetologica. 1992;48(1):31-9.

53. Christiansen F, Esteban N, Mortimer JA, Dujon AM, Hays GC. Diel and seasonal patterns in activity and home range size of green turtles on their foraging grounds revealed by extended Fastloc-GPS tracking. Marine Biology. 2016;164(1):10. doi: 10.1007/s00227-016-3048-y.

54. Ketten DR, Bartol SM. Functional measures of sea turtle hearing. Woods Hole Oceanographic Inst. Mar. Biology Dept, 2005.

55. Grap NJ, Monzel AS, Kohl T, Bleckmann H. *Crocodylus niloticus* (Crocodilia) is highly sensitive to water surface waves. Zoology. 2015;118(5):320-4. doi: https://doi.org/10.1016/j.zool.2015.03.004.

56. Bierman HS, Carr CE. Sound localization in the alligator. Hearing Research. 2015;329(Supplement C):11-20. doi: https://doi.org/10.1016/j.heares.2015.05.009.

57. Elsey RM, Trosclair III PL. The Use of an Unmanned Aerial Vehicle to Locate Alligator Nests. Southeastern Naturalist. 2016.

58. Evans LJ, Jones TH, Pang K, Saimin S, Goossens B. Spatial Ecology of Estuarine Crocodile (*Crocodylus porosus*) Nesting in a Fragmented Landscape. Sensors. 2016;16(9):1527.

59. Evans I, Jones TH, Pang K, Evans MN, Saimin S, Goossens B. Use of drone technology as a tool for behavioral research: a case study of crocodilian nesting. Herpetological Conservation and Biology. 2015;10(1):90-8.

60. Service QPaW. Standard operating procedure for drone use: Raine Island National Park (Scientific). 2017 June 2017. Report No.

61. Giuliano C, Guinea ML. A recently formed Crested Tern (*Thalasseus bergii*) colony on a sandbank in Fog Bay (Northern Territory), and associated predation. Northern Territory Naturalist. 2015;26:13.

COMPARISON OF BEACH TEMPERATURES IN THE NESTING RANGE OF THE KEMP'S RIDLEY SEA TURTLE IN THE GULF OF MEXICO, MEXICO AND USA

by

E. M. BEVAN, T. WIBBELS, D. SHAVER, J. S. WALKER, F. I. MARTINEZ, J. M. CUEVAS, J. ORTIZ, J. PEÑA, L. SARTI, B.M.Z. NAJERA, AND P. BURCHFIELD

In preparation for *Endangered Species Research*

Format adapted for dissertation

CHAPTER 4

COMPARISON OF BEACH TEMPERATURES IN THE NESTING RANGE OF THE KEMP’S RIDLEY SEA TURTLE IN THE GULF OF MEXICO, MEXICO AND USA

ABSTRACT

Rising environmental temperatures associated with climate change can adversely affect species like sea turtles whose hatchling sex determination is temperature dependent. One hypothetical response of sea turtles to near-future elevated temperatures is a shift in nesting distribution to maintain suitable thermal conditions. Assessing sea turtle responses to climate warming involves evaluating: 1) how temperatures in a habitat will be altered, 2) a species’ capacity to respond to these changes, and 3) whether the response could ultimately mitigate the impacts of a warming environment. Our study evaluated sand temperatures across primary nesting habitat of the critically endangered Kemp’s ridley sea turtle, Lepidochelys kempii, in the western Gulf of Mexico. Most nesting occurs on a 30-km stretch of beach in Tamaulipas, Mexico, but was historically more widely distributed. Applying conservative climate projections, we assessed whether a hypothetical shift in the epicenter of nesting to the northern extent of the present distribution would maintain incubation temperatures suitable to produce a viable ratio of hatchlings of both sexes. Coupling our temperature measurements with known impacts of temperature on the reproductive physiology of the Kemp’s ridley, we predict that the northernmost beaches will support the production of mixed sex ratios in the short-term.

However, given the rapid rate of warming and long generation time for the Kemp's ridley, a northward shift in nesting distribution is unlikely to ultimately mitigate the effects of elevated temperatures on hatchling sex ratios and mortality. Given its single, primary nesting location, the Kemp's ridley provides insights on developing strategies for the survival of thermally-sensitive species in a warming world.

INTRODUCTION

Large-scale changes in climatic patterns influence an array of taxa across diverse habitats and are driving observed changes in species phenology, behavior, and distribution (Walther et al. 2002). Ectothermic species are particularly vulnerable to the impacts of climate change and understanding historic and current responses of thermally-sensitive species to environmental changes is key for anticipating how such species will respond in the near-future (within the next 100 years), predicting extinction risk, and ensuring that effective conservation management strategies are applied (Walther et al. 2002, Parmesan 2006, Williams et al. 2008, Telemeco et al. 2013, Keith et al. 2014). Responses to climate change, however, often differ across taxa, confounding projections of population trends and emphasizing the need for studies evaluating species-specific responses at regional scales (Parmesan 2006, Weishampel et al. 2010, Pike 2014). Contemporary climate change is anticipated to directly and indirectly affect various life history stages of thermally-sensitive species. Sea turtles are especially vulnerable through loss of nesting habitat due to rising sea levels and intensified beach erosion, skewed sex ratios due to temperature-dependent sex determination (TSD), altered nesting phenology, and increases in nest and hatchling mortality (Poloczanska et al. 1973, Hawkes et al.

2007b, 2009, Fuentes & Hawkes 2011, Laloe et al. 2016). The ability to avoid stressful thermal conditions in sea turtles is most restricted in ontogenetic stages where movement is limited such as during embryonic development (Godley et al. 2001, Hawkes et al. 2007a, 2007b, Telemeco et al. 2009, 2013). Elevated incubation temperatures at nesting beaches can impair embryonic development at a constant incubation temperature above 33-35˚C (Ackerman 1997), and in studies when temperatures fluctuate above 35˚C, hatching success is reduced in some species (Howard et al. 2014). While exposure to brief periods of temperatures above 35˚C during incubation may not reduce hatching success, the impacts of prolonged periods of incubation spent above 35˚C are not well understood and may reduce hatching success (Howard et al. 2014). However, these specific findings are not based on an investigation of thermal limits for all sea turtle species and interspecific differences in thermal tolerances are likely to exist (Howard et al. 2014). In fact, relatively high hatching success (above 77%) has been reported for Kemp’s ridley, Lepidochelys kempii, nests with incubation temperatures exceeding 35˚C, particularly during the last third of the incubation period when metabolic heat rises, although incubation temperatures reaching 38.0-40.2˚C have been associated with higher rates of embryonic mortality (Shaver & Caillouet 2015, Shaver & Chaney 1989, Shaver et al. 1988). The Kemp’s ridley may have a higher lethal temperature threshold due to a shallow average nest depth, greater daily nest temperature fluctuation, and higher pivotal temperature compared to other sea turtle species (Howard et al. 2014, Caillouet et al. 2015b, Shaver et al. 1988, Shaver & Chaney 1989). Thus, the relationship between hatching success and duration of time during incubation spent above 35˚C may not apply to Kemp’s ridleys considering the thermal tolerance of this species has yet to be evaluated.

Sea turtles have experienced large-scale environmental changes in the past and have responded with shifts in phenology, and changes in behavior and population dynamics to maintain favorable thermal conditions in habitats that span their life history (Weishampel et al. 2004, Hawkes et al. 2007b, Mazaris et al. 2008, Pike 2009). However, given the rapidity of anthropogenic climate warming, whether sea turtles can adapt to abrupt large-scale ecosystem changes remains unknown (Poloczanska et al. 1973, Walther et al. 2002, Parmesan 2006, Fuentes & Hawkes 2011). As nest incubation temperatures continue to rise they may soon approach conditions that ultimately become unsuitable for successful hatchling production. If sea turtles lack the physiological or behavioral plasticity to rapidly respond, wildlife resource managers will be faced with identifying alternative strategies including active nest management (e.g. egg hatcheries, shading nests, watering nests) and artificially shifting nest distributions to mitigate the impacts of climate warming. To evaluate the plasticity of different species of sea turtles to respond to climate warming, studies are especially needed in species with restricted distributions, such as Kemp’s ridley, to better understand whether suitable nesting habitat will remain available under predicted near-future climate change.

The Kemp’s ridley sea turtle is distributed throughout the Gulf of Mexico and along the Atlantic coast of the United States (Pritchard and Marquez 1973, Marquez 1994). The species occurs in the coastal zone within approximately 20 km from the coast, and at depths less than approximately 50 m (Chavez et al. 1968, Marquez 1994, Shaver et al. 2016). Between 1990 and 2009, the Kemp’s ridley exhibited an exponential increase as it rebounded from near-extinction due to factors including human harvesting in the mid 1980's (Heppell et al. 2007, Gallaway et al. 2013, Caillouet 2014). In 2010, a drastic decline and unexpected deviation from that recovery trajectory occurred and following 2010, the annual number of nests has fluctuated around 20,000 nests each nesting season (Gallaway et al. 2013, 2015). The basis for this perturbation remains unclear (Caillouet 2011, 2014, Gallaway et al. 2013, Caillouet et al. 2015a). Approximately 96% of Kemp's ridley nesting occurs along a 196 km stretch of beach in Tamaulipas, Mexico, and about 60% of this nesting is concentrated at a single, roughly 30 km stretch of remote beach at Rancho Nuevo, Tamaulipas, Mexico. Historic documentation suggests that the geographic range of nesting in this species was once widely distributed throughout the western Gulf of Mexico, prior to its near extinction in the mid 1980's (Marquez 1994, Shaver et al. 2016, TEWG 2000).

As air temperatures at current nesting beaches increase and nesting habitat is lost due to climate change induced sea level rise and coastal erosion, one hypothesized response of the Kemp's ridley could be a range shift to exploit new, thermally suitable nesting habitats, although a variety of factors may confound this option (Hawkes et al. 2009). The ability of sea turtles to adapt to changing environmental conditions may depend on taxon specific variables, with species demonstrating lower site fidelity and greater behavioral flexibility potentially reducing their extinction risk under conditions of habitat loss (Pike & Stiner 2007, Kamel & Mrosovsky 2005, Mrosovsky 2006). Unique among sea turtles, the Kemp's ridley exhibits comparatively high fidelity to a single region of beach in the western Gulf of Mexico (Pritchard and Marquez 1973, Marquez 1994, Burchfield 2014). This limited geographic distribution increases the vulnerability of this federally endangered species and reduces its options for adapting to the impacts of rapid anthropogenic climate change.

A key concern regarding rapid climate warming and sea turtles is that warming directly influences embryonic development through the process of temperature-dependent sex determination (TSD), characterized by the sex of the embryo being determined by the incubation temperature of the nest during the middle third of the incubation period (Mrosovsky 1980, 1994, Wibbels 2003). Although many aspects of the sea turtle life history are thermally-sensitive (e.g. timing of reproductive activities, foraging abilities, metabolism), TSD can significantly influence reproductive output, reproductive success, and ultimately, the recovery of a thermally-sensitive endangered species (Coyne 2000, Wibbels 2007). Among sea turtles, cooler nest temperatures produce more males, while warmer temperatures result in more females (Mrosovsky 1980). The range over which 100% male hatchling production shifts to 100% female is termed the transitional range of temperatures (TRT), with the temperature resulting in a 1:1 M:F sex ratio known as the pivotal temperature (Yntema & Mrosovsky 1979). For the Kemp’s ridley, specifically, the TRT ranges from approximately 29.0 to 32.5˚C, with a 1:1 M:F sex ratio estimated to occur when the temperature during the middle third of the incubation period is approximately 29.9–30.2˚C (Shaver et al. 1988, Mrosovsky & Pieau 1991, Mrosovsky 1994, Godfrey & Mrosovsky 1999, LeBlanc et al. 2012). The TRT for sea turtles in general is rather narrow (1-3˚C) suggesting that relatively minor changes in global air temperatures could significantly alter hatchling sex ratios. Climate models generated by the Intergovernmental Panel on Climate Change (IPCC) project an increase in global temperature of 0.3 to 4.8°C by the year 2100 (Pachauri et al. 2014). Rising global temperatures could lead to extreme female bias and male-limited populations (Wibbels 2003, Fuentes et al. 2010, Fuentes & Hawkes 2011, McNeill et al. 2016, Laloë et al. 2016, Marcovaldi et al. 2016).

Near-future anthropogenic climate change has implications for a variety of taxa across diverse habitats and can alter the dynamics of entire ecosystems (Walther et al. 2002). In the process, the ability of thermally-sensitive species such as sea turtles to demonstrate plasticity and ultimately adapt to rapid environmental changes through behavioral and/or physiological responses remains uncertain. Thus, it is necessary to identify potential strategies to mitigate the impacts of climate change and best avoid the extinction of already endangered species. As highly migratory species, a possible response of sea turtles to a warming environment is a shift in nesting range and distribution. Studies are needed that evaluate the availability of alternative beaches that could provide temperature-suitable nesting habitat for sea turtles to protect and manage those future critical habitats.

The present study compares beach thermal profiles across most of the expanded historic nesting range of the critically endangered Kemp’s ridley sea turtle to evaluate the availability of thermally-suitable nesting habitat for this species under predicted near-future environmental conditions. Although relatively minimal Kemp’s ridley nesting occurs on beaches to the south of those included in the present study at Veracruz, Mexico, beach temperatures from Veracruz were not included in the current analysis. The single, primary nesting location in the western Gulf of Mexico, makes the Kemp’s ridley a model species to evaluate the implications of near-future anthropogenic climate change on the life history and survival of an entire, thermally-sensitive, endangered species.

MATERIALS AND METHODS

Field Protocols

A total of 130–140 data loggers (Onset HOBO Pendant®) were buried at a depth of 35 cm each year (2014–2017) on sandy beaches every 300 m at La Pesca (LP), Tepehuajes (TEP), Rancho Nuevo (RN), Barra Del Tordo (BT), Altamira (A), and Miramar (MIR) beaches in Tamaulipas, Mexico. Data loggers were buried at a depth of 35 cm each year (2014–2016) every 800 m at Padre Island National Seashore (PAIS) and South Padre Island (SPI), Texas, (Figure 1). The depth of the loggers chosen coincides with the mean nest depth of the Kemp ridley (Pritchard and Marquez 1973). Data loggers had an accuracy of ±0.3°C and each was calibrated prior to the beginning of a given nesting season in the laboratory at the University of Alabama at Birmingham (UAB) for deployment in Mexico or in the laboratory at PAIS for deployment in Texas. The timing of when a given data logger was buried in the sand varied by the beach and year of the study, but on average data loggers were placed prior to the beginning of the annual nesting season for Kemp's ridley (between March and April). Data loggers were removed at the end of the season after all nests had emerged (August–September). Two data loggers each were buried along transects perpendicular to the beach. The positioning of the two data loggers on each transect were such that one was buried between the base of the dune and the seaward facing slope of the primary dune (the region where most nesting occurred, position 3), and the other buried on the seaward beach in front of the dune (position 2) (Marquez 1994). Only data loggers located in the zone where most nesting occurred, position 3, were used for analysis. For comparative purposes, only data from 11 April to 20 August in each of the years, 2014 – 2017 were analyzed, a time period that was selected so as to encompass the primary peak nesting season for the Kemp's ridley (Pritchard & Marquez 1973).

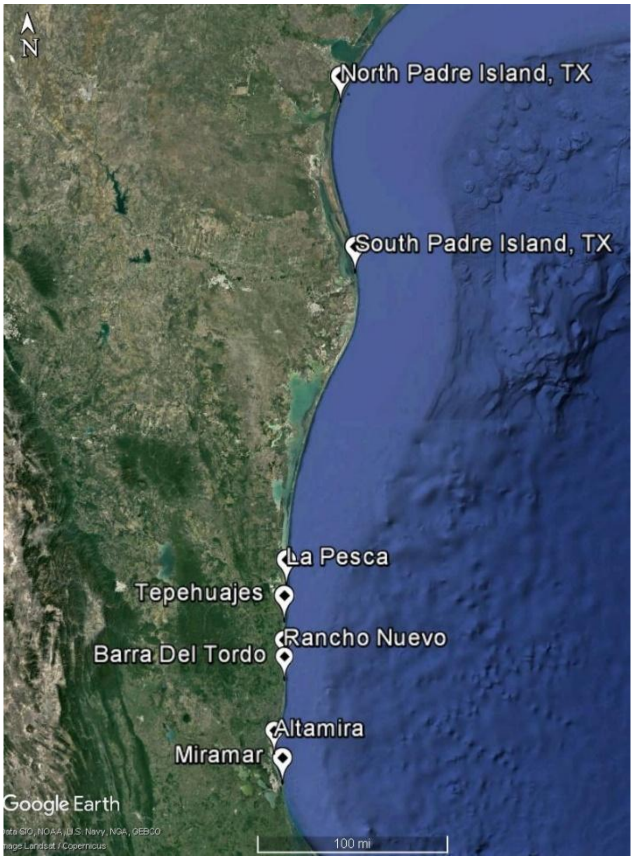

Figure 1. Study sites across Kemp's ridley primary nesting habitat in the State of Tamaulipas, Mexico, as well as Padre Island, Texas. Locations represent beaches on which data loggers were buried to a depth of 35 cm to record sand temperatures throughout the Kemp ridley nesting season for all locations in Mexico and Texas from 2014 – 2016, and for only locations in Mexico used in the present study for the 2017 nesting season.

