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Implications Of Hatchling Sex Ratios And Survival In The Recovery Program For The Endangered Kemp'S Ridley Sea Turtle

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IMPLICATIONS OF HATCHLING SEX RATIOS AND SURVIVAL IN THE RECOVERY PROGRAM FOR THE ENDANGERED KEMP'S RIDLEY SEA TURTLE

by

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A THESIS

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IMPLICATIONS OF HATCHLING SEX RATIOS AND SURVIVAL IN THE RECOVERY PROGRAM FOR THE ENDANGERED KEMP'S RIDLEY SEA TURTLE

ELIZABETH BEVAN

BIOLOGY

ABSTRACT

The Kemp's ridley (*Lepidochelys kempii*) sea turtle neared extinction during the mid-1980s, but due to intense conservation efforts its population is now gradually recovering. Hatchling sex ratios and natural predation on nests and hatchlings have been monitored at Rancho Nuevo, Mexico to optimize this species' recovery. Sand and nest temperatures were evaluated for the 2009 - 2012 nesting seasons in the egg corrals and on the nesting beach. Temperatures were cool during the start of the nesting seasons (i.e. below pivotal temperature), and gradually rose and were at or above pivotal temperatures by mid-May. Temperatures remained warm for the remainder of the nesting seasons, except when tropical weather systems impacted the area and lowered incubation temperatures. Thus, a female bias was predicted from 2009 - 2012, but some nests early in the nesting season or those subjected to tropical weather systems during the middle third of incubation were predicted to produce males. The nesting beach was also warm (suggesting a female bias) but it was cooler than the egg corrals.

Sex ratios for the egg corrals and nesting beach were recalculated using incubation temperatures that were raised by 1°C to hypothetically simulate the effects of increasing global temperatures on hatchling sex ratios. Increases in sand temperatures due to global climate change could result in extreme female biases for the egg corrals and the nesting beach.

Subsets of *in situ* nests from arribadas in 2011 and 2012 were monitored for predation throughout incubation and hatching success was determined following emergence. Predation on *in situ* nests was low and hatching success relatively high. Additionally, survival of hatchlings during seafinding was evaluated for *in situ* nests in 2012 and results suggest relatively high survival rates. Evaluation of predation data supports the concept that arribadas may achieve predator satiation, thus enhancing nest and hatchling survival. Leaving arribada nests *in situ* may be an effective conservation strategy. These sex ratio and predation studies provide data to facilitate an effective transition from the use of egg corrals back to the use of the natural nesting beach as the Kemp's ridley recovers.

Keywords: temperature-dependent sex determination, *Lepidochelys kempii*, sea turtle, sex ratios

DEDICATION

This thesis is ultimately possible because of the loving support of my family and friends who have done more than their fair share of listening to me whine.

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NEST AND HATCHLING SURVIVAL AT RANCHO NUEVO, THE PRIMARY NESTING BEACH OF THE KEMP'S RIDLEY SEA TURTLE

LIST OF ABBREVIATIONS

PSH	predator satiation hypothesis
TRT	transitional range of temperatures
TSD	temperature-dependent sex determination
TSP	thermosensitive period

GENERAL INTRODUCTION

History and Conservation Status

Once abundant in the Gulf of Mexico, the Kemp's ridley (*Lepidochelys kempii)* became the world's most endangered sea turtle as its numbers fell to near extinction during the 1980's. In the mid 1900's, juvenile Kemp's ridleys were frequently encountered in the Gulf of Mexico, but information on adults was scarce. At that time, there was no scientific documentation on nesting in this species. This prompted some scientists to investigate the "riddle of the ridley", and led some fishermen to develop the misconstrued notion that the Kemp's ridley could potentially be a hybrid of the loggerhead sea turtle, *Caretta caretta*, and the hawksbill sea turtle, *Eretmochelys imbricata*, earning it the nickname "bastard turtle" (Carr and Caldwell, 1958). The mystery was finally revealed to the scientific community in 1963 when Hildebrand discovered previous footage of a Kemp's ridley mass nesting event on remote beach in the western Gulf of Mexico near Rancho Nuevo, Mexico. The film that Hildebrand discovered was shot by Andres Herrera in June of 1947 and showed an estimated 40,000 Kemp's ridleys nesting during a single arribada (mass nesting event) (Hildebrand, 1963). This astonishing abundance, however, dwindled to a mere 740 nests for an entire nesting season by the mid 1980's due to intense exploitation of eggs and incidental by-catch in commercial fisheries (Marquez, 1994).

Kemp's ridleys feed primarily on benthic crustaceans which has resulted in a high rate of mortality from incidental capture in shrimp trawls and significantly hindered the recovery of this species. At one point, the turtles were caught 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 (Carr and Caldwell, 1958). The drastic decline of the Kemp's ridley population prompted intense conservation efforts. In 1966, a conservation program was started 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" (Burchfield, 1998; Marquez, 1994). Before this program was initiated the majority of sea turtle nests were harvested by humans or destroyed by predators. Despite this effort at the nesting beach, the numbers of nesting females continued to dwindle. Due to the continued decline of the Kemp's ridley, the conservation program was expanded in 1978 to a bi-national collaboration between the United States and Mexico to enhance the restoration of this species (Fontaine et al., 1989; Marquez, 1984; Woody, 1989). From 1978 to 1988, in hopes of instigating a second nesting site, up to 2,000 eggs were transported yearly to Padre Island for "imprinting" and incubation (Owens et al., 1982a; Shaver and Wibbels, 2007). 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 (Shaver and Wibbels, 2007). 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 (Witzell, 1983; Shaver et al., 1988a; Frazer, 1992; Wibbels et al., 1998b). Imprinting efforts were ended in 1988 and starting in 1989 all hatchlings remained in Mexican sand during incubation before a subset was sent to

Galveston, Texas, for headstarting. This protocol was continued with Kemps ridley hatchlings until the program's end in 1992 (Klima and McVey, 1982; Shaver and Wibbels, 2007). Following the implementation of turtle excluder devices, the Kemp's ridley population began to slowly recover in the 1990's. As the number of nesting females slowly rose, additional egg corrals were added on the beach to the north and south of Rancho Nuevo (NMFS and USFWS, 2007). Kemp's ridley nesting steadily increased through 2009 with a relatively rapid rate of recovery, reaching approximately 20,000 nests laid annually on the coast of Tamaulipas in 2009. However, a significant decline in nesting occurred in 2010 to approximately 13,000 nests, followed by an increase back to approximately 20,000 nests annually in 2011 and 2012. The reason for the decline of nesting numbers in 2010 is not clear but could relate to environmental factors such as cold stunning and the Deepwater Horizon oil spill. Further, the recent leveling off of nesting numbers could also be due to these factors, as well as other factors such as nearing the Gulf of Mexico's carrying capacity for the species.