Data Analysis

Data loggers were set to record ambient sand temperature every hour throughout the duration of the 5-month nesting and hatching season. Following data logger recovery and transportation to UAB or PAIS the data were downloaded to a computer. Hourly sand temperatures for each data logger were averaged to generate a daily average (±SD) temperature. After testing the data for normality and identifying and removing statistically significant outliers from the data set, daily sand temperatures from all data loggers were analyzed using a repeated measures random effects model with “data logger” as a random effect in the nlme package in R (Pinheiro et al. 2009). A post-HOC Tukey HSD comparison test was used to compare daily and seasonal mean temperatures among the different beaches and group the beaches according to similarity for each year.

RESULTS

Data analysis indicates that Kemp ridley mean nesting beach temperatures during the period of the nesting season used in this study (11 April – 20 August) were significantly different from each other in each of the three years where beaches in Tamaulipas, Mexico and Padre Island, Texas, USA were examined (2014, 2015, 2016) (ANOVA: 2014 – df = 7, F = 42.95, $p<0.0001$; 2015 – df = 8, F = 131.82, $p < 0.0001$; 2016 – df = 7, F = 107.67, $p < 0.0001$). In the 2017 nesting season only temperatures at beaches in Mexico were examined and results indicated that mean nesting beach temperatures for the nesting season were significantly different from each other (ANOVA, df = 5, F = 10.5, $p < 0.0001$) (Figure 1).

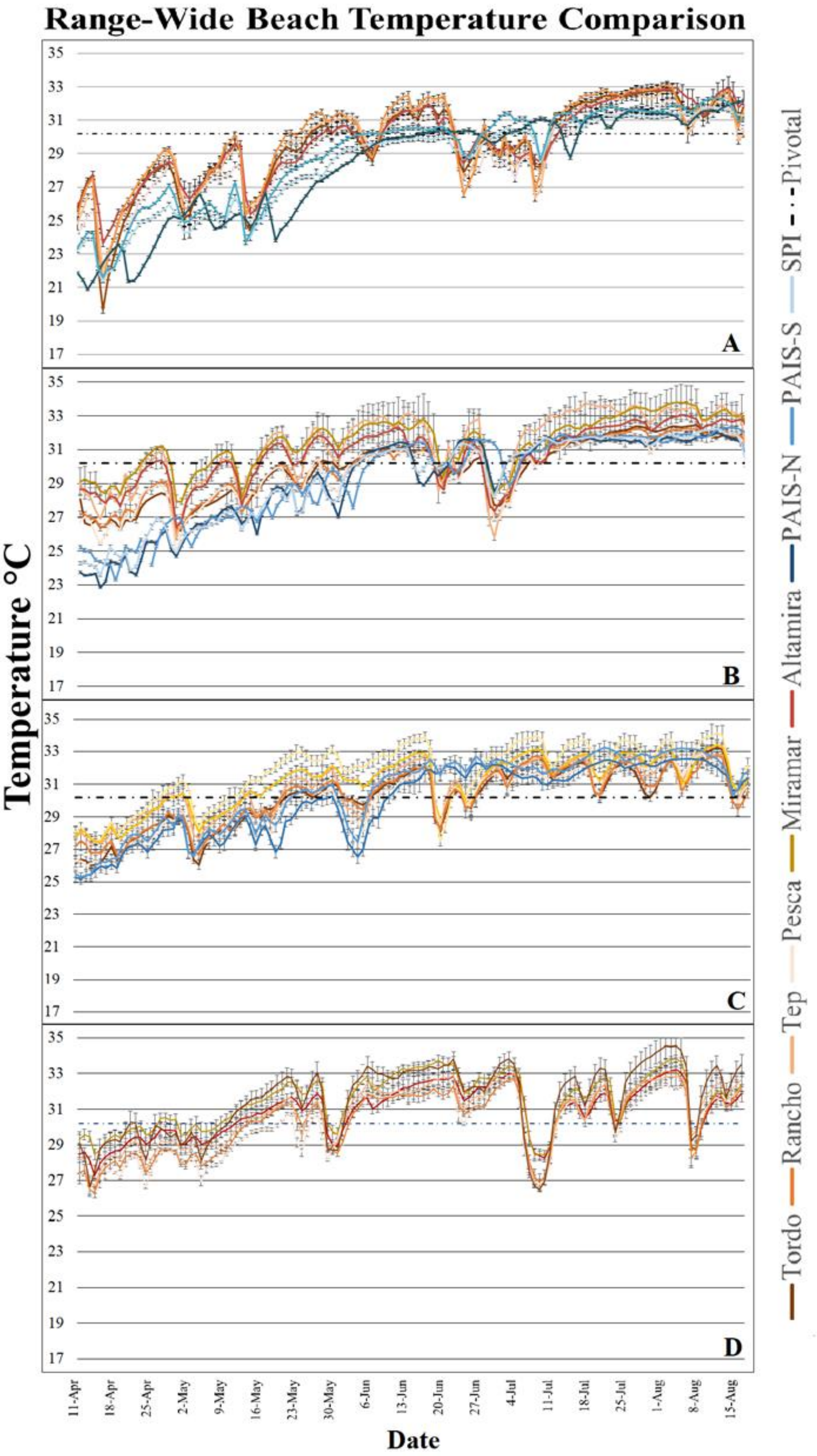
Range-Wide Beach Temperature Comparison
Temperature °C
35
33
31
29
27
25
23
21
19
17
A
B
C
D
11-Apr
18-Apr
25-Apr
2-May
9-May
16-May
23-May
30-May
6-Jun
13-Jun
20-Jun
27-Jun
4-Jul
11-Jul
18-Jul
25-Jul
1-Aug
8-Aug
15-Aug
Date
Tordo
Rancho
Tep
Pesca
Miramar
Altamira
PAIS-N
PAIS-S
SPI
Pivotal

Figure 2. Average daily sand temperatures (±SD) recorded at study locations throughout the Kemp's ridley nesting range in Tamaulipas, Mexico, and Padre Island, Texas during a) 2014, b) 2015, c) 2016. Mean daily beach temperatures recorded only at study locations in Mexico during the 2017 nesting season are represented in graph d. The dashed line represents the pivotal temperature that results in an approximate 1F:1M hatchling sex ratio in *Lepidochelys kempii*.

Comparing the mean nesting beach temperatures recorded during the nesting season from 2014–2016 at study sites in Texas, USA, and Mexico, the largest difference between the highest and lowest mean beach temperature was recorded during the 2015 nesting season at 2.16˚C (Table 1). Comparing mean beach temperatures recorded at study sites only in Mexico, the greatest difference between the maximum and minimum mean beach temperature was 1.67˚C during the 2015 nesting season. The highest mean beach temperature for a nesting season observed during this study was 31.55±1.98˚C recorded at MIR beach in 2016 (Table 1).

Table 1. Minimum and maximum nesting season mean beach temperatures recorded at study sites across the Kemp's ridley, *Lepidochelys kempii*, nesting range in 2014–2016 when beach locations in the State of Tamaulipas, Mexico, and Padre Island, Texas, USA, were examined. Minimum and maximum mean nesting beach temperatures in the 2017 nesting season are given for only beach locations in Mexico that were examined. Northern Padre Island National Seashore (NPAIS), Rancho Nuevo (RN), Miramar (MIR), La Pesca (LP), and Barra Del Tordo (BT).

Year	Min Temp (Location) (˚C)	Max Temp (Location) (˚C)	Difference (˚C)
2014	27.36±3.88˚C (NPAIS)	29.29±2.92˚C (RN)	1.93˚C
2015	29.30±2.65˚C (NPAIS)	31.46±1.57˚C (MIR)	2.16˚C
2016	29.83±2.44˚C (NPAIS)	31.55±1.98˚C (MIR)	1.72˚C
2017	30.1918±1.85˚C (LP)	31.4957±2.14˚C (BT)	1.3˚C

Post-hoc Tukey HSD comparisons of mean beach temperatures at study locations in Texas and Mexico during the 2014–2016 nesting seasons and at study locations only in Mexico during the 2017 nesting season grouped mean beach temperatures into 2–4 temperature subsets depending on the year (Table 2).

Table 2. Tukey HSD comparisons of mean beach temperatures (±SD) recorded from 11-April to 20-Aug from 2014–2016 at study sites throughout the Kemp's ridley, *Lepidochelys kempii*, nesting range in Tamaulipas, Mexico and Padre Island, Texas, USA. Tukey HSD analysis of mean beach temperatures during the 2017 nesting season represent temperatures recorded only at study sites in Mexico. Northern Padre Island National Seashore (NPAIS), southern Padre Island National Seashore (SPAIS), South Padre Island (SPI), La Pesca (LP), Barra Del Tordo (BT), Tepehuajes (TEP), Altamira (A), and Rancho Nuevo (RN).

Year	Beach	Cool	Mid-Temp	Mid-Temp	Warm
2014	NPAIS	27.36 (±3.88)			
	SPI	27.64 (±3.43)			
	SPAIS	28.11 (±3.53)	28.11 (±3.53)		
	LP	28.37 (±2.83)	28.37 (±2.83)		28.37 (±2.83)
	BT		28.99 (±2.96)		28.99 (±2.96)
	TEP		29.02 (±2.82)		29.02 (±2.82)
	A		29.13 (±2.69)		29.13 (±2.69)
	RN				29.28 (±2.92)
2015	NPAIS	29.29 (±2.65)			
	SPI	29.39 (±2.52)			
	SPAIS	29.50 (±2.52)			
	LP	29.79 (±1.83)			
	BT	29.96 (±1.82)			
	RN	30.00 (±1.76)			
	A				30.83 (±1.67)
	TEP				31.30 (±2.04)
	MIR				31.46 (±1.57)
2016	NPAIS	29.83 (±2.44)			
	LP	29.96 (±2.12)	29.96 (±2.12)		

	BT	30.04 (±2.16)	30.04 (±2.16)		
	RN	30.14 (±1.96)	30.14 (±1.96)		
	SPAIS	30.42 (±2.44)	30.42 (±2.44)	30.42 (±2.44)	
	TEP		30.65 (±1.79)	30.65 (±1.79)	
	A			30.99 (±1.77)	30.99 (±1.77)
	MIR				31.55 (±1.98)
2017	LP	30.19 (±1.85)			
	RN	30.37 (±2.00)			
	TEP		30.72 (±1.79)		
	A		30.87 (±1.68)		
	MIR				31.48 (±1.67)
	BT				31.50 (±2.14)

Collectively, the results from the current study indicate that mean nesting beach temperatures throughout Mexico and Texas were statistically different from each other throughout the 2014–2016 nesting seasons. Similarly, mean nesting beach temperatures at study sites in Mexico were statistically different from each other in the 2017 nesting season. In all four years (2014–2017) of the present study MIR beach in Mexico was consistently grouped among the nesting beaches with the highest mean beach temperatures, while LP beach in Mexico and NPAIS in Texas, USA, were consistently grouped among the lowest temperature nesting beaches in each year.

DISCUSSION

Our findings suggest that northern beaches in Texas and Mexico, such as LP, SPI, and PAIS, could provide cooler natural incubation temperatures under a predicted near future climate warming scenario than beaches to the south, where the majority of Kemp’s ridley nesting currently occurs. These northern beaches could therefore provide alternative, suitable thermal nesting habitat for Kemp ridley sea turtles and should receive priority when considering their conservation. Mean nesting beach temperatures observed for the 11 April – 20 August period during each nesting season at the northern end of PAIS and LP fell below the temperature producing a 1:1 M:F sex ratio, approximately 30˚C, Wibbels (2003)) during some nesting seasons, though temperatures within nests would be higher due to metabolic heating. It is important to note that the results in the present study document the mean sand temperatures at 35 cm depth for these beaches during the 11April – 20 August period. Nests laid in the early portion of this period will experience incubation temperatures cooler than the mean, while nests laid later in the warmer portion of this period will experience middle third temperatures that are higher than the mean for that beach generated in our analyses. Though RN and BT had mean beach temperatures that reached this cooler range during some years as well, applying a conservative climate warming scenario of an increase in beach temperatures of 1–2˚C by the year 2100 (Pachauri et al. 2014), beach temperatures could increase to at least an estimated mean of 30˚C at PAIS. Under this scenario, temperatures on cooler beaches (LP, SPI, and PAIS) could still favor the production of mixed hatchling sex ratios, with at least some production of male hatchlings for the species.

The present study indicates that a relatively narrow range of nesting beach temperatures occur over the nesting season throughout the nesting range of the Kemp’s ridley sea turtle, yet critical biological events, such as the determination of hatchling sex occur within this narrow thermal window (Wibbels 2003). This narrow biological range could be disadvantageous to the ultimate survival of the Kemp’s ridley and other sea turtle species considering that conservative IPCC climate models project increases in environmental temperatures of approximately 1°C (Pachauri et al. 2014). Though increases in surface temperatures will not cause equivalent and simultaneous increases in sand incubation temperatures, due to protection that incubation depth provides, even small increases in incubation temperatures can skew hatchling sex ratios and potentially lead to a severely male-limited population (Janzen 1994, Hawkes et al. 2007b). Minor increases in environmental temperatures (~1°C) can also alter the timing of migration and foraging activities in adults, and adversely impact the timing and success of Kemp's ridley hatchlings (Weishampel et al. 2004, Weishampel et al. 2010, Fuentes & Hawkes 2011). Further, these changes could disrupt the timing of linkages between the movements of temperature-sensitive species and the availability of critical resources such as prey (Walther et al. 2002, Parmesan 2006, Schwanz & Janzen 2008). Developing effective management strategies to ensure the survival and continued recovery of an endangered species in light of anthropogenic climate change necessitates a better understanding of how that species will respond to these changes. The present study demonstrates that the Kemp's ridley provides a rare opportunity to investigate the impacts of rapid thermal shifts on the biology and ecology of the species due to a uniquely limited geographic nesting range and a temperature-sensitive reproductive physiology. Our study also emphasizes that for some species opportunities to adapt to long-term anthropogenic environmental changes may be limited.

One anticipated response of sea turtles to rapid climate change is a shift in their geographic distribution to maintain a suitable thermal habitat (Walther et al. 2002). We observed several distinct trends in nesting beach temperatures at primary nesting beaches for the Kemp’s ridley near RN, Mexico and beaches that currently experience relatively minor nesting levels. Beaches in Mexico and Texas with fewer annual nests represent some areas for potential range expansion for this species. Altamira and MIR beaches are located closest to the equator among the beaches thermally monitored in this study (latitude 22.494056˚ and 22.344267˚, respectively). As such, A and MIR beaches are among the warmest locations we examined given the strong inverse correlation between latitude and rising environmental temperatures (Rind 1998, Hays et al. 2001). At the northernmost extent of the beaches thermally monitored in this study, mean nesting beach temperatures at LP (monitored from 2014 – 2017) and PAIS (monitored from 2014 – 2016) provide additional support for this pattern and were consistently the lowest of the beaches monitored in the current study. However, certain beaches thermally monitored in our study were inconsistent with a strict latitudinal gradient in sand temperatures. There was no consistent latitudinal pattern in temperature for the beaches at RN, TEP, and BT with respect to the other beaches in Mexico. These exceptions suggest that the patterns of seasonal nesting temperatures recorded on these beaches are more influenced by local factors such as weather (Nagy et al. 2016), topographical features (e.g. beach width, sand albedo, Hays et al. (1995), Hays et al. (2003)), coastal ocean currents (Hawkes et al. 2009), or vegetation type and coverage, Morreale et al. (1982), than by latitude. It is also possible that the geographic distances separating the beaches of TEP, RN, and BT are not sufficient to allow detection of large-scale trends in beach temperature driven by latitude. The maximum distance separating TEP and BT is only 50 km. In contrast, the beaches of LP and MIR, separated by a distance nearly three times greater than TEP and BT, exhibit mean beach temperatures consistent with a latitudinal gradient.

Despite the potential of northern beaches to offer respite under a near-future climate change scenario and support the production of at least some proportion of male hatchlings for each nesting season, the lengthy age to maturity (approximately 11 years, Caillouet et al. 2011) and fidelity of this species to southern beaches in its nesting range diminishes the likelihood that a natural shift in nesting distribution will occur rapidly enough to compensate for the impacts of anthropogenic climate change (Poloczanska et al. 2009). A significant geographic shift in the concentration of nesting (only approximately 10% of annual nesting currently occurs on northern beaches in Texas and Mexico, Peña pers. comm.) would need to occur to naturally compensate for increasing nesting beach temperatures in the western Gulf of Mexico. Further, beaches in Texas are farther removed from the current epicenter of nesting in this species. As such, an even greater shift in primary nesting beaches would be necessary for this species to significantly buffer the negative reproductive consequences of anthropogenic climate warming and such a dramatic population level relocation seems unlikely.

Though unlikely, a shift in the current nesting distribution for the Kemps ridley could mitigate or avoid potentially lethal temperatures for hatchling sea turtles on nesting beaches. Although northern beaches in the Kemp’s ridley’s current nesting range could provide short-term respite from the impacts of climate warming, most nesting (approximately 90% of total annual nests) for this species currently occurs on warmer beaches further south in Mexico, resulting in an overall female-biased hatchling sex ratio (approximately 3.4F:1M) that has occurred since the initiation of Mexico-U.S. bi-national conservation efforts in 1978 (Marquez, 1994; Geis et al 2002; Eich 2009; Bevan 2013). It is possible that under recent and current climatic conditions, a female-biased hatchling sex ratio has facilitated the growth and recovery of the Kemp’s ridley sea turtle. Population growth trajectory models indicate that a hatchling sex ratio of approximately 3F:1M is optimal for population recovery in sea turtles (Coyne 2000). Yet, under a conservative near-future climate warming scenario, beach temperatures in Mexico throughout the southern portion of the Kemp’s ridley’s nesting range may reach temperatures that could be detrimental to hatching success, yield extreme female bias, or even result in nearly all female hatchlings. Although the increase in female hatchlings could initially result in greater reproductive output and population growth, decreasing numbers of male turtles would eventually lead to an increase in infertility throughout the population (Jensen et al. 2018). Elevated incubation temperatures could also result in increased pre- and post-hatch mortality, as has been suggested in some species of sea turtle (Fuentes & Porter 2013). As an example, mean sand temperatures at 35-cm depth could increase to a high of approximately 34˚C at MIR beach in Mexico, and this temperature does not account for the additional increase in incubation temperatures due to metabolic heating. These sand temperatures would approach the reported upper thermal limit for embryonic development in some species, such as green and loggerhead sea turtles (above approximately 33–35°C, reviewed by Howard et al. (2014)) without accounting for metabolic heating that would further elevate temperatures within nests. This scenario could result in reduced hatching success in nests (Ackerman 1997, Howard et al. 2014), though the impacts of such higher temperatures on Kemp’s ridley nests have not been evaluated (Howard et al. 2014). Additionally, it is important to note that the mean nesting beach temperatures reported in the current study represent a range of temperatures observed at each study location over a period that encompasses nearly the entire nesting and hatching season for each year. Thus, individual nest incubation periods would occur over only a portion of the entire nesting and hatching period used in our study. The temperatures experienced by eggs within nests with temperature-sensitive periods of incubation that occur during the warmest portion of the nesting season could experience prolonged exposure to the highest end of each temperature range (e.g. nests could currently experience mean temperatures as high as approximately 36˚C at MIR beach), a situation that could be further exacerbated by metabolic heating leading into the later third of incubation (Howard et al. 2014). With the additional metabolic heating, high late-season sand temperatures could cause increased rates of pre- and post-hatch mortality, yet the Kemp's ridley may be more tolerant to the higher sand incubation temperatures projected throughout most of its nesting range due to climate change, which could help to mitigate the consequences of a warming environment. Regardless, though many factors influence nesting beach temperatures, as incubation temperatures continue to warm, nesting seasons that are cool enough to produce mixed sex ratios are likely to become scarce and we can expect the yearly sex ratios generated at relatively cooler northern beaches, such as LP and PAIS to become more female-biased under conservative climate projections for the near future.

The IPCC has also generated climate models projecting greater increases in global mean surface temperature of 2.6 to 4.8˚C by the year 2100 (Pachauri et al. 2014), though thermal energy attenuates with depth during transmission from air to sand which can dampen extreme fluctuations in air temperatures (Hays et al. 2002). Thus, an extreme increase in surface/air temperature of 4.8˚C would not directly and immediately translate to an increase in sand temperature at nest depth of the same magnitude. Yet, to provide insight on the impacts of an extreme increase in sand incubation temperatures, we evaluated the results from the present study in the context of a hypothetical increase in sand temperatures of approximately 4˚C. An end-of-century increase in sand temperatures of up to 4˚C due to anthropogenic climate warming could increase mean nesting beach temperatures on north PAIS to an estimated 31˚C, which would favor the overall production of nearly all female hatchlings given current physiological constraints. It is possible that despite statistically different mean sand temperatures between Mexico and Texas beaches, these differences are not great enough under an extreme warming scenario to ultimately compensate for the impacts of rising sand and environmental temperatures associated with a warming climate and could render the northern beaches in our study area such as PAIS and LP beach no longer capable of supporting of the critical production of at least some male hatchlings for the Kemp's ridley.

Conservation strategies to address rapid anthropogenic environmental warming throughout the nesting range for the Kemp's ridley include identifying and protecting future critical nesting habitat, as well as human intervention to manipulate nest incubation conditions (Jourdan & Fuentes 2015). Possible strategies involving human intervention range from relocating nests from suboptimal beaches to hatcheries or artificial incubators such as polystyrene boxes, shading, sprinkling with water or using shade from native vegetation to cool the sand incubation temperatures of in situ nests (Kamel & Mrosovsky 2006, Fuentes et al. 2012). Although these procedures (shading and watering) have been used successfully for decades to protect Kemp's ridley eggs and to form a secondary nesting colony (Shaver & Caillouet 2015), the effectiveness of these approaches on mitigating the impacts of increasing sand temperatures on sea turtle nest incubation conditions has not been adequately quantified (Jourdan & Fuentes 2015). Sprinkling water on sand at night has been shown to decrease sand temperature by approximately 1–3°C for sand representative of the beaches near Townsville, Australia, but the effectiveness of this strategy likely depends on the specific beach environment (Jourdan & Fuentes 2015).

Nest management strategies currently used in Tamaulipas, Mexico involve relocating most Kemp's ridley nests to nearby hatcheries throughout the nesting season and moderating nest incubation conditions by using mesh shading across the top of the hatchery and sprinkling the sand with water (Peña, pers. comm.). To protect nests from predator or anthropogenic disturbance Kemp's ridley nests laid at PAIS are relocated to either egg hatcheries or facilities that allow optimal incubation conditions to be closely monitored and maintained (LeBlanc et al. 2012). Since maintaining optimal hatchling sex ratios and high hatching success at primary nesting beaches in Mexico and Texas also currently necessitates the use of these protocols, it is possible that the efficacy of these methods alone may be diminished given the higher sand temperatures anticipated by the end of the century.

Considering alternative future strategies, annually relocating more than approximately 24,000 Kemp's ridley nests (24,591 total registered Kemp's ridley nests in the 2017 season, Peña pers. comm.) from warmer beaches in the nesting range to relatively cooler beaches may not be financially or logistically feasible or sustainable through the end of the century (Fuentes & Hawkes 2011). However, it is possible that a subset of nests could be relocated from beaches in Mexico to artificial incubation facilities or reburied on thermally-suitable beaches at the northern extent of the Kemp's ridley nesting range. Artificial incubation facilities, such as those currently used at PAIS, can reliably result in hatching success rates that are comparable to and higher than those for in situ nests (Shaver & Wibbels 2003; Shaver & Caillouet 2015) when movement-induced mortality is not a factor (Eckert & Eckert, 1990). This approach would ensure the survival of at least a portion of the total annual nests for the species and the continued production of a portion of male hatchlings for the species under a near-future climate change scenario.

Relocating Kemp's ridley nests from beaches in Mexico to incubation facilities in Texas is a method that has been previously used from 1978 – 1988 as part of the Kemp's Ridley Restoration and Enhancement Program (KRREP) (Shaver & Caillouet 2015). One of the goals of the KRREP was to reintroduce the species to form a secondary Kemp's ridley nesting colony on PAIS (Caillouet et al. 2015b, Shaver & Caillouet 2015). Relying on the natal homing instinct of all sea turtles, it was anticipated that the turtles would eventually return to PAIS beaches to nest once reaching sexual maturity (Shaver & Wibbels 2007). The KRREP enhanced the numbers of turtles nesting in Texas, but those from the translocated eggs are only a small portion of the secondary nesting colony that is expanding at PAIS, where 219 nests were recorded during 2017, which nears the number found at some of the smaller Kemp's ridley nesting beaches in Mexico (Shaver & Caillouet Jr. 2015). However, relocating a portion of Kemp's ridley nests from primary beaches in Mexico to artificial incubation facilities or alternative nesting beaches in Texas represents a reliable protocol that, if necessary, could be integrated into the larger context of mitigating the impacts of a warming nesting range for this species.

In summary, the range of collective temperatures experienced at beaches throughout the nesting distribution for the Kemp’s ridley sea turtle are significantly different from each other, with some beaches at the northernmost extent of this range providing incubation temperatures that could proximally mitigate increasing environmental temperatures due to end-of-century climate warming. However, these beaches are unlikely to ultimately provide long-term temperature-suitable nesting sites for the Kemp’s ridley given the behavioral, physiological, and evolutionary thermal constraints of the species. Additionally, the differences in mean beach temperatures across the nesting range may not be sufficient to support a healthy mixed hatchling sex ratio for the Kemp’s ridley under extreme climate change scenarios. Considering nearly the entire species nests in a relatively limited geographic range, the Kemp’s ridley represents a species with limited options for adapting to climate change. As such, the Kemp’s ridley is a sentinel species by which to evaluate the impacts of near-future, anthropogenic climate change on the survival of a thermally-sensitive species of sea turtle in the western Gulf of Mexico.

ACKNOWLEDGMENTS

This research was conducted as part of the Binational Kemp’s Ridley Recovery Program which is coordinated in Mexico by the General Directorate for Wildlife of the Secretariat of the Environment and Natural Resources (SEMARNAT), the National Commission of Natural Protected Areas (CONANP), and the Tamaulipas State Wildlife Agency (SEDUMA). The Binational Recovery Program includes the U.S. agencies U.S. Fish and Wildlife Service, NOAA Fisheries, National Park Service, and Texas Parks and

Wildlife Department. Texas sand temperature data was provided by the National Park Service at Padre Island National Seashore. Special thanks to the pivotal team of biologists who buried and retrieved data loggers each nesting season along the beaches they monitored throughout Tamaulipas and Padre Island, and Thomas Backof of the National Park Service, who managed and processed data retrieved from dataloggers they installed on PAIS and Sea Turtle, Inc. installed on SPI. Funding was provided, in part, by the UAB Department of Biology, the National Park Service, and the NOAA Fisheries and the U.S. Fish and Wildlife Service through the Marine Turtle Conservation Fund.

LITERATURE CITED

Ackerman RA (1997) The nest environment and the embryonic development of sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles, Vol 1**.** CRC Press, Boca Raton, p 83—106

Bevan E (2013) Implications of hatchling sex ratios and survival in the recovery program for the endangered Kemp's ridley sea turtle. Masters Thesis, University of Alabama at Birmingham, Birmingham, AL

Burchfield PM (2014) Report on the Mexico/United States of America population restoration project for the Kemp's ridley sea turtle, *Lepidochelys kempii*, on the coast of Tamaulipas, Mexico. Gladys Porter Zoo, Brownsville, TX

Caillouet CW (2011) Guest Editorial: Did the BP-Deepwater Horizon-Macondo oil spill change the age structure of the Kemp's ridley population? Mar Turtle Newsl 130:1-2

Caillouet CW (2014) Interruption of the Kemp’s ridley population’s pre-2010 exponential growth in the Gulf of Mexico and its aftermath: one hypothesis. Mar Turtle Newsl 143:1–7

Caillouet CW, Shaver DJ, Landry AM, Owens DW, Pritchard PC (2011) Kemp’s ridley sea turtle (*Lepidochelys kempii*) age at first nesting. Chelonian Conserv Biol 10(2): 288 – 293

Caillouet CW, Gallaway BJ, Landry AM (2015a) Cause and call for modification of the bi-national recovery plan for the Kemp's ridley sea turtle (*Lepidochelys kempii*) - Second revision. Mar Turtle Newsl 145:1–4

Caillouet CW, Shaver DJ, Landry AM (2015b) Kemp's ridley sea turtle (*Lepidochelys kempii*) head-start and reintroduction to Padre Island National Seashore, Texas. Herpetol Conserv Biol 10**:**31–99

Chavez H, Contreras M, Hernandez T (1968) On the coast of Tamaulipas. International Turtle and Tortoise Society 2**:**20–29

Coyne MS (2000) Population sex ratio of the Kemp's ridley sea turtle (*Lepidochelys kempii*): problems in population modeling. PhD Dissertation, Texas A&M University, College Station, TX

Eckert KL, Eckert SA (1990) Embryo mortality and hatch success in in situ and translocated leatherback sea turtle *Dermochelys coriacea* eggs. Biol Conser 53**:**37–46

Fuentes M, Fish M, Maynard J (2012) Management strategies to mitigate the impacts of climate change on sea turtle’s terrestrial reproductive phase. Mitig Adapt Strategies Glob Change 17**:**51–63

Fuentes M, Hamann M, Limpus C (2010) Past, current and future thermal profiles of green turtle nesting grounds: implications from climate change. J of Exp Mar Biol Ecol 383**:**56–64

Fuentes M, Hawkes L (2011) How will sea turtles cope with climate change? SWOT Report 6**:**12–13

Fuentes M, Porter W (2013) Using a microclimate model to evaluate impacts of climate change on sea turtles. Ecol Modell 251**:**150–157

Gallaway BJ, Caillouet CW, Plotkin PT, Gazey JGC, Raborn SW (2013) Kemp's ridley stock assessment project final report. Gulf States Marine Fisheries Commission, Ocean Springs, Mississippi

Gallaway BJ, Gazey WJ, Wibbels T, Bevan E (2015) Evaluation of the status of the Kemp's ridley sea turtle following the 2010 Deepwater Horizon oil spill. Gulf Mex Sci 33:192–202

Geis A, Wibbels T, Garduno M, Marquez R, Burchfield P, Schroeder B (2002) Evaluation of Kemp's ridley hatchling sex ratios within egg corral and in situ nests at the primary nesting beach. Integr Comp Biol 42**:**1234

Godfrey MH, Mrosovsky N (1999) Estimating hatchling sex ratios. In: Eckert KL, Bjorndal, KA, Abreu-Grobois FA, Donnelly M (Eds) Research and management techniques for the conservation of sea turtles. IUCN/SSC Marine Turtle Specialist Group, Blanchard, p 136–138

Godley BJ, Broderick AC, Downie JR, Glen F, Houghton JD, Kirkwood I, Reece S, Hays GC (2001) Thermal conditions in nests of loggerhead turtles: further evidence suggesting female skewed sex ratios of hatchling production in the Mediterranean. J of Exp Mar Biol Ecol 263**:**45–63

Hawkes LA, Broderick AC, Coyne MS, Godfrey MH, Godley BJ (2007a) Only some like it hot—quantifying the environmental niche of the loggerhead sea turtle. Divers Distrib 13**:**447–457

Hawkes LA, Broderick AC, Godfrey MH, Godley BJ (2007b) Investigating the potential impacts of climate change on a marine turtle population. Glob Change Biol 13**:**923–932

Hawkes LA, Broderick AC, Godfrey MH, Godley BJ (2009) Climate change and marine turtles. Endang Species Res 7:137–154

Hays CG, Broderick AC, Glen F, Godley BJ (2003) Climate change and sea turtles: a 150-year reconstruction of incubation temperatures at major marine turtle rookery. Glob Change Biol 9:642–646

Hays CG, Ashworth A, Barnsley MJ, Broderick AC, Emery DR, Godley BJ, Henwood A, Jones EL (2001) The importance of sand albedo for the thermal conditions on sea turtle nesting beaches. Oikos 93**:**87–95

Hays GC, Mackay A, Adams CR, Mortimer JA, Speakman JR, Boerema M (1995) Nest site selection by sea turtles. J Mar Biol Assoc UK 75**:**667–674

Hendrickson JR (1958) The green sea turtle, Chelonia mydas (Linn.) in Malaya and Sarawak. J Zool 130(4):455–535