Biology and Ecology

As adults, the grey-colored Kemp's ridley is the smallest of all sea turtle species with adults generally ranging from approximately 60 to 65 cm straight carapace lengths and weights of 32 to 49 kg (Heppell et al., 2005). They are opportunistic feeders, feeding primarily on crustaceans and tunicates, particularly crabs (Marquez, 1994; Witzell and Schmid, 2005). Though there may be differences in diet between life stages, Kemp's ridleys show a strong preference for benthic crabs (primarily spider, purse, calico or blue crabs) and generally feed in waters less than 50 meters deep (Ogren, 1989; Witzell and

Schmid, 2005; Marquez, 1994). *Lepidochelys kempii* 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). However, growth rate and age to maturity estimates vary and may reflect the particular habitat of the turtle (Schmid and Witzell, 1997; Snover et al., 2007). 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 (NMFS and USFWS, 2007). Growth rate and activity levels have been directly correlated to temperature for captive hatchling and juvenile Kemp's ridleys (Márquez, 1994). The swimming speed and behavior of the Kemp's ridley are affected by temperature, which partially determine its geographic distribution (O'Hara, 1980).

Distribution/Nesting Range

Subadult Kemp's ridleys inhabit coastal waters from Texas to Massachusetts, while adults remain mainly in the Gulf of Mexico (Marquez, 1994). Swimming offshore from Rancho Nuevo, hatchlings ride the gyres of the Gulf of Mexico's currents, possibly associated with mats of seagrasses, until about two years of age. 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), although a few ridleys have been documented in northeastern Atlantic (Carr, 1980; Carr and Caldwell, 1956). It is believed that main foraging areas for ridleys include the eastern Gulf of Mexico including Florida Bay, the Northern Gulf of Mexico associated with the Mississippi river drainage, and Campeche Sound (Marquez, 1994). These crustacean-rich feeding grounds are important areas for juveniles through adult stages. Though the range for juveniles and subadults may include the Atlantic coast of the U.S., adult Kemp's ridleys are primarily found in the Gulf of Mexico (Pritchard and Marquez-M, 1973). This limited distribution and nesting range make the Kemp's ridley exceptionally vulnerable to extinction from anthropogenic and other causes of mortality. Unlike other sea turtle species, almost all Kemp's ridley nesting occurs from Texas to Campeche with the majority concentrated on a single, 40 km stretch of beach near Rancho Nuevo, Tamaulipas, Mexico during the months of April through July (Marquez, 1994).

A unique characteristic of sea turtles is the ability to return to natal beaches as adults to nest. Though not thoroughly understood, this characteristic plays a major role in the ability of the majority of the Kemp's ridley population to navigate their migratory routes back to the same stretch of beach along the western Gulf of Mexico (Grassman and Owens, 1989). As female Kemp's ridleys emerge from the ocean, they push their beak into the sand, a behavior unique to ridley turtles and thought to potentially aid in nest site selection. This could also be potentially useful in the perception of beach characteristics such as grain size, humidity, temperature, roots and other obstacles or the odor of millions of incubating eggs that could play a role in finding the nesting beach and in arribada synchronization (Pritchard, 1969).

Arribada Nesting Behavior

Lepidochelys is the only genus known to consistently nest in synchronized events termed "*arribadas*", although some may nest alone (Eckrich and Owens, 1995; Pritchard and Marquez-M., 1973). These events average approximately 25 days apart, but this timing can be quite unpredictable (Bernardo and Plotkin, 2007). Though various physiological and environmental factors have been suggested as possible cues instigating an arribada, such as strong winds, tidal cycle, lunar phase, and changes in temperature, the exact stimuli for this phenomenon remain unknown (Pritchard and Marquez-M., 1973; Pritchard, 1969; Owens et al., 1982b). Nesting during high winds may help to erase shallow tracks on the beach that could reveal the presence or location of a nest to a predator. Wind may also carry away any olfactory cues emitted during the nesting process that predators may also use to hone in on nest location (Bernardo and Plotkin, 2007).

One possible justification for the maintenance of arribadas is its potential facilitation of mating. The occurrence of multiple mating, and thus multiple paternities among sea turtles suggests it plays an important role in the reproductive success and fitness for both males and females (Pearse and Avise, 2001). It is possible that arribada aggregations have evolved to facilitate a multiple mating strategy by drawing males and females to a common breeding area, and thus preserve greater reproductive fitness for the species (Bernardo and Plotkin, 2007). Another potential advantage of arribada behavior would be to enhance hatchling survival through predator satiation (see discussion below under predation).

The migration to Rancho Nuevo, along with events leading to an arribada could involve a variety of factors and cues. Characteristics of the natal beach, such as odor, humidity, temperature, and other chemical factors, could represent important cues for “imprinting” in hatchling sea turtles, enabling the females to return to their beach of origin to lay nests of their own. The natal homing of sea turtles likely plays an important role in the return of nesting females to Rancho Nuevo for each reproductive season

(Grassman and Owens, 1989). In addition to the imprinting hypothesis, it is also plausible that "social facilitation" could play a role in natal homing as well as arribada behavior (Hendrickson, 1958; Owens et al., 1982b). In this hypothesis, neophyte females would follow "experienced" nesters to previously established nesting areas to "learn" the unique cues of that beach to aid in future nesting migrations.

It is plausible that social interaction/communication involved in arribada behavior and/or migrations could be chemical-based. *Lepidochelys* is the only genus of marine turtle to possess inframarginal pores, called "Rathke glands" that secrete pheromone-like substances. It has been hypothesized that such pheromones could aid in the coordination of arribadas (Pritchard, 1969; Pritchard and Trebbau, 1984; Marquez, 1990).

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). In addition to Kemp's ridleys, Green (*Chelonia mydas*), loggerhead (*Caretta caretta*), and occasionally leatherback sea turtles (*Dermochelys coriacea*) also nest on the beaches of Rancho Nuevo, though their lower numbers have generally prevented competition for nesting space with the Kemp's ridley. Seasonal separation and different preferred nest site locations on the beach dune also prevent competition between the species nesting on these beaches (Marquez, 1994).

Nesting Behavior

Spending only 50-60 minutes on the nesting process, Kemp's ridleys lay the shallowest (35-40 cm deep) of all marine turtles. Their crawls are relatively light for a sea turtle species and are easily blown away or covered with high winds. When covering their nest, they use lateral blows of their uniquely round and depressed bodies to compact sand over freshly-laid nests (Marquez, 1994). The remigration interval for Kemp's ridleys has been estimated to be approximately 1.8 (Rostal and Plotkin, 2007) to 2.0 years (TEWG, 2000). Females are estimated to lay approximately 3.075 nests per season with an average of 94-97 eggs per nest. Nests incubate for approximately 45-58 days before hatching (Rostal and Plotkin, 2007; Marquez, 1994). The eggs typically turn pure white with the start of incubation (one day after being laid) and require at least 15-18% humidity within the incubation environment to become turgid (Marquez, 1994). However, eggs may also become dark, yellow, grey or rose-colored if infertile (Marquez, 1994).

Hatchlings

Upon completion of incubation, hatchlings pip their shells, allowing the amniotic fluid to drain into the surrounding nest chamber. Sea turtle hatchlings have been reported to take between 3 and 7 days from hatching to first emergence from the nest (Balazs and Ross, 1974; Christens, 1990), but this subject has never been addressed in the Kemp's ridley. Carr and Ogren (1960) showed that hatchlings synchronize their efforts in digging to the surface with spastic activity of turtles on the bottom of the clutch instigating activity in those above. Once the clutch reaches the surface, activity of the hatchlings below is determined by hatchlings at the top that are exposed to the temperature fluctuations on the surface of the sand (Bustard and Greenham, 1968).

Once the "roof" of sand over the nest collapses, forming a depression, hatchlings may rest for one to two days just beneath the sand surface and then emerge, causing the sand to appear to "boil" with hatchlings (Hernández et al., 1967; Pritchard and Marquez-M, 1973). Traditionally, sea turtle hatchlings have been thought to emerge collectively (Carr, 1986; Dodd, 1988; LeBuff Jr, 1990; Nelson, 1988), thereby increasing their chances of successful ascent through the sand through social facilitation (Carr and Hirth, 1961) and satiation of predators in their escape from the nest to the sea (Pritchard, 1969; Hendrickson, 1980; Eckrich and Owens, 1995; Bustard, 1972; Delm, 1990) . However, there is substantial documentation that emergence from a single nest may span several nights (Limpus, 1985; Hendrickson, 1958; Diamond, 1976; Witherington et al., 1990). Hendrickson (1958) noted that approximately half of all nests have hatchlings emerge on more than one night. Hatchlings typically emerge during the cooler hours of night from the nest usually in less than an hour (Hernández et al., 1967; Pritchard and Marquez-M., 1973), though small numbers of diurnally emerging hatchlings have been reported (Balazs and Ross, 1974; Drake and Spotila, 2002; Glen et al., 2005; Bustard and Greenham, 1968). A nighttime emergence not only reduces the risk of heat stress and desiccation, but also the chance of being visually detected by predators (Marquez, 1990). However, with more time spent waiting for these ideal conditions, the chance that hatchlings will be detected by predators (Godley and Broderick, 1992) or the nest will become infested with insects (McGowan et al., 2001) increases. Waiting also uses up a hatchling's crucial energy reserves that would otherwise be used in their frenzied activity to get to offshore waters (Hays et al., 1992). Ensuring that the nest emerges at an optimum time is therefore of importance to the survival of sea turtle hatchlings.

Most studies have pointed to temperature as an important cue in distinguishing the optimal time of day to emerge, yet the exact mechanism by which temperature initiates emergence is not known (Hays et al., 1992; Witherington et al., 1990; Mrosovsky and Shettleworth, 1968; Bustard and Greenham, 1968; Moran et al., 1999; Hendrickson, 1958). Reports of hatchling emergence following rain showers would support rapidly cooling sand temperatures as a potential cue for emergence (Witherington et al., 1990).

Sex Determination and Secondary Sexual Characteristics

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 egg. In all sea turtles, cooler incubation temperatures produce males while warmer temperatures result in females. Previous studies have shown that temperature affects sex determination during the middle third of incubation (Mrosovsky and Yntema, 1980; Merchant-Larios et al., 1989; Mrosovsky and Pieau, 1991). The temperature range over which the sex ratio shifts from 100% male hatchlings to 100% female hatchlings is termed the "transitional range of temperatures" (TRT). Within the TRT there is a "pivotal temperature" at which a 1:1 sex ratio is produced (Mrosovsky and Yntema, 1980). These parameters have been determined by incubating groups of eggs in laboratory incubators at constant temperatures and then verifying the sex ratio of each group through histological examination of hatchling gonads.

Estimating Sea Turtle Sex Ratios

Secondary sexual characteristics in sea turtles are not exhibited until reaching pubescence, at which point the males develop long muscular tails, a somewhat softened plastron, and more pronounced claws on their front flippers in comparison to females. These secondary sex characteristics are not present in immature sea turtles. The sex of immature sea turtles can be determined by viewing internal features using laparoscopy on live individuals or necropsy of dead turtles. Other, less-invasive methods have also been used to distinguish between males and females, such as measuring blood testosterone levels (Wibbels et al., 2000). Although testosterone affects the reproductive physiology of both sexes, serum testosterone levels are generally higher in males than females in immature sea turtles (Owens et al., 1978; Wibbels et al., 2000). Unfortunately, the logistics associated with evaluating the sex of immature sea turtles (e.g. laparoscopy, dissection) has generally limited large scale studies for sex ratio estimates for most sea turtle populations. This also extends to studies evaluating hatchling sex ratios produced in sea turtle populations. Estimating hatchling sex ratios is even more limited because testosterone levels have not been shown to be a clear predictor of sex in hatchlings (Wibbels et al., 2000; Gross et al., 1995). Traditionally, hatchling sex ratio studies have examined gonadal histology to verify sex. However, a major drawback to this method when working with endangered sea turtles is that it requires the killing of hatchlings, therefore, non-lethal methods of estimating sex ratios are preferred.

If the pivotal temperature and TRT for a sea turtle population are known, the mean temperature experienced during the thermosensitive period, or middle third of incubation, has been used to estimate hatchling sex ratios on the beach(Valenzuela, 2001;

Hanson et al., 1998; Wibbels et al., 1998a; Merchant-Larios et al., 1997; Shaver and Wibbels, 2007; LeBlanc et al., 2012; Eich, 2009). Previous data suggest that the TRTs for sea turtles are rather narrow (e.g. 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).

Several studies have addressed the TRT and pivotal temperature in the Kemp's ridley sea turtle. Shaver et al. (1988) studied the effects of temperature on sex ratios for nests between 1982 and 1987 and estimated the pivotal temperature for the Kemp's ridley to be approximately 30.2˚C. From 1978 to 1988 the effects of incubating eggs in Styrofoam boxes at Padre Island National Seashore and shading egg corrals were not known (Shaver et al., 1988b; Wibbels et al., 1989). Based on the pivotal temperature from 1985, the majority of hatchlings produced in the early years of the recovery program (1978 to 1984) were estimated to be male and incubation temperatures were then raised in an effort to produce predominantly female cohorts until 1992 (Shaver et al., 1988b; Wibbels et al., 1989).

From an evolutionary perspective, a 1:1 sex ratio could be predicted for a population in which parental investment in both sexes is equal (Fisher, 1930). However, previous studies suggest that TSD has the potential to produce a wide variety of sex ratios (Shine, 1999; Wibbels, 2003). For example, the majority of hatchling sex ratios reported in previous studies do not adhere to the expected 1:1 value, including the Kemp's ridleys at Rancho Nuevo (Wibbels, 2003). Biased sex ratios could prove to be advantageous to endangered populations. Female biases has been reported for many sea turtle populations and a greater percentage of females could facilitate an endangered population's recovery through greater egg production (Wibbels, 2003; Coyne et al., 2007). TSD could therefore be used as a conservation tool for enhancing the recovery of endangered populations (Coyne et al., 2007; Wibbels, 2003; Witzell et al., 2005).

Previous studies estimate a 75.6% and 76.1% female bias for the egg corral at Rancho Nuevo during the 2007 and 2008 nesting seasons, respectively (Eich, 2009). Due to conservation measures, most Kemp's ridley nests have been moved to the egg corral since 1966 (Hernández et al., 1967). Temperature data from the egg corral during each nesting season since 1998 show a similar temperature regime to temperatures recorded during the 2007 and 2008 sex ratio study. These data thus suggest a long-term, female-biased sex ratio has been produced from the Rancho Nuevo egg corral (NMFS and USFWS, 2007).