Heppell SS, Burchfield PM, Pena LJ (2007) Kemp's ridley recovery. In: Plotkin PT (ed) Biology and conservation of ridley sea turtles. Johns Hopkins University Press, Baltimore, p 325–335

Howard R, Bell I, Pike DA (2014) Thermal tolerances of sea turtle embryos: current understanding and future directions. Endang Species Res 26(1):75–86

Janzen FJ (1994) Climate change and temperature-dependent sex determination in reptiles. Proc Natl Acad Sci USA 91(16)**:**7487–7490

Jensen MP, Allen CD, Eguchi T, Bell IP, LaCasella EL, Hilton WA, Hof CAM, Dutton PH (2018) Environmental warming and feminization of one of the largest sea turtle populations in the world. Curr Biol 28(1):154–159

Jourdan J, Fuentes M (2015) Effectiveness of strategies at reducing sand temperature to mitigate potential impacts from changes in environmental temperature on sea turtle reproductive output. Mitig Adapt Strategies Glob Change 20**:**121–133

Kamel SJ, Mrosovsky N (2005) Repeatability of nesting preferences in the hawksbill sea turtle, *Eretmochelys imbricata*, and their fitness consequences. J Anim Behav 70**:**819–828

Kamel SJ, Mrosovsky N (2006) Inter-seasonal maintenance of individual nest site preferences in hawksbill sea turtles. Ecology 87**:**2947–2952

Keith DA, Mahony M, Hines H, Elith J, Regan TJ, Baumgartner JB, Hunter D, Heard GW, Mitchell NJ, Parris KM (2014) Detecting extinction risk from climate change by IUCN Red List criteria. Conserv Biol 28**:**810–819

Laloë J-O, Esteban N, Berkel J, Hays GC (2016) Sand temperatures for nesting sea turtles in the Caribbean: implications for hatchling sex ratios in the face of climate change. J of Exp Mar Biol Ecol 474**:**92–99

Leblanc AM, Wibbels T, Shaver D, Walker JS (2012) Temperature-dependent sex determination in the Kemp’s ridley sea turtle: effects of incubation temperatures on sex ratios. Endang Species Res 19(2):123–128

Marcovaldi MGD, López-Mendilaharsu M, Santos AS, Lopez GG, Godfrey MH, Tognin F, Baptistotte C, Thomé JC, Dias ACC, De Castilhos JC, Fuentes MMPB (2016) Identification of loggerhead male producing beaches in the south Atlantic: implications for conservation. J of Exp Mar Biol Ecol 477**:**14–22

Marquez MR (1994) Synopsis of biological data on the kemp's ridley sea turtle, *Lepidochelys kempi* (Garman, 1880). NOAA Tech Memo NMFS-SEFC-343. U. S. Department of Commerce, Miami, FL

Mazaris AD, Kallimanis AS, Sgardelis SP, Pantis JD (2008) Do long-term changes in sea surface temperature at the breeding areas affect the breeding dates and reproduction performance of Mediterranean loggerhead turtles? Implications for climate change. J of Exp Mar Biol Ecol 367**:** 219–226

McNeill JB, Avens L, Goodman Hall A, Goshe LR, Harms CA, Owens DW (2016) Female-bias in a long-term study of a species with temperature-dependent sex determination: monitoring sex ratios for climate change research. PLoS ONE 11(8):e0160911

Morreale SJ, Ruiz GJ, Spotila JR, Standora EA (1982) Temperature dependent sex determination: current practices threaten conservation of sea turtles. Science 216:1245–1247

Mrosovsky N (1980) Thermal biology of sea turtles. Am Zool 20:531–547

Mrosovsky N (1994) Sex ratios of sea turtles. J Exp Zoolog 270:16–27

Mrosovsky N (2006) Distorting gene pools by conservation: assessing the case of doomed turtle eggs. Environ Manage 38**:**523–531

Mrosovsky N, Pieau C (1991) Transitional range of temperature, pivotal temperatures and thermosensitive stages for sex determination in reptiles. Amphib-reptil 12:169–179

Pachauri RK, Allen MR, Barros V, Broome J, Cramer W, Christ R, Church J, Clarke L, Dahe Q, Dasgupta P (2014) Climate change 2014: synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change. IPCC, Geneva, Switzerland

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37:637–669

Pike DA (2009) Do green turtles modify their nesting seasons in response to environmental temperatures? Chelonian Conserv Biol 8(1)43–47

Pike DA, Stiner JC (2007) Sea turtle species vary in their susceptibility to tropical cyclones. Oecologia 153**:**471–478

Pinheiro J, Bates D, Debroy S, Sarkar D, Team RC (2009) nlme: Linear and nonlinear mixed effects models. R package version 3:96

Poloczanska ES, Limpus CJ, Hays GC (2009) Vulnerability of marine turtles to climate change. Adv Mar Biol 56**:**151–211

Pritchard PCH, Marquez R (1973) Kemp's ridley turtle or Atlantic ridley. IUCN Monograph No. 2, Morges, Switzerland.

Rind D (1998) Latitudinal temperature gradients and climate change. J Geophys Res Atmos 103**:**5943–5971

Schwanz LE, Janzen FJ (2008) Climate change and temperature- dependent sex determination: can individual plasticity in nesting phenology prevent extreme sex ratios? Physiol Biochem Zool 81**:**826–834

Shaver DJ, Caillouet CW (2015) Reintroduction of Kemp's ridley (*Lepidochelys kempii*) sea turtle to Padre Island National Seashore, Texas and its connection to head-starting. Herpetol Conserv Biol 10**:**114–171

Shaver DJ, Chaney AH (1989) An analysis of unhatched Kemp's ridley sea turtle eggs. In: Caillouet CW, Landry AM (eds) Proceedings of the First Symposium on the Kemp’s Ridley Sea Turtle Biology, Conservation and Management. Texas A&M Univ. Sea Grant College Program, Galveston p 82–89

Shaver DJ, Hart KM, Fujisaki I, Rubio C, Sartain-Iverson AR, Peña J, Gamez DG, De Jesus R, Burchfield PM, Martinez HJ, Ortiz J (2016) Migratory corridors of adult female Kemp's ridley turtles in the Gulf of Mexico. Biol Conserv 194**:**158–167

Shaver DJ, Owens DW, Chaney AH, Caillouet CW, Burchfield P, Marquez R (1988) Styrofoam box and beach temperatures in relation to incubation and sex ratios of Kemp's ridley sea turtles. In: Schroeder BA (ed) Proceedings of the eighth annual workshop on sea turtle biology and conservation, Fort Fisher, NC. NOAA Tech. Memo., Miami, p 103–108

Shaver DJ, Wibbels T (2007) Head-starting the Kemp's ridley sea turtle. In: Biology and conservation of ridley sea turtles. Plotkin, PT (ed). Johns Hopkins University Press, Baltimore, p 297–324

Telemeco RS, Abbott KC, Janzen FJ (2013) Modeling the effects of climate change-induced shifts in reproductive phenology on temperature-dependent traits. Am Nat 181**:**637–648

Telemeco RS, Elphick MJ, Shine R (2009) Nesting lizards (*Bassiana duperreyi*) compensate partly, but not completely, for climate change. Ecology 90**:**17–22

TEWG (2000) Assessment update for the Kemp's ridley and loggerhead sea turtle populations in the western north Atlantic. NOAA Tech Memo NMFS-SEFSC-444. U. S. Department of Commerce, Miami, FL

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416**:**389–395

Weishampel JF, Bagley DA, Ehrhart LM (2004) Earlier nesting by loggerhead sea turtles following sea surface warming. Glob Change Biol 10**:**1424–1427

Weishampel JF, Bagley DA, Ehrhart LM, Weishampel AC (2010) Nesting phenologies of two sympatric sea turtle species related to sea surface temperatures. Endang Species Res 12**:**41–47

Wibbels T (2003) Critical approaches to sex determination in sea turtles. In: Lutz PL, Musick JA Wyneken J (eds.) The biology of sea turtles. CRC Press, Boca Raton, FL

Wibbels, T (2007) Sex determination and sex ratios in ridley turtles. In: Plotkin P, Bernardo J (eds) Biology and conservation of ridley sea turtles. Johns Hopkins University Press, Baltimore, MD

Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. PLOS Biol 6:e325

Wyneken J, Burke TJ, Salmon M, Pedersen DK (1988) Egg failure in natural and relocated sea turtle nests. J Herpetol 22:88–96

Yntema CL, Mrosovsky N (1979) Incubation temperature and sex ratio in hatchling loggerhead turtles: a preliminary report. Mar Turtle Newsl 11:9–10

PREDICTED HATCHLING SEX RATIOS OF THE KEMP'S RIDLEY SEA TURTLE AT RANCHO NUEVO, MEXICO: IMPACTS OF A WARMING NESTING HABITAT

by

E. M. BEVAN, T. WIBBELS, F.I. MARTINEZ, J.M. CUEVAS, J. ORTIZ, B.M.Z. NAJERA, L. SARTI, L.J. PEÑA, AND P.M. BURCHFIELD

In preparation for *Chelonian Conservation Biology*

Format adapted for dissertation

CHAPTER 5

PREDICTED HATCHLING SEX RATIOS OF THE KEMP’S RIDLEY SEA TURTLE AT RANCHO NUEVO, MEXICO: IMPACTS OF A WARMING NESTING HABITAT

ABSTRACT

Average global surface temperatures are projected to rise between 0.3 and 4.8°C by the end of the century, and ectothermic species worldwide are particularly vulnerable to such rapid and large-scale changes. In sea turtles, incubation temperature determines the sex of hatchlings, with more females produced at warmer temperatures and more males produced at cooler temperatures. As a result of this temperature-sensitive characteristic, numerous studies have highlighted the consequences of potential feminizing trends and increases in incubation temperatures for sea turtle populations. In particular, the Kemp’s ridley (Lepidochelys kempii) faces unique challenges, namely the species’ single, primary nesting beach (Rancho Nuevo, Gulf of Mexico) that could limit its capacity to respond to rising environmental temperatures. This characteristic renders the species a model for investigating the impacts of rapid anthropogenic climate change on a thermally-sensitive species in the Gulf of Mexico. The present study evaluates long-term trends in egg hatchery, nesting beach sand temperatures, and nesting chronology then uses this information to make predictions about hatchling sex ratios for the Kemp’s ridley at Rancho Nuevo. Although we did not detect a significant increase in mean sand temperatures or hatchling sex ratios over an 18-year period, we did detect a significant

shift in the mean date of nesting over a 36-year period. These findings provide insights for the conservation and management of the Kemp’s ridley and should be considered when developing strategies to ensure its survival and successful recovery in the face of major environmental changes.

INTRODUCTION

As the world’s most endangered marine turtle, the Kemp’s ridley (Lepidochelys kempii) is unique among sea turtles in that it has a single primary nesting beach located at Rancho Nuevo, Tamaulipas, Mexico (Pritchard and Marquez 1973). Approximately 66% of the nesting for the species occurs in this restricted 30 km stretch of beach and nearly all (~97%) nesting occurs within the region of Tamaulipas, Mexico (Pritchard and Marquez 1973, Marquez 1994, Peña pers. comm). Due to the imminent extinction of this species, the United States joined Mexico in a binational collaborative effort to save the species in 1978 and initiated the Binational Kemp’s Ridley Recovery Program (KRRP) (Woody 1989). The program expanded and enhanced efforts to transport all the Kemp’s ridley nests to the protection of a single egg hatchery at Rancho Nuevo. This hatchery has consistently been used in the same location each nesting season and has remained the primary repository for up to 10,000 – 12,000 nests each year (Burchfield 2014).

Beginning in 1998, an integral component of the Kemp’s ridley conservation efforts involved recording sand incubation temperatures in the main egg corral as a proxy for monitoring the hatchling sex ratios produced each nesting season (Wibbels 2007, Burchfield 2014). Sea turtles exhibit temperature-dependent sex determination (TSD), where the temperature in the nest during the approximate middle third of incubation determines the sex of embryos (Mrosovsky 1994; Wibbels 2003, 2007). For the Kemp's ridley, temperatures above approximately 32.5°C produce 100% females and temperatures below 28.0°C produce 100% males, while temperatures between these two values result in mixed sex ratios (LeBlanc et al. 2012; Wibbels 2003). The temperature when a 1:1 hatchling sex ratio of males to females is produced (termed the "pivotal" temperature) is approximately 30.0°C for the Kemp's ridley (LeBlanc et al. 2012). A previous study based on Kemp's ridley nesting trends modeled the effect of hatchling sex ratios on population recovery and indicated a hatchling sex ratio of approximately 3 females to 1 male is optimal for promoting a faster population recovery (Coyne and Landry 2007). Thus, the sand temperatures in the main egg corral at the Kemp's ridley's primary nesting beach have been maintained to promote optimal hatchling sex ratios for the recovery of the species due to TSD. Sand incubation temperatures provide a non-invasive proxy for predicting hatchling sex ratios (Merchant-Larios et al. 1997). Though other methods of determining the sex of sea turtles are used (laparoscopy, necropsy of stranded turtles, testosterone assays), sand temperatures and histological analysis of gonadal tissue from deceased hatchlings that remain in the nest after emergence are the most feasible and accurate methods for predicting the sex ratio of hatchlings (Yntema and Mrosovsky 1980; Wibbels 2003).

Species with TSD are particularly sensitive to changes in environmental temperatures. Accordingly, rapid anthropogenic climate change can directly influence hatchling sex ratios that in turn have significant implications for the recovery and conservation of a species (Walther et al. 2002; Hulin et al. 2009). Increasing sand temperatures on nesting beaches can lead to the feminization of hatchling sex ratios, reduced hatchling survival and fitness, and potentially result in the lack of male sea turtles in the population (Booth et al. 2004; Burgess et al. 2006; Booth and Evans 2011; Micheli- Campbell et al. 2011; Jensen et al. 2018). If sea turtles lack the physiological or behavioral plasticity to rapidly respond, wildlife resource managers may need to identify alternative strategies including directly or indirectly manipulating incubation conditions or relocating nests to more favorable nesting locations to mitigate the impacts of climate warming. Studies are needed that provide insight on what options are available for thermally-sensitive species to respond to predicted near-future climate change, in addition to studies that establish current baselines for population sex ratios by which to monitor the consequences of climate change on a given species. Furthermore, warming environmental temperatures at breeding habitats can alter the timing of reproductive migrations, breeding and nesting, and disrupt the distribution of prey available for sea turtles at foraging habitats (Walther et al. 2002; Parmesan 2006).

In the present study, we evaluated sand temperatures in the primary egg hatchery and on the natural nesting beach of the Kemp's ridley over the last 18 years at Rancho Nuevo, Mexico. Combining the daily number of nests laid at Rancho Nuevo and relocated to the main egg hatchery with the mean temperature during the middle third of incubation for all nests, we generated an 18-year dataset for hatchling sex ratios in the binational KRRP. In addition, observed daily nesting data available since 1977 were further evaluated for long-term trends in nesting chronology (Figure 1).

The results from the present study provide a critical initial step in understanding how the current nesting habitat may be changing in response to climate change and provides insights on the ultimate impact these changes could have on the survival and conservation status of the most critically endangered species of sea turtle in the world.

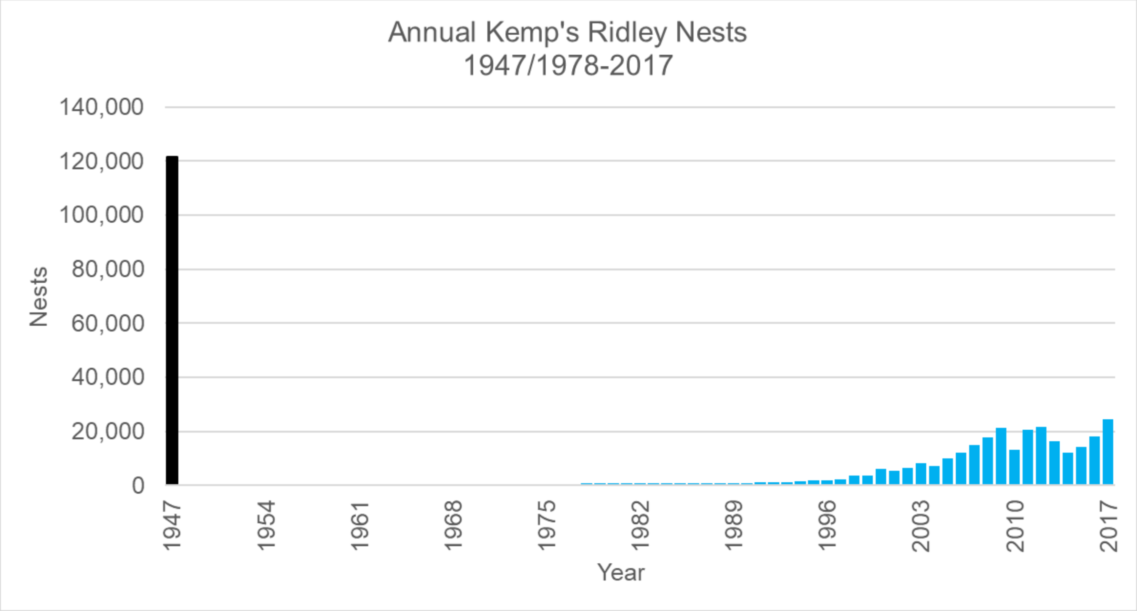

Figure 1. Annual Kemp’s ridley nests, the estimated benchmark in 1947 (black) from Bevan et al. 2016 and observed nesting from 1978-2017 (blue) (Peña, *pers. comm.*).