Temperature data since 1998 have also shown that the egg corral is typically warmer than temperatures on the natural nesting beach (Geis et al., 2001; Geis, 2004; Geis et al., 2005; Park, 2006; Eich, 2009). Thus, in general, nests moved to the egg corral tend to produce more female hatchlings than nests left out on the natural nesting beach to incubate (Eich, 2009). The egg corral has therefore generally produced a greater female bias than the natural nesting beach, though the natural nesting beach has still produced a female bias (Eich, 2009). Hypothetically, if the nests that were moved to the egg corral in 2007 and 2008 were left to incubate *in situ* on the natural nesting beach, the predicted sex ratios for each year would have been 53.7 % and 56.1%, respectively (Eich, 2009).

As the Kemp's ridley continues to recover, a greater portion of nests from each season will be left out on the natural nesting beach to incubate *in situ* once the egg corrals reach maximum capacity. The Recovery Program is therefore shifting from using egg corrals to leaving nests *in situ*, thus potentially changing the sex ratio and likewise the recovery rate for this species. A lower female biased sex ratio may, however, reflect a more natural sex ratio for the Kemp's ridley (Geis et al., 2000; Geis et al., 2001; Geis et al., 2002; Geis, 2004; Geis et al., 2005).

Other Factors That Influence Sex Ratio

Factors such as vegetation, rainfall, metabolic heating from within nests, and seasonal variation in beach temperatures can influence the incubation environment and therefore also affect hatchling sex ratios. Over the course of incubation in the nest, the metabolic rate and oxygen consumption of each embryo increases with development (Ackerman and Prange, 1972; Ackerman, 1977). This results in a corresponding rise in nest temperature above that of the surrounding sand during incubation (Bustard and Greenham, 1968; Godfrey et al., 1997; Bustard, 1972; Broderick et al., 2001). Sex ratios are also influenced by rain events throughout the season that can have a cooling effect on incubation temperatures (Mrosovsky et al., 1984; LeBlanc, 2004; Eich, 2009). Long-term data on beach temperatures and hatchling sex ratios for sea turtles is generally lacking. However, the Kemp's ridley nesting beach at Rancho Nuevo represents a unique opportunity to generate such a data base since the great majority of the species nests in a single location, and that beach has been the subject of intense conservation work for several decades.

Climactic changes can significantly impact species with TSD (Janzen, 1994). Changes in incubation temperatures can alter sex ratios and reproductive biology, which in turn directly influence the reproductive ecology of a population. Since many species with TSD are threatened or endangered, it is of conservational interest to monitor sex ratios in light of mounting evidence of global climate change. It is plausible that as temperatures increase we could see extreme female biases where males become limited in the population, increases in hatchling mortality (see below), and changes in nesting phenology (Janzen, 1994; Schwanz and Janzen, 2008).

Egg and Hatchling Survival

The successful incubation of eggs and production of hatchlings is critical to the conservation of endangered sea turtles. A variety of factors can affect nest survival and hatchling production including excessive rainfall, tidal inundation, beach erosion due to weather events, predation, translocation of nests in conservation programs, and extreme temperatures (Marquez, 1994). Saturating nests with excessive rainfall can drown the embryos or stimulate the growth of fungus within the nest (Burchfield et al., 1985). Fungus within the nest has been shown to cause higher rates of deformity in embryos and increase egg mortality (Burchfield et al., 1985). Counter-intuitively, conservation related activities can also increase mortality of sea turtle embryos by handling and transporting eggs to hatcheries (Mickelson and Downie, 2010). Studies on both hawksbills (Goodwin, 1981) and olive ridleys (Marquez et al., 1976) found that embryos are the most sensitive to movement during the early part of incubation and handling the eggs 6-48 hours after being laid can result in up to 100% mortality of nests. Similar results were found among Australian loggerhead and green sea turtle populations with mere gentle movement between 12 hours and 14 days after deposition resulting in significant decreases in nest success (Mickelson and Downie, 2010).

Predation also represents a major threat to sea turtle egg and hatchling survival. A nesting female can potentially emit certain scents, noises and other cues during the nesting process that may attract predators (Stancyk et al., 1980). Nests are therefore typically more easily detected by predators on the night they are laid, with the ease of detection diminishing as these signs fade with rain, wind and time in the environment (Fowler, 1979; Anderson, 1981). The risk of predation may also increase near the time of hatching and emergence due to the odor emitted from released amniotic fluid and decomposing shells (Marquez, 1994). Previous studies note coyotes, raccoons, skunks, ghost crabs, and birds are some of the primary predators that impact Kemp’s ridley nests and hatchlings (Eich, 2009). These predators may only devour a portion of the eggs, but this leaves the nest open and susceptible to infestation by ants, fly maggots, mites, and bacteria. Buzzards, caracara and grackles opportunistically feed upon eggs that have already been uncovered and although birds, such as herons, avocets, terns, gulls, and gallinules have been sighted around nests, including those at Rancho Nuevo, none have been observed to dig up sea turtle eggs directly (Eich, 2009; Marquez-M.R., 1994). Many of these infestations and predators gain access to the nest through ghost crab burrows (Cornelius and Robinson, 1982). Ghost crab predation can also be a significant source of nest mortality, both by the direct consuming eggs or providing access to eggs for other predators.

Sea turtle hatchlings are particularly vulnerable to predation on their crawl from the nest to the water following emergence. The hatchlings begin a period of constant activity, or a “frenzy period”, to hasten seafinding and facilitate transport to offshore habitat (Carr, 1963; Wyneken and Salmon, 1992; Salmon and Wyneken, 1987). This frenzied activity, however, can also make hatchlings more easily detected by predators. This threat of predation continues after reaching the sea as risk of attack continues from carnivorous birds, fishes and sharks (Marquez-M.R., 1994).

Synchronized nesting in ridleys could be an adaptive response to high predation pressure on nests and hatchlings. Overwhelming predators with an abundance of prey (i.e. nests or hatchlings) in a short period of time has been termed the “predator satiation hypothesis” (PSH) (Hendrickson, 1980). The combined odors of many females nesting 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). It is therefore possible that ridleys nest in *arribadas* to decrease predation through predator satiation (Bernardo and Plotkin, 2007).

Overview of Thesis Objectives

The purpose of the current thesis is to address several major topics related to the biology and conservation of the Kemp’s ridley sea turtle. The first chapter of this study evaluates the hatchling sex ratio being produced at Rancho Nuevo, Mexico. Sand and nest temperatures from the egg corrals and natural nesting beach were monitored throughout the 2009, 2010, 2011, and 2012 nesting seasons. These data were used to predict sex ratios produced in the Kemp's Ridley Recovery Program. Further, this study compared the two different incubation environments, the egg corral and the natural nesting beach, to evaluate the effects that leaving nests to incubate *in situ* has on hatchling sex ratios. These data aid in the analysis of long-term effects of incubation temperatures on hatchling sex ratios and ultimately the recovery rate of this species. Additionally, a hypothetical model was also developed to simulate the effects of global climate change on the sex ratios produced in the Recovery Program. This model could prove valuable for future decisions regarding the conservation and management of this species.

The second chapter of this thesis evaluated the survival of nests and hatchlings on the natural nesting beach. A subset of *in situ* nests from arribadas during the 2011 and 2012 nesting seasons were monitored daily for signs of predation to evaluate natural predation rate on nests during the period of incubation. Hatching success, emergence success, and hatchling survival from the nest to the surf were recorded for these *in situ* nests. These data were used to evaluate arribada nesting as a means of reducing the natural predation rate through predator satiation. These data support the use of the arribada nesting strategy as a useful management tool as the number of Kemp's ridley nests continues to grow with the recovery of the species.

Collectively, the data gathered in this thesis provide basic information on the biology and ecology of the Kemp's ridley. Further, this information will be used to optimize the management strategy for the Kemp’s ridley and thus enhance the recovery of this critically endangered sea turtle.

HATCHLING SEX RATIOS AT THE PRIMARY NESTING BEACH OF THE KEMP'S RIDLEY SEA TURTLE

by

Elizabeth Bevan and Thane Wibbels

In Preparation for *Ecosphere*

Format adapted for thesis

Abstract

The Kemp's ridley sea turtle was almost extinct by the mid 1980's, but due to intense conservation efforts, the species is gradually recovering. Hatchling sex ratios produced at Rancho Nuevo, Mexico have been monitored in an effort to optimize the recovery rate of this species. In the current study, sand and nest temperatures were evaluated during the 2009 -- 2012 nesting seasons. Beach and egg corral temperatures were monitored at nest depth using temperature data loggers. Incubation temperatures were also monitored in a subset of nests in egg corrals and on the natural nesting beach from each season. In general, temperatures were relatively cool (i.e. below pivotal temperature) at the start of the nesting seasons, but gradually rose and were at, or above, pivotal temperature by mid-May. Temperatures remained relatively high for the remainder of the nesting seasons unless the area was affected by tropical weather systems that significantly lowered incubation temperatures to near or below the pivotal temperature. Thus, an overall female bias was predicted for each nesting season. However, some nests laid early in the nesting season or those affected by tropical weather systems during the critical period of incubation were predicted to produce a male bias. The nesting beach was also relatively warm, thus suggesting a female bias, but it was generally cooler than the egg corrals. Collectively, the data suggest that female-biased sex ratios were produced during the 2009 --2012 nesting seasons at Rancho Nuevo. The results have ecological and conservation implications for the Kemp's ridley. The production of a female bias in the Kemp's Ridley Recovery Program may be accelerating the recovery rate of this endangered sea turtle. Therefore, leaving arribada nests *in situ*, may be an effective conservation strategy. Sex ratio studies provide data which are

helping to facilitate an effective transition from the use of egg corrals back to the use of the natural nesting beach as the Kemp’s ridley recovers.

Introduction

The Kemp’s ridley was historically the world’s most endangered sea turtle. The number of nesting females fell from an estimated 40,000 turtles in a single arribada in 1947 to approximately 250 turtles for an entire nesting season in the mid 1980’s (Hildebrand, 1963; Marquez, 1994). This was mainly due to intense exploitation of eggs and incidental capture in fishing trawls (Marquez, 1994). The startling decline of the Kemp’s ridley prompted initial conservation measures by the Mexican government in 1966 and later the development of a binational recovery program with the United States in 1978. The Kemp’s Ridley Recovery Program called for a ban on egg harvest, the protection of nesting females, and the relocation of all Kemp’s ridley nests to protected egg hatcheries (i.e. egg corrals) (Burchfield, 1998; Marquez, 1994). The main egg corral at the primary nesting beach near Rancho Nuevo, MX, is constructed in roughly the same location each year. It is located relatively high up on the beach profile where nests are less likely to be inundated by water or lost due to tropical storms. The relocation of most Kemp’s ridley nests to the egg corral therefore subjects the eggs to a similar thermal environment. This can significantly influence the sex ratio of the Kemp’s ridley since this species, like all other sea turtles, exhibits temperature-dependent sex determination (TSD).

Previous studies of sea turtles have shown that TSD can produce a variety of sex ratios and these can have a variety of effects on the reproductive ecology of a population (Wibbels, 2003). The sex ratio of a population determines its reproductive output and therefore affects the recovery rate for an endangered species. Sea turtles exhibit a male-female pattern of sex determination where males are produced from cooler temperatures, females from warmer temperatures, and at a given pivotal temperature in between, an approximately 50/50 mixture of males to females is produced (Mrosovsky and Yntema, 1980). The range over which mixed sex ratios are produced (i.e. range of temperatures over which 100% male production shifts to 100% female production) is the transitional range of temperatures (TRT). The pivotal temperature for the Kemp's ridley was determined to be approximately 30.2°C by Shaver et al. (1988), and more recently estimated to be 30.0°C (LeBlanc et al., 2012). The pivotal temperature and TRT can be used to predict the sex ratio of a nest (LeBlanc et al., 2012). Sex is determined in the approximate middle third of incubation for sea turtles and sand temperatures at nest depth during this period have been shown to be a practical method for predicting hatchling sex (Valenzuela, 2001; Hanson et al., 1998; Wibbels et al., 1998). Monitoring sand temperatures can therefore be an effective means of estimating the sex ratio of nests that are laid on the beaches at Rancho Nuevo. Further, an overall sex ratio for each nesting season based on thousands of nests can then be generated to collectively look at long-term changes in the sex ratio for the Kemp's ridley over time in response to changes in environmental conditions.

Long-term analysis of hatchling sex ratios can provide insight on the ecological, evolutionary, and conservational implications of TSD. For example, in the case of the

Kemp's ridley, hatchling sex ratios produced at Rancho Nuevo could be affecting the recovery rate of this endangered sea turtle. Further, long term analysis of hatchling sex ratios at Rancho Nuevo could shed light on potential changes in sex ratio associated with global climate change. It could also provide insight on how the recovery program may have to adjust their management strategy to avoid extreme sex ratios associated with global climate change. The beauty of generating a long-term database on Kemp's ridley sex ratios is that this can act as a model for how temperature change can impact a sea turtle species. The Kemp's ridley is an ideal species for such a study, since its sex determination is highly sensitive to environmental temperature and the majority of the species nests in the same location. The latest models from the IPCC project an increase in temperatures of 1-4°C by the year 2100 and possibly even higher given the Earth's current trajectory (Solomon et al., 2007). It is possible that even the most conservative of these estimates (i.e. a 1°C increase in temperatures) could lead to extreme female biases in the Kemp's ridley.

The purpose of the current study is to produce relatively high resolution hatchling sex ratio predictions for the egg corrals at Rancho Nuevo for the 2009–2012 nesting season. These data will be evaluated relative to temperature data from previous years that provide a general indication of previous sex ratios. This will represent the initial endeavor to assemble a long-term database examining sex ratio production from the Kemp's Ridley Recovery Program.

This study also investigates hatchling sex ratios produced on the natural nesting beach. The results provide insight on "natural" sex ratios and have conservational implications. The Recovery Program is in the midst of a transition from using egg corrals to leaving arribada nests *in situ* as a management strategy. It is therefore crucial to monitor nesting beach temperatures and *in situ* nest incubation temperatures in addition to egg corral temperatures to predict the effect that this shift in thermal environments will have on the species.