METHODS

A total of 5 – 10 data loggers (Onset HOBO Pendant®) were buried at a depth of 35 cm each year (1998 – 2016) in the sand of the primary egg hatchery at Rancho Nuevo, Tamaulipas, Mexico. The data loggers were evenly positioned throughout the egg corral to represent the variation in sand temperatures to which incubating nests would have been exposed throughout the nesting season. The data logger depth represents the mean nest depth for the Kemp’s ridley sea turtle (Pritchard and Marquez 1973). An additional 10 –

36 data loggers, depending on year, were buried at the same depth along a 30 km stretch of natural nesting beach at Rancho Nuevo, from Barra Carrizo at the northern end to Barra Del Tordo at the south (Figure 2). One data logger was buried every 300 m along the beach from 1998 – 2000, and two data loggers were buried along perpendicular transects from 2001 – 2016. In years when two data loggers per transect were used, one data logger was buried between the base of the dune and the seaward facing slope of the primary dune (the region where most nesting occurred, termed “position 3”), and the second was buried seaward in front of the face of the dune (termed “position 2”) (Marquez 1994). Only data loggers located at position 3 where most nesting occurred were used for this analysis. For comparative purposes, only data from a common period in all years of the current study (2 May to 28 June) were analyzed. This time period is coincident with the critical portion of embryonic incubation in the Kemps ridley during which hatchling sex is determined in approximately the middle third of embryonic development (Mrosovsky 1994, Wibbels 2003) for nests laid between 17 April and 29 May, which encompasses the peak nesting season (Pritchard and Marquez 1973).

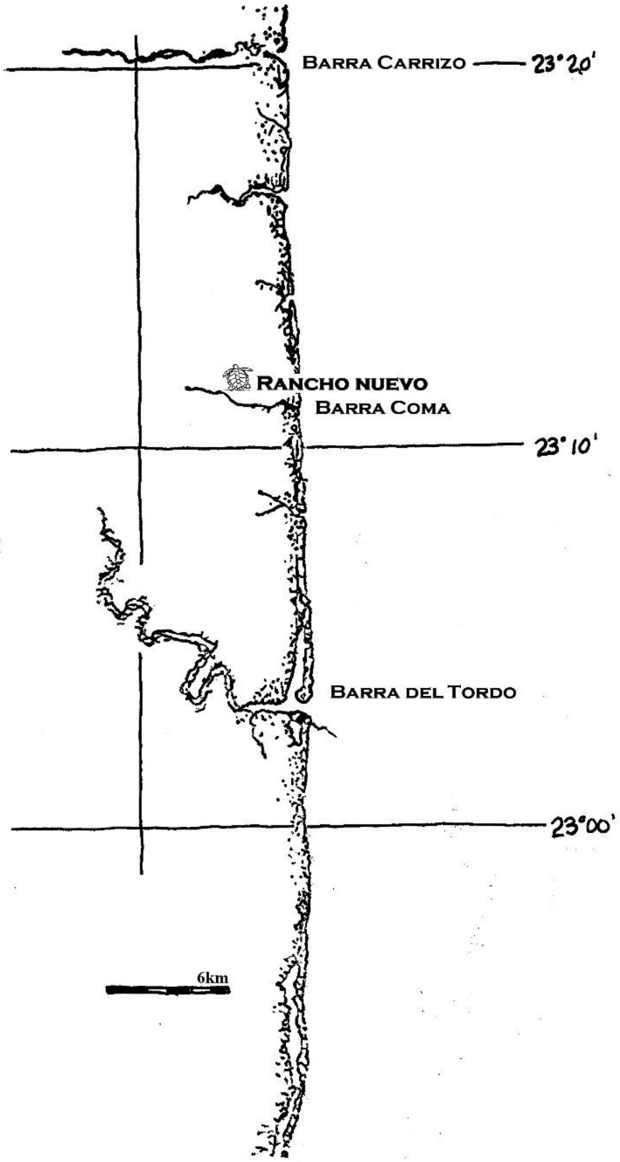

Figure 2. The location of the primary egg hatchery at Rancho Nuevo, Tamaulipas, Mexico used throughout the nesting season each year by the Kemp's Ridley Recovery Program from 1978 to the present. Data loggers use in the present study were buried to a depth of 35 cm to record sand temperatures in the primary egg hatchery and along a 30 km stretch of natural nesting beach from Barra Carrizo to Barra Del Tordo from 1998 – 2016.

The data loggers employed had a resolution of ±0.3°C and each was calibrated in the laboratory at the University of Alabama at Birmingham (UAB) prior to the beginning of a given nesting season. The timing of when a given data logger was buried in the sand varied by the year of the study, but typically, data loggers were buried in place prior to the beginning of the annual nesting season of the Kemp's ridley (between March and April). Data loggers were removed after the hatchlings had emerged from nests (August-September).

Sex Ratio Predictions

Each data logger was set to record ambient sand temperature every hour throughout the duration of the nesting and hatching season (April – August). Following data logger retrieval and transportation to UAB, the data were downloaded to a computer. Hourly sand temperatures for each data logger were averaged to generate a daily (24 h) mean (±SD) temperature. After removing statistically significant outliers (temperature recordings that were erroneous and biologically impossible on the nesting beach) from the data set (using the outlier function in R, Komsta 2015), for each day of the nesting season a 15-day mean temperature, offset from the original date of lay by 15 days, was calculated to represent the average temperature during the middle third of the incubation period for nests laid on that day. This calculation generated an offset 15-day mean temperature profile for the nesting season that represented the average sand temperature during the portion of incubation when hatchling sex is determined (the middle third of the incubation period). The incubation period for Kemp's ridleys (from the day of nest deposition to the day of hatchling emergence) varies depending on incubation temperature from 45 to 58 days with an average of 51 days (Pritchard and Marquez 1973). However, after hatching, hatchling sea turtles spend an average of 4-5 days in the nest prior to emergence (Godfrey and Mrosovsky 1997). Therefore, we used an average incubation period of 45 days, resulting in a duration of 15-days for the middle third of incubation.

The sex ratio for each nest relocated to the egg hatchery on a given day was predicted by comparing the mean temperature during the middle third of incubation (discussed above) to the thermal reaction norm of sex determination generated for the Kemp's ridley in LeBlanc et al. (2012). The sex ratio predicted for each nest based on the thermal reaction norm was multiplied by the total number of eggs per nest to generate the number of predicted male and female hatchlings in that nest. We assumed a total of 70 hatchlings per nest based on an approximate clutch size of 100 eggs per nest for the Kemp's ridley (Rostal and Plotkin 2007; Burchfield 2013) and an estimated 70% hatching success (Burchfield 1998). After repeating this process for all nests relocated to the main egg corral throughout the nesting season, the overall sex ratio for each nesting season was calculated from the total number of male and female hatchlings predicted to have been produced in the main egg corral. We used a random effects regression analysis to analyze long-term trends in the hatchling sex ratios predicted for each nesting season from 1998 – 2016 and fitted a linear trendline to the data. The total number of nests laid on each day of the nesting season from 1998 – 2016 was provided by Comision National Areas Naturales Protegidas (CONANP, *pers comm*.).

To simulate a conservative end of century climate warming scenario (Pachauri et al. 2014), we added 1°C to the 15-day middle third average sand temperatures for each day throughout the nesting season. This modified temperature profile was then used to predict the total number of male and female hatchlings estimated for each nest and calculate the overall hatchling sex ratios for each year that would be expected given a conservative increase in incubation conditions.

Nesting Phenology

Data on the number of Kemp’s ridley nests laid daily at Rancho Nuevo from 1998 – 2016 was provided by CONANP as part of the sex ratio analyses (discussed above) and nesting data prior to 1998 obtained from archived data held by the Gladys Porter Zoo in Brownsville, TX (Pritchard and Marquez 1973, Marquez 1994, CONANP, pers. comm). These data were evaluated using two approaches in the present study, a regression analysis of the weighted mean date of nesting and regression analyses of the dates by which 20, 40, 60, and 80% of nesting was completed in each nesting season. These percentages were chosen to evaluate the approximate timing of the first, second, and third large mass nesting events of each nesting season and were based on the proportion of total nesting for a season represented by recent mass nesting events at Rancho Nuevo (20%=first arribada, 40%=second arribada, 60%=third arribada, Burchfield 2014). The 80% of nesting metric was chosen to represent the final portion of nesting at the end of the season. To standardize the survey period for each nesting season, only nesting data between 1-April and 31-July of each nesting season were used in the present analysis. This period represented the majority of all Kemp’s ridley nesting for each nesting season (mean of 99.7% of nesting for each season). The mean date of nesting for each nesting season was calculated after weighting each day by the total number of nests laid on that day (Julian date x number of nests laid on that day). This dataset was then evaluated using a linear regression analysis. This approach was used due to the pulsatile nature of

Kemp’s ridley mass nesting involving hundreds to thousands of turtles nesting in relatively restricted area of beach (a few hundred to several hundred meters of linear beach) and over several hours for each mass nesting event. Approximately one mass nesting event occurs each month of the peak nesting season from April through June for a total of one to three events each nesting season with solitary, scattered nesting that occurs between these events (Lutz et al. 2003).

RESULTS

Sand Temperatures

Our analyses did not detect a significant increase in annual mean sand temperatures in the primary egg corral or on the natural nesting beach at Rancho Nuevo from 1998 to 2016 (Corral: R2=0.18, F=3.70, df=18, P=0.07; Beach: R2 =0.04, F=0.71, df=18, P=0.41) (Figure 3). However, trendlines for mean sand temperatures in the primary egg corral and on the natural nesting beach (0.04 and 0.02°C per year, respectively) indicate a potentially increasing trend in temperatures over time. A comparison of sand temperatures in the egg corral and on the natural nesting beach indicate that sand temperatures in the main egg corral are on average 0.87°C ± 0.23°C (T=2.59, df=196, P=0.01) warmer than sand temperatures on the natural nesting beach.

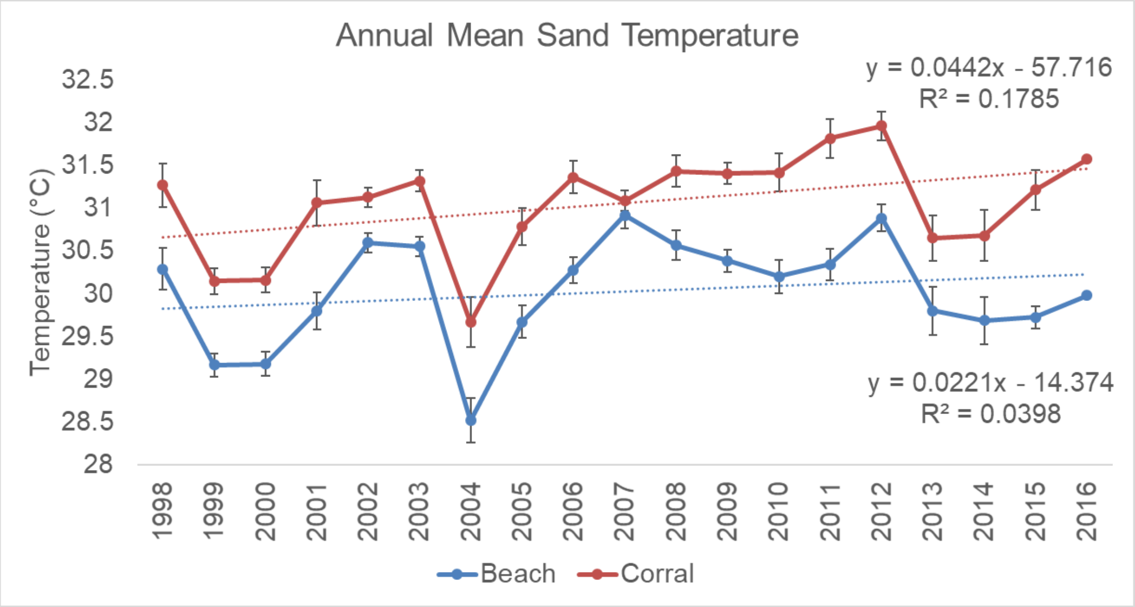

Figure 3. Mean sand temperatures in the primary egg hatchery (red) and on the natural nesting beach (blue) between 2-May and 28-June each nesting season (1998 – 2016) at Rancho Nuevo, Mexico.

Sex ratio predictions

We found no significant increase in the predicted female-bias of nests in the main egg corral with the middle third of incubation between 2-May and 28-June from 1998 to 2016 (R2 = 0.22, F = 4.40, df = 17, P =0.05). The trendline for predicted hatchling sex ratios in the main egg corral indicates a potential increase of 0.01% female bias over the 18-year study period (Figure 4). Using the average sand temperatures on the natural nesting beach to predict hatchling sex ratios instead of the sand temperatures in the egg hatchery, our analyses provide insight on the hatchling sex ratios that would have resulted if nests had been left to incubate in situ on the natural nesting beach, instead of the nest being relocated to the egg hatchery. Under this scenario, the consistently cooler temperatures of the nesting beach compared to that of the egg hatchery in a given year would likely have resulted in an overall reduced female-biased hatchling sex ratio

(R2=0.522, F=37.07, df=34, P<0.0001) (Figure 4). However, our analyses of natural nesting beach temperatures over the 18-year time period did not indicate a significant increase in predicted hatchling sex ratios (R2=0.003, F=0.05, df=17, P=0.84) and the trendline for these sex ratios showed nearly no change over the 18-year period of the current study (an increase of 0.0016% female per year).

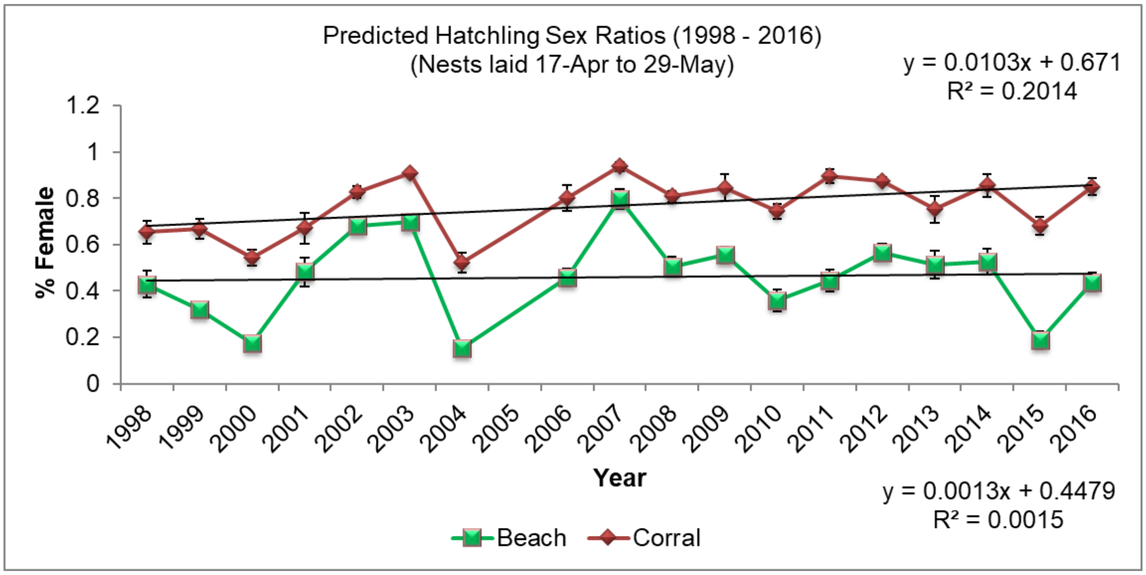

Figure 4. Annual hatchling sex ratios predicted for nests laid in the main egg corral (red) and sex ratios predicted for nests hypothetically left on the natural nesting beach (green) to incubate from 1998 to 2016. Sex ratio predictions were based on mean sand temperature during the middle third of incubation for nests laid on each day between 17-April to 29-May.

Hypothetical Climate Change Scenario

Under current climate conditions, applying a conservative end-of-century increase in environmental temperatures of ~1°C to the most recent year of sand temperatures recorded during the present study (during 2016), the annual mean sand temperature would increase to approximately 31.0°C on the natural nesting beach and approximately 32.6°C in the primary egg corral. Using these mean sand temperatures and the nesting trends observed in the 2016 nesting season, the predicted hatchling sex ratio for nests laid between 17-April to 29-May and relocated to the primary egg corral would be 95.7 ± 0.015% female. If the nests laid during the 2016 nesting season had remained in situ on the natural nesting beach, then predicted hatchling sex ratios under a conservative end-of-century temperature scenario would be 81.1 ± 0.04% female.

Timing of Nesting

Our analyses of Kemp's ridley nesting phenology at Rancho Nuevo indicate several trends over the 1977 – 2016 period of the present study (Figure 5). The mean date of nesting has shifted earlier by 16 days, from a mean of 22-May to 5-May with a trendline slope of -0.423 days per year (R2=0.368, F=5.32, df=37, p<0.0001). Similarly, the dates by which 20 (R2=0.298, F=15.27, df=37, p=0.0004, slope of trendline=-0.401), 40 (R2=0.394, F=23.37, df=37, p<0.0001, slope of trendline=-0.612), 60 (R2=0.339, F=18.44, df=37, p=0.0001, slope of trendline=-0.587), and 80% (R2=0.151, F=6.38, df=37, p=0.0161, slope of trendline=-0.368) of total nesting for each season have also shifted earlier in the nesting season.

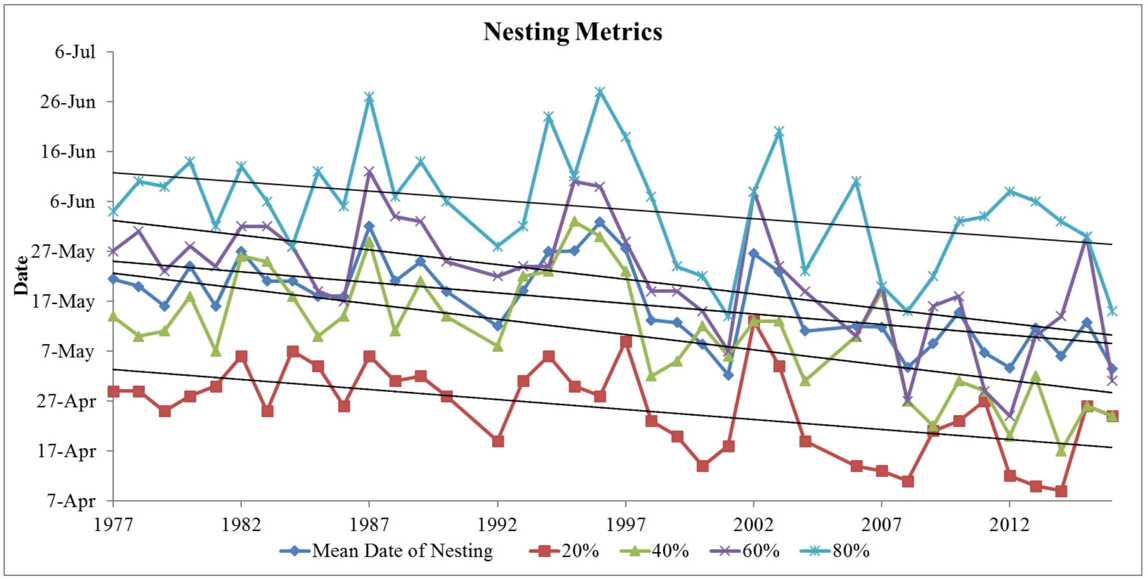

Figure 5. Dates when 20, 40, 60, and 80 % of all Kemp’s ridley nests were laid at Rancho Nuevo, Mexico, during each nesting season from 1977 – 2016. Completion of a percentage of nesting was used to represent the episodic mass nesting events (“arribadas”) characteristic of the genus *Lepidochelys*.

DISCUSSION

Intense conservation efforts such as relocating the majority of Kemps ridley nests to protective egg hatcheries have been implemented since the beginning of the binational KRRP in 1978 at Rancho Nuevo, Mexico. These actions have been an integral factor in minimizing turtle mortality due to a variety of threats (i.e. natural predation, exploitation for human consumption, mortality in fishing gear) ultimately preserving the species from likely extinction (Pritchard and Marquez 1973). Our analyses of sand temperatures and predicted hatchling sex ratios at the consistent location of the egg hatchery since the beginning of the binational KRRP suggest that despite environmental changes projected for Kemp’s ridley habitat, we may not yet be able to detect the impacts of these long-term changes at the primary nesting beach. By relocating the majority of Kemp’s ridley nests to the egg hatchery, the data generated by the binational KRRP conservation efforts and used in the present study reflect decades of artificial manipulation of thermal incubation conditions to promote an optimal recovery rate. Additionally, these data provide an opportunity to evaluate the impacts of these management decisions on the survival of the species in the context of a warming world.

The present study provides a critical initial step in understanding the potential implications of past, current, and future environmental warming on the reproductive biology and survival of the Kemp's ridley sea turtle. This information is critical for evaluating the efficacy of current conservation methodologies as well as developing future strategies for mitigating the impacts of climate change and managing the survival of this endangered species. Along with consistently moving all nests to the protection of egg hatcheries at Rancho Nuevo, additional measures to cool incubation conditions (e.g. shading the hatchery with mesh and sprinkling the sand with water) are currently being implemented to maintain incubation conditions that are cool enough to produce a current hatchling sex ratio of approximately 3 females to 1 male (Coyne and Landry 2007) and prevent increases in hatchling mortality (Peña, pers comm). These additional efforts underway are indicative of sub-optimal temperatures at the nesting beach for this species and suggest that egg hatcheries and recent techniques for modifying incubation conditions alone are likely to be insufficient in the future to sustain ideal thermal incubation conditions.

Collectively, long-term data on sand temperatures, hatchling sex ratios (determined by histology, Wibbels 2007, Leblanc et al. 2012), and predicted near-future hatchling sex ratios at Rancho Nuevo provide insights into the potential impact of near-future warming on population growth and recovery of the Kemp's ridley. Using a conservative estimate for a projected increase in egg hatchery sand temperature of ~1°C, near-future hatchling sex ratios are predicted to be highly female-biased (~95% female bias) by the end of the century. Although not significant in the current study, the upward trends in observed sand temperatures and hatchling sex ratios could be indicative of more gradual warming of beach habitats in the Gulf of Mexico region than in other regions, including at higher latitudes (Walther et al. 2002, Ringot et al. 2008). This regional heterogeneity in environmental warming could be contributing to the findings of the current study and may suggest that thermally-sensitive species in the Gulf of Mexico region could have more time to respond to environmental changes than species in regions experiencing faster rates of environmental warming (Ringot et al. 2008). This highlights the need to continue monitoring environmental conditions at critical habitat for the Kemp's ridley as a model species for observing impacts of climate change in the Gulf of Mexico.

Conservation strategies must focus on mitigating the potentially detrimental impacts of rapid climate change on the survival, fitness, and sex ratios of hatchlings, as well as the timing of reproductive activities in adult sea turtles. Given the anticipated increases in global environmental temperatures projected by the end of the century (0.3 – 4.8°C, Pachauri et al. 2014), and the potential impacts of these increases on hatchling sex ratios that are already female-biased, it is possible that extreme female-biased sex ratios could be observed by the end of the century. Under an extreme climate warming scenario (Pachauri et al. 2014), hyper-feminized hatchling cohorts could ultimately result in a lack of sufficient male sea turtles available to fertilize eggs and higher rates of infertile nests at the nesting beach (Laloë et al. 2016; Hays et al. 2017). Extreme temperatures at Rancho Nuevo could also result in abnormal development and result in increased nest mortality (Ackerman 1997; Howard et al. 2014). In addition to impacts on hatchlings, environmental warming could impact the timing of reproductive migrations, breeding and the nesting in adult sea turtles (Weishampel et al. 2004, 2010).

It should be noted that the hypothetical end-of-century climate warming scenarios discussed above assume that the timing of nesting will be identical or a least similar at Rancho Nuevo in the future. The results from the current study indicate that the timing of Kemp's ridley nesting is shifting earlier which could be an attempt to maintain optimal thermal incubation conditions by nesting earlier during a relatively cooler portion of the season (Weishampel et al. 2010). However, it is also possible that earlier nesting at beaches is a result of earlier reproductive migrations from foraging areas that are cued in part by ocean temperatures in these habitats (Poloczanska et al. 2009). The northern Gulf of Mexico is primary foraging habitat for nearly 80% of adult Kemp's ridleys (Shaver et al. 2016) and it is possible that warming sea surface temperatures in this region could be driving earlier reproductive migrations (Weishampel et al. 2004). Yet despite shifting the timing of nesting to earlier in the season, whether this gradual response is rapid enough to compensate for the rate of increase in environmental temperatures has not yet been evaluated. It is possible that the longer time period used in the analysis of nesting phenology (1977 – 2016) has confounded our analysis of trends in nesting phenology. However, we feel that the significant shift in nesting date supports the concept that environmental warming and hatchling feminization trends at Rancho Nuevo could be occurring more gradually than in other regions and may require a longer time period to detect.

Although end-of-century predictions presented in the current study can be concerning, the consequences of an increase in nesting beach temperatures may not be as detrimental for the Kemp's ridley as anticipated based on studies of other sea turtle species (Howard et al. 2014). The Kemp's ridley exhibits one of the highest pivotal temperatures among sea turtles, and this may indicate a higher lethal temperature threshold over embryonic development (Leblanc et al. 2012, Howard et al. 2014; Shaver and Caillouet 2015). It has been suggested that up to some thermal maxima increases in sand incubation temperatures could lead to an increase in the rate of population growth through an increase in the number of breeding females (Hays et al. 2017). Despite a reduction in the proportion of male hatchling produced under such a scenario, the ability of male sea turtles to inseminate multiple females coupled with the annual breeding cycle of male sea turtles compared to the 2-3-year breeding periodicity of female sea turtles may help to offset the impacts of extreme female biases in sea turtle populations (Lasala et al. 2013, Hays et al. 2010, 2014, 2017; Schofield et al. 2017). However, under extreme climate warming projections (increases of approximately 4°C by end of century, Pachauri et al. 2014), sand incubation conditions may become lethal for embryonic development in some populations of sea turtles (Poloczanska et al. 2009; Laloë et al. 2016; Hays et al. 2017). Increases in hatchling mortality and reduced hatching success for sea turtle nests have been reported to occur in some species held at constant incubation temperatures in the range of 33-35°C, and above 35˚C for species held under fluctuating incubation temperatures (Ackerman 1997; Howard et al. 2014). However, these studies did not evaluate the upper thermal limits for embryonic development in all sea turtle species and interspecific differences may occur (Howard et al. 2014). Therefore, it is important to continue to evaluate how the Kemp's ridley responds to large-scale environmental changes to ensure that optimal management decisions are implemented in key habitats.

The survival of each individual species of sea turtle will depend on its unique life history characteristics and inherent capacity to adapt to climate change. Multiple responses of sea turtles to such large-scale environmental changes have been hypothesized to maintain optimal thermal conditions including shifts in nesting phenology and distribution, behavioral changes, and changes in population dynamics (Weishampel et al. 2004; Hawkes et al. 2007; Mazaris et al. 2008; Pike 2009). Despite the results from the present study suggesting that sea turtles in the Gulf of Mexico region may have more time to adapt to warming environmental conditions, the facts remain that sea turtles are long-lived, slow to mature, and each species exhibits some degree of site fidelity to its natal nesting beaches (Lutz et al. 2002). These factors may hinder the ability of sea turtles to respond rapidly enough to adequately compensate for the current and projected rate of climate change (Walther et al. 2002; Fuentes and Hawkes 2011). As an example, species demonstrating greater variation in nest site location could reduce nest mortality and risk of species extinction under conditions of rising temperatures or beach erosion and habitat loss associated with climate change (Kamel and Mrosovsky 2005; Mrosovsky 2006; Pike and Stiner 2007).

There are a variety of strategies for possibly mitigating the impacts of climate change on the Kemps ridley sea turtle. One approach would be to stop the use of egg hatcheries and leave each season's nests in situ on the natal nesting beach. This approach would offer short-term respite from sub-optimal sand temperatures in the egg corral as sand temperatures on the nesting beach are on average 1.0°C cooler than the in the egg hatcheries currently in use at Rancho Nuevo. This difference is primarily due to the egg hatchery being constructed higher up on the slope of the beach, closer to the primary dune and farther from mean water level to protect nests from inundation and erosion (Peña, pers. comm). Yet with higher elevation and greater distance to mean water level, fluctuations in temperature, moisture, and salinity of the sand are greater (Wood and Bjorndal 2000), thus average sand temperatures are warmer, and eggs are more prone to desiccation in the egg hatchery in comparison to the natural nesting beach. However, sand temperatures on the natural nesting beach may gradually increase and and thus would no longer mitigate the impacts of warming. Additionally, it is possible that leaving nests in situ on the natal nesting beach would increase nest and hatchling predation rates, along with increases in other threats such as nest failure due to inundation and erosion (Mrosovsky 2006). Although previous studies at Rancho Nuevo have shown that the current predation rates on the natural nesting beach are minimal (Eich 2009; Bevan 2013), it is unknown how predator populations would respond to the greater availability of prey (i.e. unprotected nests).

Additional strategies for mitigating the impacts of climate warming might include relocating nests to alternative beaches that are cooler throughout the nesting range for the Kemp’s ridley or developing artificial incubation facilities to ensure some portion of the nests survive. However, each of these approaches entails its own unique set of challenges and involves numerous implications for the biology and conservation of the Kemp’s ridley. It is probably not logistically feasible to annually relocate more than 20,000 nests (approximately 27,000 nests registered in Tamaulipas, Mexico in 2017, Peña, pers comm.) from beaches in Mexico to either artificial incubation facilities or alternative nesting beaches with thermally suitable incubation conditions. Relocating a portion of Kemp's ridley nests has previously been employed as a conservation method. This relocation occurred during the first decade of the Kemp's Ridley Recovery Program (1978-1988), and those that implemented the plan demonstrated that this approach may be useful as a component of a larger conservation strategy (Caillouet et al. 2015; Shaver and Caillouet 2015). It is possible that beaches at the northern extent of the Kemp's ridley's nesting range could support the production of mixed sex ratios under an end-of-century climate warming scenario (Bevan et al. unpub. data). However, it is unlikely that relocating nests to these northern beaches would instigate a larger scale shift in the distribution of nesting for the Kemp's ridley given the rapid rate of anthropogenic climate change and the long age to maturity in sea turtles (Fuentes and Hawkes 2011).

Key components of mitigating the impacts of near-future anthropogenic climate change on thermally-sensitive species are understanding how changes in environmental conditions affect a given species and predicting the physiological and behavioral responses. By monitoring trends in sea turtle nesting beach temperatures and predicted hatchling sex ratios, the present study provides a crucial step in understanding how climate change could impact the Kemp's ridley sea turtle in its natal nesting habitat. However, developing sound management strategies to ensure the survival of this species necessitates continued evaluation of individual and population-level responses to environmental changes. The present study suggests that the Kemp's ridley may have more time yet limited options for evolutionary adaption to anthropogenic climate change.

Importantly, due to its restricted range, the Kemp’s ridley serves as a rare model for evaluating the impacts of rapid environmental changes on the survival of a thermally-sensitive species.

ACKNOWLEDGMENTS

This research was conducted as part of the Binational Kemp’s Ridley Recovery Program which is coordinated in Mexico by the General Directorate for Wildlife of the Secretariat of the Environment and Natural Resources (SEMARNAT), the National Commission of Natural Protected Areas (CONANP), and the Tamaulipas State Wildlife Agency (SEDUMA). The program encompasses a variety of U.S. agencies including the U.S. Fish and Wildlife Service, NOAA Fisheries, National Park Service, and Texas Parks and Wildlife. Funding was provided, in part, by the UAB Department of Biology, NOAA Fisheries and the U.S. Fish and Wildlife Service through the Marine Turtle Conservation Fund. Special thanks to the dedicated personnel whose efforts were pivotal in collecting the data for this project.

LITERATURE CITED

ACKERMAN, R.A. 1997. The nest environment and the embryonic development of sea turtles. The biology of sea turtles 1:83-106.

BEVAN, E. 2013. Implications of hatchling sex ratios and survival in the recovery program for the endangered Kemp's ridley sea turtle. MS Thesis, University of Alabama at Birmingham, Birmingham, AL.