Thus, the current study investigates hatchling sex ratios from both the egg corrals and the natural beach at the primary nesting location for the Kemp's ridley. The results provide insight on a variety of implications that TSD has for this species, including the potential long-term changes in sex ratio associated with future climate change.

Materials and Methods

Sand Temperatures in Egg Corrals

Sand temperatures were monitored in the main egg corral (located adjacent to the main turtle camp) and in two satellite egg corrals at Rancho Nuevo: the main egg corral (RN, 0 km), the south corral (SRN, 5 km south of main egg corral) and the north corral (NRN, 16 km north of main egg corral). All three egg corrals were rectangular in shape running north to south, and located on the beach at the base of the dune bordering the beach. The main egg corral is the primary egg corral used at Rancho Nuevo and holds the majority of the nests that are relocated to corrals. Historically, the main egg corral was the original and only corral used during the initial years of the Kemp's Ridley Recovery Program. The south and north corrals have been used in recent years as "satellite" corrals that generally hold a smaller number of eggs, and reduce the distance required to transfer nests to the main egg corral.

Temperature data loggers (HOBO® H8 or HOBO® Pendant loggers, Onset Computer Corp.) were buried at mid nest depth (35 cm) in the sand of all three egg corrals to record temperature profiles over the 2009, 2010, 2011 and 2012 nesting seasons. Three temperature transects running east to west with 3 data loggers per transect were used in the main egg corral (total of 9 data loggers), whereas a single transect with 3 data loggers running north to south along the center of the corral was used in each of the satellite corrals. These data loggers were calibrated and set to record temperature at one hour intervals.

Nest Temperatures in Egg Corrals

Temperatures were also monitored directly in a subset of nests in all three corrals for 2009 (n= 19 RN, 8 SRN, 5 NRN), 2010 (n=11 RN, 6 SRN, 5 NRN), 2011 (n=12 RN, 4 SRN, 4 NRN), and 2012 (n=28 RN, 6 SRN, 5 NRN). Data loggers were placed in the middle of each clutch of eggs as the eggs were relocated to the egg corral. Data loggers were placed into nests throughout each nesting season, including in nests from all major arribadas.

Sand Temperatures on the Natural Nesting Beach

Temperatures were also monitored on the natural nesting beach. Eight temperature transects running east to west (perpendicular to the surf) with two data loggers per transect were used to record temperature profiles at mid nest depth (35 cm) for the natural nesting beach over each nesting season from 2009-2012. These transects were placed at approximately 1 km intervals on the beach directly north and south of the main egg corral (an area that was historically known for a large percentage of the nesting).

Nest Temperatures on the Natural Nesting Beach

Temperature data loggers were also placed into the middle of the clutch of eggs in a subset of nests left to incubate *in situ* on the natural nesting beach. Each nesting season, approximately 10-15 data loggers were placed in nests that were laid in areas where most of the Kemp's ridley nesting occurs (i.e. on the portion of the beach flat adjacent to the dune bordering the beach).

Comparison between Sand and Nest Temperatures in Egg Corrals at Rancho Nuevo

Average nest temperatures during the middle third of incubation for nests in the egg corral were compared to sand temperatures in the egg corral over those same dates to determine if sand temperature was an accurate predictor of nest temperature.

Sand temperature data analysis

Average daily temperatures were generated for each data logger based on their one hour sampling interval (i.e. 24 temperature recordings per day). These daily averages were used to generate seasonal temperature profiles for corral and natural beach sand temperatures.

Predicting Sex Ratios for Egg Corral Nests and In Situ Nests at Rancho Nuevo

Previous studies have indicated that in many turtles including sea turtles, the sex is determined by temperatures during the approximate middle third of incubation (Yntema and Mrosovsky, 1982; Merchant-Larios, 1999; Wibbels et al., 1991). A variety of studies have used beach temperature to predict hatchling sex ratios produced from nesting beaches (Wibbels, 2003; Godfrey and Mrosovsky, 1997; Marcovaldi et al., 1997; Godley et al., 2001). In the current study sex ratios were estimated for both egg corral and *in situ* nests based on the average temperature experienced over the middle third of the total incubation period. This was possible because the effects of specific incubation temperatures have been evaluated in the Kemp's ridley (Shaver et al., 1988; LeBlanc et al., 2012). Those studies indicate that temperatures above 31.0°C produced 100% females, temperatures of approximately 30.2°C produce an approximate 1:1 sex ratio (i.e. the pivotal temperature), and temperatures of approximately 28.0°C or below produce 100% males. A conservative approach was adopted in which each nest was assigned one of four sex ratio categories: 100% female for average middle third temperatures of 31.0°C or above, 75% female for temperatures between 30.9°C and the pivotal temperature (30.2°C), 25% female for temperatures between pivotal temperature and 28.1°C, and 0% female for temperatures of 28.0°C or below.

The period from the day of lay to the day of emergence for the Kemp's ridley varies depending on temperature from approximately 45 to 58 days with an average of approximately 51 days (Pritchard and Marquez-M., 1973). Previous studies of sea turtles suggest that hatchlings spend approximately 4 to 5 days in the nest prior to emergence (Godfrey and Mrosovsky, 1997). Therefore, in the current study, an estimated average incubation duration of 45 days was used, resulting in a predicted 15-day duration of the middle third of incubation. Average temperature was calculated over this 15-day duration representing the middle third of incubation for corral and *in situ* nests (i.e. average temperature from day 16 through day 31 of incubation).

Based on the sand temperatures in the egg corrals, an average temperature over the 15-day middle third period was calculated for each lay date of the nesting season, resulting in a "sliding" middle third average temperature profile for the entire nesting season. This "sliding" middle third average temperature profile was used to predict the sex ratio for each nest moved to the egg corrals over the entire season (based on the temperature categories discussed above). The nesting data for the 2009 – 2012 nesting seasons (i.e. number of nests laid on each day of the four nesting seasons and then relocated to the egg corral) were provided by Comisión National Áreas Naturales Protegidas (CONANP). Nest sex ratios were also predicted for a subset of corral and *in situ* nests based on actual incubation temperatures that were recorded from data loggers placed into the nests.

The overall sex ratio for the egg corrals was calculated from the estimated total number of male and female hatchlings produced from all nests in each nesting season. In order to determine the predicted number of males and females in each nest, the following information was used. Kemp's ridleys lay an average of 100 eggs per nest (Burchfield and Pena, 2008; Rostal and Plotkin, 2007) and experience approximately 70% hatching success (Burchfield, 1998): thus it was estimated that 70 hatchlings were produced per nest at Rancho Nuevo. Therefore, for each nest in the egg corrals, the estimated numbers of males and females was calculated using the predicted sex ratio and a predicted total of 70 hatchlings per nest.