BOOTH, D.T., BURGESS, E., MCCOSKER, J., AND LANYON, J.M. 2004. The influence of incubation temperature on post-hatching fitness characteristics of turtles. In: International Congress Series, 226-233.

BOOTH, D.T., AND EVANS, A. 2011. Warm water and cool nests are best. How global warming might influence hatchling green turtle swimming performance. PloS ONE 6:e23162.

BURCHFIELD, P.M. 2014. Report on the Mexico/United States of America population restoration project for the Kemp's ridley sea turtle, *Lepidochelys kempii*, on the coast of Tamaulipas, Mexico.

BURGESS, E.A., BOOTH, D.T., AND LANYON, J.M. 2006. Swimming performance of hatchling green turtles is affected by incubation temperature. Coral Reefs 25:341-349.

CAILLOUET, C.W., SHAVER, D.J., AND LANDRY JR, A.M. 2015. Kemp's ridley sea turtle (*Lepidochelys kempii*) head-start and reintroduction to Padre Island National Seashore, Texas. Herpetological Conservation and Biology 10:31-99.

COYNE, M., AND LANDRY, A.M. 2007. Population sex ratios and its impact on population models. (ed) PLOTKIN, P. In: Biology and conservation of ridley sea turtles. Baltimore, Maryland Johns Hopkins University Press, 191 – 211.

EICH, A.M.L. 2009. Evolutionary and conservation implications of sex determination and hatchling depredation in Kemp's ridley sea turtles 71(1).

FUENTES, M., AND HAWKES, L. 2011. How will sea turtles cope with climate change? SWOT Report 6:12-13.

GODFREY, M.H., AND MROSOVSKY, N. 1997. Estimating the time between hatching of sea turtles and their emergence from the nest. Chel. Conserv. Biol. 2:581-585.

HAWKES, L.A., BRODERICK, A.C., GODFREY, M.H., AND GODLEY, B.J. 2007. Investigating the potential impacts of climate change on a marine turtle population. Global Change Biology 13:923-932.

HAYS, G.C., FOSSETTE, S., KATSELIDIS, K.A., SCHOFIELD, G., AND GRAVENOR, M.B. 2010. Breeding periodicity for male sea turtles, operational sex ratios, and implications in the face of climate change. Conservation Biology 24:1636-1643.

HAYS, G.C., MAZARIS, A.D., AND SCHOFIELD, G. 2014. Different male vs. female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. Marine Megafauna 1:43.

HAYS, G.C., MAZARIS, A.D., SCHOFIELD, G., AND LALOË, J.-O. 2017. Population viability at extreme sex-ratio skews produced by temperature-dependent sex determination. Proceedings of the Royal Society B: Biological Sciences 284.

HEPPELL, S.S., BURCHFIELD, P.M., AND PEÑA, L.J. 2007. Kemp's ridley recovery In: PLOTKIN, P (ed) Biology and conservation of ridley sea turtles: 325.

HILDEBRAND, H.H. 1963. Hallazgo del area de anidacion de la tortuga marina "lora", *Lepidochelys kempi* (Garman), en la costa occidental del Golfo de Mexico. Rept. Chel. Ciencia, Mexico 22:105-112.

HOWARD, R., BELL, I., AND PIKE, D.A. 2014. Thermal tolerances of sea turtle embryos: current understanding and future directions. Endangered Species Research 26(1): 75-86.

HULIN, V., DELMAS, V., GIRONDOT, M., GODFREY, M.H., AND GUILLON, J.-M. 2009. Temperature-dependent sex determination and global change: are some species at greater risk? Oecologia 160:493-506.

JENSEN, M.P., ALLEN, C.D., EGUCHI, T., BELL, I.P., LACASELLA, E.L., HILTON, W.A., HOF, C.A.M., AND DUTTON, P.H. 2018. Environmental warming and feminization of one of the largest sea turtle populations in the world. Current Biology 28:154-159.e154.

KAMEL, S.J., AND MROSOVSKY, N. 2005. Repeatability of nesting preferences in the hawksbill sea turtle, *Eretmochelys imbricata*, and their fitness consequences. Animal Behaviour 70:819-828.

KOMSTA, L. 2006. Processing data for outliers. The Newsletter of the R Project 6 (2), 10.

LALOË, J.-O., ESTEBAN, N., BERKEL, J., AND HAYS, G.C. 2016. Sand temperatures for nesting sea turtles in the Caribbean: Implications for hatchling sex ratios in the face of climate change. Journal of Experimental Marine Biology and Ecology 474:92-99.

LASALA, J.A., HARRISON, J.S., WILLIAMS, K.L., AND ROSTAL, D.C. 2013. Strong male-biased operational sex ratio in a breeding population of loggerhead turtles (Caretta caretta) inferred by paternal genotype reconstruction analysis. Ecology and Evolution 3:4736-4747.

LUTZ, P.L., MUSICK, J.A., AND WYNEKEN, J. 2003. The biology of sea turtles. CRC press, 472 pp.

MAZARIS, A.D., KALLIMANIS, A.S., SGARDELIS, S.P., AND PANTIS, J.D. 2008. Do long-term changes in sea surface temperature at the breeding areas affect the breeding dates and reproduction performance of Mediterranean loggerhead turtles? Implications for climate change. Journal of Experimental Marine Biology and Ecology 367:219-226.

MERCHANT-LARIOS, H., RUIZ-RAMIREZ, S., MORENO-MENDOZA, N., AND MARMOLEJO-VALENCIA, A. 1997. Correlation among thermosensitive period, estradiol response, and gonad differentiation in the sea turtle *Lepidochelys olivacea*. General and Comparative Endocrinology 107:373-385.

MICHELI- CAMPBELL, M., CAMPBELL, H., CRAMP, R., BOOTH, D., AND FRANKLIN, C. 2011. Staying cool, keeping strong: incubation temperature affects performance in a freshwater turtle. Journal of Zoology 285:266-273.

MROSOVSKY, N. 1994. Sex ratios of sea turtles. J. Exp. Zool. 270:16-27.

MROSOVSKY, N. 2006. Distorting gene pools by conservation: assessing the case of doomed turtle eggs. Environmental Management 38:523-531.

PACHAURI, R.K., ALLEN, M.R., BARROS, V., BROOME, J., CRAMER, W., CHRIST, R., CHURCH, J., CLARKE, L., DAHE, Q. AND DASGUPTA, P. 2014. Climate change 2014: synthesis Report. Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change. IPCC.

PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics:637-669.

PIKE, D.A. 2009. Do green turtles modify their nesting seasons in response to environmental temperatures? Chelonian Conservation and Biology 8(1), 43-47.

PIKE, D.A., AND STINER, J.C. 2007. Sea turtle species vary in their susceptibility to tropical cyclones. Oecologia 153:471-478.

POLOCZANSKA, E.S., LIMPUS, C.J., AND HAYS, G.C. 2009. Vulnerability of marine turtles to climate change. Advances in marine biology 56:151-211.

PRITCHARD, P.C.H., AND MARQUEZ, R. 1973. Kemp's ridley turtle or Atlantic ridley. IUCN Monograph No. 2, Morges, Switzerland..

RIGNOT, E., BAMBER, J.L., VAN DEN BROEKE, M.R., DAVIS, C., LI, Y., VAN DE BERG, W.J. AND VAN MEIJGAARD, E. 2008. Recent Antarctic ice mass loss from radar interferometry and regional climate modelling. Nature Geoscience, 1(2):106.

ROSTAL, D.C., AND PLOTKIN, P.T. 2007. Reproductive physiology of the ridley sea turtle. In: Biology and conservation of ridley sea turtles. Johns Hopkins University Press, Baltimore, Maryland:151-165.

SCHOFIELD, G., KATSELIDIS, K.A., LILLEY, M.K.S., REINA, R.D., AND HAYS, G.C. 2017. Detecting elusive aspects of wildlife ecology using drones: New insights on the mating dynamics and operational sex ratios of sea turtles. Functional Ecology.

SHAVER, D.J., AND CAILLOUET, C.W. 2015. Reintroduction of Kemp's ridley (*Lepidochelys kempii*) sea turtle to Padre Island National Seashore, Texas and its connection to head-starting. Herpetological Conservation and Biology 10:114-171.

SHAVER, D.J., HART, K.M., FUJISAKI, I., RUBIO, C., SARTAIN-IVERSON, A.R., PEÑA, J., GAMEZ, D.G., MIRON, R.D.J.G.D., BURCHFIELD, P.M., MARTINEZ, H.J. AND ORTIZ, J., 2016. Migratory corridors of adult female Kemp's ridley turtles in the Gulf of Mexico. Biological conservation, 194:158-167.

WALTHER, G.-R., POST, E., CONVEY, P., MENZEL, A., PARMESAN, C., BEEBEE, T.J.C., FROMENTIN, J.-M., HOEGH-GULDBERG, O., AND BAIRLEIN, F. 2002. Ecological responses to recent climate change. Nature 416:389-395.

WEISHAMPEL, J.F., BAGLEY, D.A., AND EHRHART, L.M. 2004. Earlier nesting by loggerhead sea turtles following sea surface warming. Global Change Biology 10:1424-1427.

WEISHAMPEL, J.F., BAGLEY, D.A., EHRHART, L.M., AND WEISHAMPEL, A.C. 2010. Nesting phenologies of two sympatric sea turtle species related to sea surface temperatures. Endangered Species Research 12:41-47.

WIBBELS, T. 2007. Sex determination and sex ratios in ridley turtles. In: Plotkin, P. (ed) Biology and conservation of ridley sea turtles. Johns Hopkins University Press, Baltimore, Maryland: 167 – 185.

WIBBELS, T. 2003. Critical approaches to sex determination in sea turtles. In: Lutz, P.L., Musick, J.A., AND Wyneken, J. (eds) The biology of sea turtles. CRC Press Boca Raton, FL, 103 – 134.

WOOD, D.W. AND BJORNDAL, K.A. 2000. Relation of temperature, moisture, salinity, and slope to nest site selection in loggerhead sea turtles. Copeia 1:119-128.

WOODY, J.B. 1989. International efforts in the conservation and management of Kemp's ridley sea turtle(*Lepidochelys kempi*).

YNTEMA, C.L., AND MROSOVSKY, N. 1980. Sexual differentiation in hatchling loggerheads (*Caretta caretta*) incubated at different controlled temperatures. Herpetologica 36:33-36.

SUMMARY

The impacts of anthropogenic climate change are already having wide-reaching effects across multiple ecosystems. Thermally-sensitive taxa such as sea turtles are particularly at risk (Fuentes and Hawkes 2011, Pachauri et al. 2014). Along with planning for continued global warming, including the management of deeper cold fronts, sea level rise, flooding rains, and more intense weather events, it is imperative that the scientific focus be placed on understanding how long-term ecosystem fluctuations will affect the life histories of thermally sensitive species, and the degree to which responses vary across taxa. The research presented in this dissertation provides valuable insights into how changes in environmental temperatures could impact a variety of aspects of the reproductive biology and ultimately, recovery and sustained conservation of endangered sea turtle populations. Re-evaluating the historic abundance of the Kemp's ridley sea turtle in the context of current nesting trends in the Gulf of Mexico demonstrates the importance of historic benchmarks in establishing recovery goals and assessing the effectiveness of conservation efforts. This re-assessment serves as a model for other sea turtle populations and could alter our perspective on the status of endangered sea turtles, as well as reform strategies for the recovery of additional species in future. Such information can also provide clues to the historic health of an ecosystem and its past ability to support large populations of marine megafauna (Gallaway et al. 2016a,b), which can frame our management decisions regarding the current and future status of a given ecosystem. The more we understand how ecosystems have changed from the past to recent years, the better we can anticipate how climate change will affect these habitats in the future.

Assessing how a given habitat is changing as a result of long-term environmental variability and the impact of these changes often requires a habitat-wide perspective and long-term data that is often not available for endangered species. A strength of the current research is the 18-year dataset generated by the collaborative recovery program for the Kemp’s ridley. These data provide the opportunity to assess the impact of climate change on the temperature-sensitive physiology of this species and ultimately its recovery. By extending our analysis of beach temperatures to the majority of the nesting habitat for the Kemps ridley, we provide an assessment of potential responses to a warming environment. This represents a critical step towards formulating optimal strategies for ensuring the survival and recovery of this endangered species under future environmental variability.

As thermally-sensitive species worldwide face unprecedented challenges, implementing novel methodologies to understand how ecosystems are changing has become key for resource managers developing response strategies. The current dissertation research capitalizes on the rapid advancement of drone technologies to advance the field of sea turtle conservation and management. We demonstrate that drone technology provides a powerful new tool to evaluate the behavioral activities of species within their dynamic habitats, especially in light of climate change. The ability to observe sea turtles in a variety of habitats and over geographic scales that have been traditionally difficult or impossible to assess, has expanded our understanding of the extent and connectivity of critical habitats including for example seasonal breeding and courtship areas adjacent to sea turtle nesting beaches. The widespread integration of drone technology into studies of wildlife has occurred rapidly, and often without full consideration of its potential biases and consequences. One key issue is that drones may alter the natural behaviors of a target species. If behavior is altered by auditory or visual drone-induced disturbance, the data collected will be biased. The current dissertation provides important baseline information essential for assessing the potential impact of drone disturbance on multiple species including sea birds, crocodiles, and sea turtles. These data will facilitate the development of ethical protocols to best facilitate non-intrusive drone-based observation of wildlife in future research studies.

Collectively, the research presented in this dissertation addresses topics regarding the broad scope of how anthropogenic climate change can drive long-term changes in ecosystems and the species that depend on these critical habitats. These results ultimately contribute to the development of more resilient conservation programs and optimal management strategies that can be used to shape the survival of endangered species worldwide. In the process, my findings and those of my collaborators demonstrate the successful use of novel methodologies to provide insight on species interactions and dynamic habitats. As such, the present dissertation paves the way for understanding the impacts of using drone technologies for marine wildlife and ecosystem studies, a giant step forward that I believe will revolutionize the way we protect, manage, and study the marine environment.

GENERAL LIST OF REFERENCES

Acevedo-Whitehouse, K., A. Rocha-Gosselin, and D. Gendron. 2010. A novel non-invasive tool for disease surveillance of free-ranging whales and its relevance to conservation programs. Animal Conservation **13**:217-225.

Ackerman, R. A. 1977. The respiratory gas exchange of sea turtle nests (Chelonia, *Caretta*). Respir. Physiol. **31**:19-38.

Ackerman, R. A., and H. D. Prange. 1972. Oxygen diffusion across a sea turtle (*Chelonia mydas*) egg shell. Comp. Biochem. Physiol. **43**:905-909.

Ackerman, R. A., R. C. Seagrave, R. Dmi'el, and A. Ar. 1985. Water and heat exchange between parchment-shelled reptile eggs and their surroundings. Copeia **1985**:703-711.

Adams, D. E. 1966. More about the ridley operation: Padre Island egg transplanting.

Aguilar, H. R. 1987. Influencia de la temperatura de incubacion sobre la determination del sexo y la duracion del periodoe incubaction en la tortuga lora (*Lepidochelys kempi*, Garman, 1880). Instituto Politecnico Nacional Mexico, D.F.

Allen, C. H. 1990. Guest editorial: Give ‘headstarting' a chance. Marine Turtle Newsletter **51**:12-16.

Bernardo, J., and P. T. Plotkin. 2007. An evolutionary perspective on the arribada phenomenon and reproductive behavioral polymorphism of olive ridley sea turtles (*Lepidochelys olivacea*). In: Biology and conservation of ridley sea turtles. The Johns Hopkins University Press, Baltimore:59-87.

Bevan, E. 2013. Implications of hatchling sex ratios and survival in the recovery program for the endangered Kemp's ridley sea turtle. MS Thesis, University of Alabama at Birmingham, Birmingham, AL.

Bevan, E., T. Wibbels, B. M. Z. Najera, M. A. C. Martine, L. A. M. Sarti, F. I. Martinez, J. M. Cuevas, T. Anderson, A. Bonka, M. H. Hernandez, L. J. Peña, and P. M. Burchfield. 2015. Unmanned Aerial Vehicles (UAVs) for monitoring sea turtles in near-shore waters. Marine Turtle Newsletter:19-22.

Bevan, E., T. Wibbels, E. Navarro, M. Rosas, B. M. Najera, L. Sarti, F. ILLESCAS, J. MONTANO, L. J. PEÑA, and P. BURCHFIELD. 2016. Using unmanned aerial vehicle (UAV) technology for locating, identifying, and monitoring courtship and mating behaviour in the green turtle (Chelonia mydas). Herpetol Rev. **47**:27-32.

Bleakney, J. S. 1965. Reports of marine turtles from New England and eastern Canada. Canadian Field-Naturalist **79**(2): 120-128.

Braun-McNeill, J., S. P. Epperly, D. W. Owens, L. Avens, E. Williams, and C. A. Harms. 2007. Seasonal reliability of testosterone radioimmunoassay (RIA) for predicting sex ratios of juvenile loggerhead (*Caretta caretta*) turtles. Herpetologica **63**:275-284.

Caillouet, C. W. 2011. Guest Editorial: Did the BP-Deepwater Horizon-Macondo oil spill change the age structure of the Kemp's ridley population? Marine Turtle Newsletter **130**: 1-2.

Caillouet, C. W. 2014. Interruption of the Kemp’s ridley population’s pre-2010 exponential growth in the Gulf of Mexico and its aftermath: one hypothesis. Marine Turtle Newsletter 143: 1-7.

Carr, A. 1952. Handbook of turtles of the United States, Canada and Baja, California. Comstock Publishing Association, Ithaca, N.Y.

Carr, A. F. 1942. Notes on sea turtles. Proc. New England Zool. Club. 16.

Chabot, D., and D. M. Bird. 2015. Wildlife research and management methods in the 21st century: Where do unmanned aircraft fit in? Journal of Unmanned Vehicle Systems **3**:137-155.

Chavez, H., M. Contreras-G, and T. Hernandez-D. 1968a. On the coast of Tamaulipas. Internat. Turt. Tort. Soc. J **2**:20-29.

Chávez, H., M. Contreras, and T. Hernandez-D. 1968b. On the coast of Tamaulipas. Part two. International Turtle and Tortoise Society Journal **2**:16-19.

Chávez, H., E. T. P. Hernández, and M. Contreras. 1967. Aspectos biologicos y proteccion de la Tortuga Lora, *Lepidochelys kempi* (Garman), en la costa de Tamaulipas, Mexico.

Clark, P., A. Weaver, E. Brook, E. Cook, T. Delworth, and K. Steffen. 2008. Introduction: Abrupt changes in the Earth’s climate system. Abrupt Climate Change:19-59.

Coyne, M., A. M. Landry Jr, and P. T. Plotkin. 2007. Population sex ratios and its impact on population models. In: Plotkin, P. T (ed) Biology and conservation of Ridley sea turtles. Johns Hopkins University Press, Baltimore, MD:191-211.

Crowder, L. B., S. R. Hopkins-Murphy, and J. A. Royle. 1995. Effects of turtle excluder devices (TEDs) on loggerhead sea turtle strandings with implications for conservation. Copeia:773-779.

Eckrich, C. E., and D. W. Owens. 1995. Solitary versus arribada nesting in the olive ridley sea turtles (*Lepidochelys olivacea*): a test of the predator-satiation hypothesis. Herpetologica:349-354.

Eich, A. M. L. 2009. Evolutionary and conservation implications of sex determination and hatchling depredation in Kemp's ridley sea turtles. PhD Diss., University of Alabama at Birmingham, Birmingham, AL.

Fisher, R. A. 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford.

Fontaine, C. T., S. A. Manzella, T. D. Williams, R. M. Harris, and W. J. Browning. 1989. Distribution, growth and survival of head-started, tagged and released Kemp's ridley sea turtles(Lepidochelys kempi) from year-classes 1978-1983.

Fuentes, M., and L. Hawkes. 2011. How will sea turtles cope with climate change? SWOT Report **6**:12-13.

Gallaway, B. J., et al. 2016 a. Development of a Kemp's ridley sea turtle stock assessment model. Gulf of Mexico Science **33**(2): 138-157.

Gallaway, B. J., W. J. Gazey, D. Shaver, T. Wibbels and E. Bevan. 2016 b. Evaluation of the status of the Kemp's ridley sea turtle following the 2010 Deepwater Horizon oil spill. Gulf of Mexico Science **33**(2): 192-202.

Garman, S. 1880. On certain species of Chelonioidae. Bulletin of the Museum of Comparative Zoology **6**:122-126.

Geis, A., T. Wibbels, R. Marquez-M, M. Garduno-D, P. Burchfield, and J. Peña-V. 2001. Predicted sex ratios of hatchling Kemp's ridleys produced in egg corrals during the 1998, 1999, and 2000 nesting seasons. *In:* Proceedings of the 21st International Sea Turtle Symposium., Philadelphia, PA.

Geis, A., T. Wibbels, B. Phillips, Z. Hillis-Starr, A. Meylan, P. Meylan, C. Diez, and R. Van Dam. 2003. Predicted Sex Ratio of Juvenile Hawksbill Seaturtles Inhabiting Buck Island Reef National Monument, US Virgin Islands. Journal of Herpetology:400-404.

Geis, A. A. 2004. Utilizing Technologies for Enhancing the Conservation of Sea Turtle Populations. 6151-6151.

Hansen, J., M. Sato, R. Ruedy, L. Nazarenko, A. Lacis, G. Schmidt, G. Russell, I. Aleinov, M. Bauer, and S. Bauer. 2005. Efficacy of climate forcings. Journal of Geophysical Research: Atmospheres **110**.

Hanson, J., T. Wibbels, and R. Martin. 1998. Predicted female bias in sex ratios of hatchling loggerhead sea turtles from a Florida nesting beach. Can. J. Zool. **76**:1-12.

Hendrickson, J. R. 1980. The ecological strategies of sea turtles. Amer. Zool. **20**:597-608.

Heppell, S. S., P. M. Burchfield, and L. J. Peña. 2007. Kemp's Ridley Recovery. In: Plotkin, P. (ed) Biology and Conservation of Ridley Sea Turtles:325.

Hildebrand, H. H. 1963. Hallazgo del area de anidacion de la tortuga marina "lora", *Lepidochelys kempi* (Garman), en la costa occidental del Golfo de Mexico (Rept., Chel.). Ciencia, Mexico **22**:105-112.

Hildebrand, H. H. 1982. Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Washington, D.C.

Hodgson, A. 2007. The distribution, abundance and conservation of dugongs and other marine megafauna in Shark Bay Marine Park, Ningaloo Reef Marine Park and Exmouth Gulf. Report to the Western Australia Department of Environment and Conservation September.

Hodgson, A., N. Kelly, and D. Peel. 2013. Unmanned aerial vehicles (UAVs) for surveying marine fauna: a dugong case study. PloS ONE **8**:e79556.

Hodgson, A., and H. Marsh. 2007. An evaluation of whale shark aerial surveys for monitoring whale shark abundance and distribution: future options.

Hodgson, J. C., S. M. Baylis, R. Mott, A. Herrod, and R. H. Clarke. 2016. Precision wildlife monitoring using unmanned aerial vehicles. **6**:22574.

Hodgson, J. C., R. Mott, S. M. Baylis, T. T. Pham, S. Wotherspoon, A. D. Kilpatrick, R. R. Segaran, I. Reid, A. Terauds, and L. P. Koh. 2017. Drones count wildlife more accurately and precisely than humans. bioRxiv:165019.

Jones, G. P., L. G. Pearlstine, and H. F. Percival. 2006. An assessment of small unmanned aerial vehicles for wildlife research. Wildlife Society Bulletin **34**:750-758.

Kroeker, K. J., R. L. Kordas, R. N. Crim, and G. G. Singh. 2010. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecology Letters **13**:1419-1434.

LeBlanc, A. M., T. Wibbels, D. Shaver, and J. S. Walker. 2012. Temperature-dependent sex determination in the Kemp’s ridley sea turtle: effects of incubation temperatures on sex ratios. Endangered Species Research, **19**(2): 123-128.

Lewison, R. L., L. B. Crowder, and D. J. Shaver. 2003. The impact of turtle excluder devices and fisheries closures on loggerhead and Kemp's ridley strandings in the western Gulf of Mexico. Conservation Biology **17**:1089-1097.

Lutz, P. L., J. A. Musick, and J. Wyneken. 2002. The biology of sea turtles. CRC press.

Marquez 1994. Synopsis of Biological Data on the Kemp's Ridley Turtle, Lepidochely kempi (Garman, 1880). NOAA Technical Memorandum NMFS-SEFC-343:91p.

Marquez, M. R. 1990. FAO species catalogue. Vol. 11. Sea turtles of the world. An annotated and illustrated catalogue of sea turtle species known to date. 125.

Marquez, M. R. 1994. Synopsis of Biological Data on the Kemp's Ridley Sea Turtle, *Lepidochelys kempi* (Garman, 1880). NOAA Technical Memorandum NMFS-SEFC-343:91p.

Marquez, R. 1984. Kemp's ridley turtle overview of biology. Pages 96-100 *In* Proceedings of the Western Atlantic Turtle Symposium. University of Miami Press, Miami.

Mickelson, L. E., and J. R. Downie. 2010. Influence of incubation temperature on morphology and locomotion performance of Leatherback (*Dermochelys coriacea*) hatchlings. Canadian Journal of Zoology-Revue Canadienne De Zoologie **88**:359-368.

O'Hara, J. 1980. Thermal influences on the swimming speed of loggerhead turtle hatchlings. Copeia:773-780.

Ogren, L. H. 1989. Distribution of juvenile and subadult Kemp’s ridley turtles: Preliminary results from the 1984-1987 surveys. *In* Proceedings from the 1st Symposium on Kemp’s ridley Sea Turtle Biology, Conservation, and Management. Sea Grant College Program, Galveston, TX.

Owens, D. W., J. R. Hendrickson, V. Lance, and I. P. Callard. 1978. A technique for determining sex of immature Chelonia mydas using radioimmunoassay. Herpetologica **34**:270-273.

Pachauri, R. K., M. R. Allen, V. Barros, J. Broome, W. Cramer, R. Christ, J. Church, L. Clarke, Q. Dahe, and P. Dasgupta. 2014. Climate change 2014: synthesis Report. Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change. IPCC.

Park, A. 2006. Sex ratios, sexing techniques, and the conservation of sea turtles. MS Thesis, University of Alabama at Birmingham, Birmingham, Alabama.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics:637-669.

Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds. 2005. Climate change and distribution shifts in marine fishes. Science **308**:1912-1915.

Poloczanska, E. S., C. J. Limpus, and G. C. Hays. 2009. Vulnerability of marine turtles to climate change. Advances in marine biology **56**:151-211.

Pritchard, P. C. H. 1969. Studies of the systematics and reproductive cycles of the genus *Lepidochelys*.

Pritchard, P. C. H., and R. Marquez 1973. Kemp's ridley turtle or Atlantic ridley., International Union for the Conservation of Nature and Natural Resources.

Pritchard, P. C. H., and P. Trebbau. 1984. The turtles of Venezuala. Contributions in Herpetology 2, Society for the Study of Amphibians and Reptiles, Caracas, Venezuela.

Putman, N. F., K. L. Mansfield, R. He, D. J. Shaver, and P. Verley. 2013. Predicting the distribution of oceanic-stage Kemp's ridley sea turtles. Biology letters **9**:20130345.

Rees, A. F., L. Avens, K. Ballorain, E. Bevan, A. C. Broderick, R. R. Carthy, M. J. A. Christianen, G. Duclos, M. R. Heithaus, D. W. Johnston, J. C. Mangel, F. Paladino, K. Pendoley, R. D. Reina, N. J. Robinson, R. Ryan, S. T. Sykora-Bodie, D. Tilley, M. R. Varela, E. R. Whitman, P. A. Whittock, T. Wibbels, and B. J. Godley. 2018. The potential of unmanned aerial systems for sea turtle research and conservation: a review and future directions. Endangered Species Research **35**:81-100.

Renaud, M., and S. F. Center. 1990. Evaluation of the impacts of turtle excluder devices (TEDs) on shrimp catch rates in the Gulf of Mexico and South Atlantic, March 1988 through July 1989. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.

Rostal, D. C., and P. T. Plotkin. 2007. Reproductive physiology of the ridley sea turtle. Biology and conservation of ridley sea turtles. Johns Hopkins University Press, Baltimore, Maryland:151-165.

Schmid, J. R., and W. N. Witzell. 1997. Age and growth of wild Kemp's ridley turtles (*Lepidochelys kempi*): cumulative results of tagging studies in Florida. Chelonian Conservation and Biology **2**:532-537.

Schofield, G., K. A. Katselidis, M. K. S. Lilley, R. D. Reina, and G. C. Hays. 2017a. Detecting elusive aspects of wildlife ecology using drones: New insights on the mating dynamics and operational sex ratios of sea turtles. Functional Ecology.

Schofield, G., K. Papafitsoros, R. Haughey, and K. Katselidis. 2017b. Aerial and underwater surveys reveal temporal variation in cleaning-station use by sea turtles at a temperate breeding area. Marine Ecology Progress Series **575**:153-164.

Shaver, D. J., D. W. Owens, A. H. Chaney, C. W. Caillouet, P. Burchfield, and R. Marquez 1988. Styrofoam box and beach temperatures in relation to incubation and sex ratios of Kemp's ridley sea turtles. Pages 103-108 In: Proceedings of the Eighth Annual Workshop on Sea Turtle Biology and Conservation.

Shaver, D. J., and T. Wibbels. 2007. Head-starting the Kemp's ridley sea turtle. In: Plotkin, PT (ed) Biology and conservation of ridley sea turtles.. The Johns Hopkins University Press, Baltimore:297-323.

Smith, C. E., S. T. Sykora-Bodie, B. Bloodworth, S. M. Pack, T. R. Spradlin, and N. R. LeBoeuf. 2016. Assessment of known impacts of unmanned aerial systems (UAS) on marine mammals: data gaps and recommendations for researchers in the United States. Journal of Unmanned Vehicle Systems **4**:31-44.

Snover, M. L., A. A. Hohn, L. B. Crowder, and S. S. Heppell. 2007. Age and growth in Kemp’s ridley sea turtles. Biology and conservation of Ridley sea turtles. Johns Hopkins University Press, Baltimore, MD:89-105.

TEWG, 2000. Assessment Update for the Kemp's Ridley and Loggerhead Sea Turtle Populations in the Western North Atlantic. U.S. Dep. Commer. NOAA Tech. Mem. NMFS-SEFSC-444:115 pp.

Valenzuela, N. 2001. Constant, shift, and natural temperature effects on sex determination in *Podocnemis expansa* turtles. Ecology **82**:3010-3024.

Vas, E., A. Lescroël, O. Duriez, G. Boguszewski, and D. Grémillet. 2015. Approaching birds with drones: first experiments and ethical guidelines. Biology letters **11**:20140754.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature **416**:389-395.

Weishampel, J. F., D. A. Bagley, and L. M. Ehrhart. 2004. Earlier nesting by loggerhead sea turtles following sea surface warming. Global Change Biology **10**:1424-1427.

Weishampel, J. F., D. A. Bagley, L. M. Ehrhart, and A. C. Weishampel. 2010. Nesting phenologies of two sympatric sea turtle species related to sea surface temperatures. Endangered Species Research **12**:41-47.

Werler, J. E. 1951. Miscellaneous notes on the eggs and young of Texan and Mexican reptiles. Zoologica **36**:37-48.

Wibbels, T. 1992. Kemp's ridley sea turtles. Science **257**:465.

Wibbels, T. 2003. Critical approaches to sex determination in sea turtles. Pages 103-134 In: P. L. Lutz, J. A. Musick, and J. Wyneken (eds) The biology of sea turtles. CRC Press Boca Raton, FL.

Wibbels, T., J. Cowan, and R. LeBoeuf. 1998. Temperature-dependent sex determination in the red-eared slider turtle, Trachemys scripta. Journal of Experimental Zoology **281**:409-416.

Wibbels, T., D. W. Owens, and C. J. Limpus. 2000. Sexing juvenile sea turtles: Is there an accurate and practical method? Chel. Conserv. Biol **3**(4): 756-761.

Wibbels, T., D. W. Owens, and D. C. Rostal. 1991. Soft plastra of adult male sea turtles: An apparent secondary sexual characteristic. Herpetol. Rev. **22**:47-49.

Witzell, W., A. Salgado-Quintero, and M. Garduño-Dionte. 2005. Reproductive parameters of the Kemp's ridley sea turtle (*Lepidochelys kempii*) at Rancho Nuevo, Tamaulipas, Mexico. Chelonian Conservation and Biology **4**:781-787.

Witzell, W. N., and J. R. Schmid. 2005. Diet of immature Kemp's ridley turtles (*Lepidochelys kempi*) from Gullivan Bay, Ten Thousand Islands, southwest Florida. Bulletin of Marine Science **77**:191-200.

Woody, J. B. 1989. International efforts in the conservation and management of Kemp's ridley sea turtle (*Lepidochelys kempi*).

Yntema, C. L., and N. Mrosovsky. 1979. Incubation temperature and sex ratio in hatchling loggerhead turtles: a preliminary report. Marine Turtle Newsletter **11**:9-10.