In 2010, the sand temperature data loggers were removed from the egg corrals on June 28th due to Hurricane Alex. Therefore, sand temperature data are not available for predicting sex ratios of a large number of nests that were laid later in the nesting season, and could potentially have a significant effect on the overall sex ratio produced in 2010. In an effort to include all the late season corral nests, a hypothetical model was used in which temperatures typical for July and August at Rancho Nuevo were used to predict the sex ratios of those nests. Since no major hurricanes or tropical storms occurred during July and August of 2010, beach temperatures would be predicted (based on previous years) to be well above pivotal temperature, falling into two of the four predicted sex ratio categories indicated above (either 75% or 100% female categories). A range of potential sex ratios during the late season was then generated using either a 75% female minimum or a 100% female maximum. Those data were then added to the sex ratio data from the early and middle season to provide an overall range of sex ratios that were potentially produced in the egg corrals during the 2010 nesting season.

Hypothetical Shift Back To the Natural Nesting Beach:

A hypothetical sex ratio for each of the four nesting seasons (2009 -2012) was also estimated for the natural nesting beach. In this model, beach temperatures rather than corral temperatures were used to predict sex ratios of every nest that was moved to the egg corrals. Sex ratios were predicted with the same methodology described above, with the exception that sand temperatures from the temperature transects on the natural nesting beach were used instead of corral temperatures.

Predicted Effects of Global Climate Change

To model the potential effects of global climate change on sex ratios in the Kemp’s ridley, a 1°C increase in the average temperature during the middle third of incubation was used in the sex ratio calculations for each nest. The IPCC has projected an increase of approximately 1-4°C in surface temperatures by the year 2100 (Solomon et al., 2007). A conservative model was simulated using only a 1°C increase in temperatures for corral nests. This approach was also used to simulate the potential effects on sex ratios on the natural nesting beach by using a conservative 1°C increase in natural nesting beach temperatures during the middle third of incubation for each nest.

Results

Sand Temperatures in Egg Corrals and on the Natural Nesting Beach

Sand temperatures in the egg corrals and on the natural nesting beach exhibited a similar profile during each of the four nesting seasons, with the exception of specific weather systems that affected certain nesting seasons (Figures 1 - 4). Typically, sand temperatures increase during the early portion of the nesting season, reaching pivotal temperature by approximately mid-April, and then remain at or above pivotal temperature during the remainder of the nesting season, with the exception of weather systems that move through the area.

The sand temperatures in the main egg corral and in the satellite egg corrals were significantly warmer than the nesting beach during all four nesting seasons (ANOVA, p=2.05032E-05 for 2009, p=0.000166 for 2010, p=2.26068E-09 for 2011, and p=0.000423 for 2012) (Figures 1 -4). The sand temperatures in the satellite egg corrals were similar to those in the main egg corrals during most years although a significant difference was indicated during 2009 (ANOVA, p= 0.044374654 for 2009, p= 0.151794611 for 2010, p= 0.207048949 for 2011, and p= 0.284728827 for 2012) in which the north egg corral was cooler than the main egg corral and the south egg corral (Tukey, p=0.0343).

During 2009 (Figure 1), temperatures were monitored in the main egg corral April 8th to August 17th with an average temperature of 31.4°C ± 1.94°C, from April 8th to June 30th in the south satellite egg corral with an average temperature of 31.1°C ± 2.0°C, and April 8th to June 30th in the north satellite egg corral with an average temperature of 30.8°C ± 1.9°C. Temperatures were monitored in the seven beach transects from April 8th to July 24th with average temperature of 30.2°C ± 1.93°C.

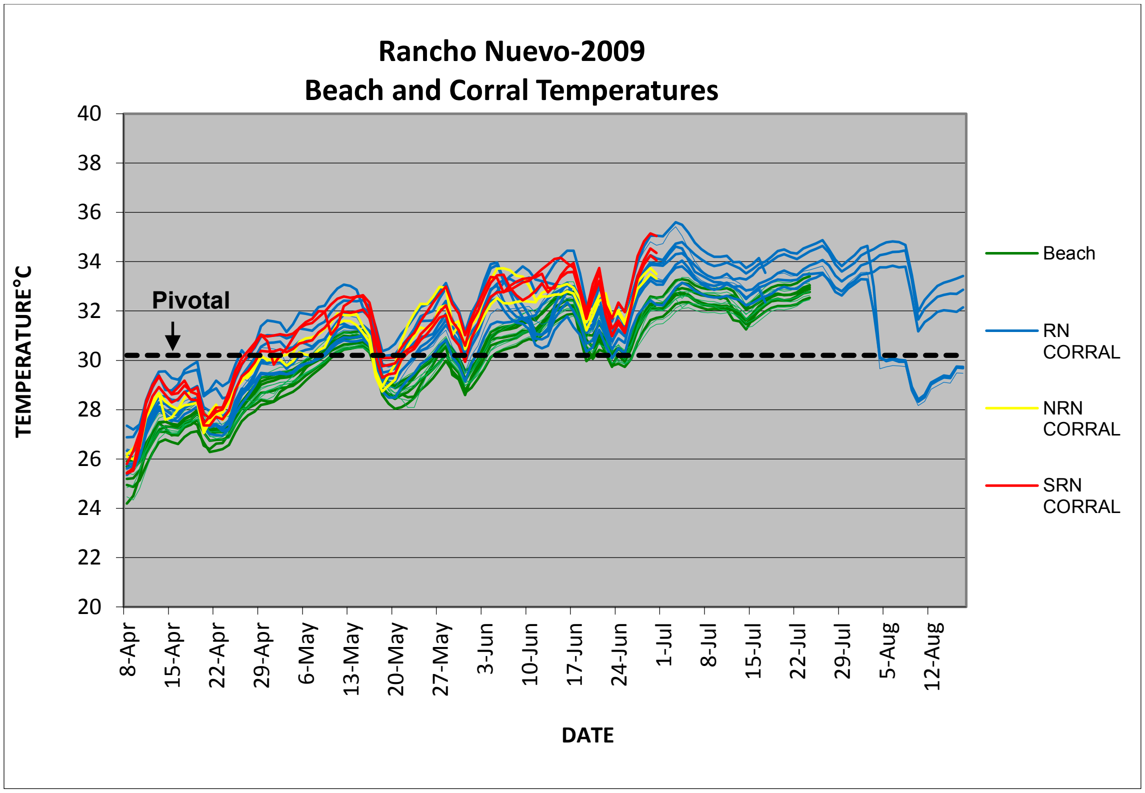


Figure 1: Sand temperatures in egg corrals at Rancho Nuevo in 2009. Blue: RN Corral; Yellow: NRN Corral; Red: SRN Corral. The dashed line at 30.2°C represents the estimated pivotal temperature based on Shaver et al., 1988.

During 2010, temperatures were monitored in the main egg corral from April 12th to June 30th with an average temperature of 30.2°C ± 2.6°C, in the south corral from April 12th to June 28th with an average temperature of 30.9°C ± 2.7°C, and in the north corral from April 12th to June 30th with an average temperature of 30.1°C ± 2.5°C. Temperatures were monitored in the seven beach transects from April 12th to June 28th, 2010 with an average temperature of 29.0°C ± 2.35°C (Figure 2).

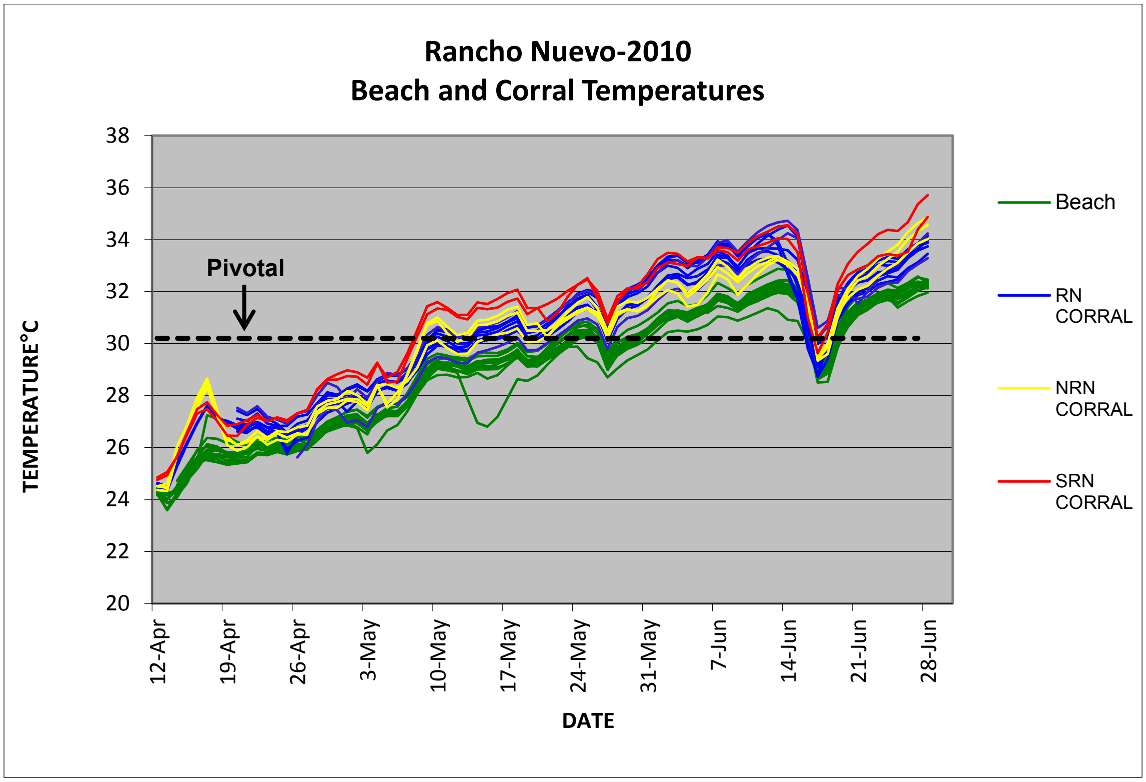


Figure 2: Sand temperatures in egg corrals at Rancho Nuevo in 2010. Blue: RN Corral; Yellow: NRN Corral; Red: SRN Corral. The dashed line at 30.2°C represents the estimated pivotal temperature based on Shaver et al., 1988.

During 2011, temperatures were monitored in the main egg corral from March 23rd to July 25th with an average temperature of 30.6°C ± 2.1°C, from March 23rd to June 29th in the south corral with an average temperature of 31.0°C ± 2.0°C, and from March 23rd to June 29th in the north corral with an average temperature of 30.5°C ± 2.3°C. Temperatures were monitored in the seven beach transects from March 23rd to July 3rd with an average temperature of 29.2°C ± 1.80°C. (Figure 3)

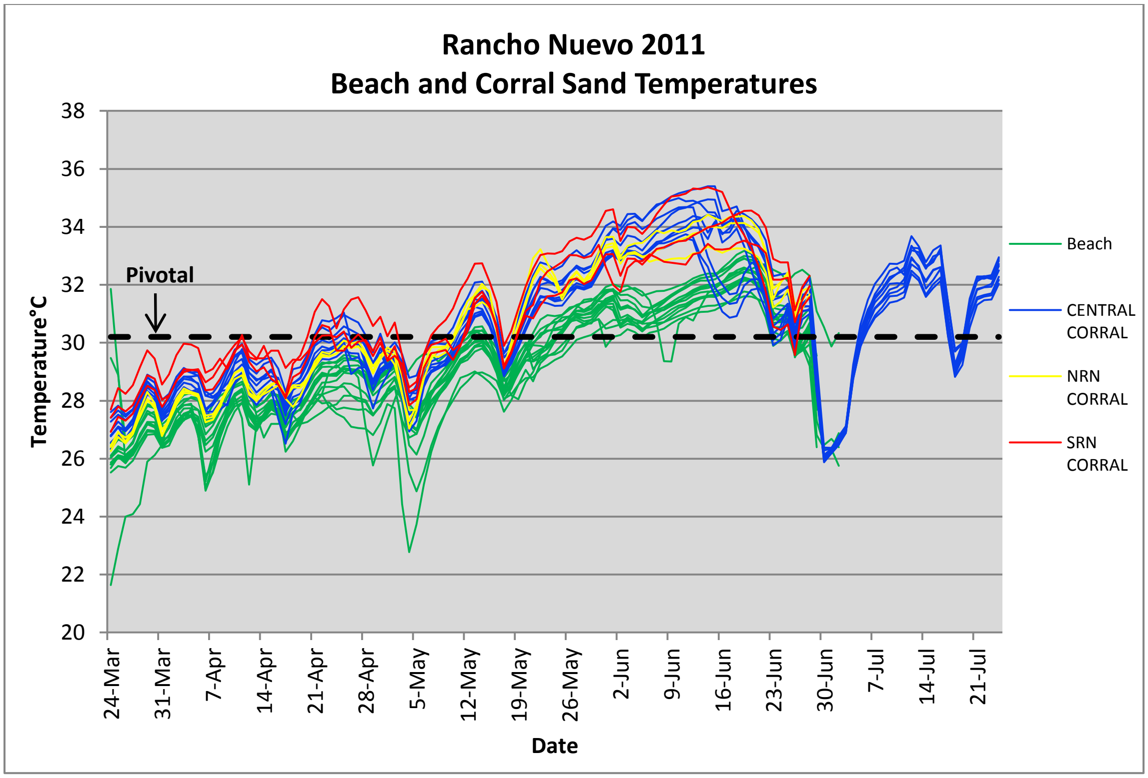


Figure 3: Sand temperatures in egg corrals at Rancho Nuevo in 2011. Blue: RN Corral; Yellow: NRN Corral; Red: SRN Corral. The dashed line at 30.2°C represents the estimated pivotal temperature based on Shaver et al., 1988.

During 2012, temperatures were monitored in the central egg corral from March 30th to August 23rd with an average temperature of 31.4°C ± 1.8°C, from March 30th to July 5th in the south corral with an average temperature of 31.3°C ± 1.9°C, and from April 19th to July 7th in the north corral with an average temperature of 31.0°C ± 1.7°C. Temperatures were monitored in the seven beach transects, though one data logger malfunctioned and therefore temperature readings were obtained from only 15 data loggers for this season. These data loggers recorded temperatures from March 30th to August 9th with an average temperature of 30.6°C ± 1.68°C. (Figure 4)

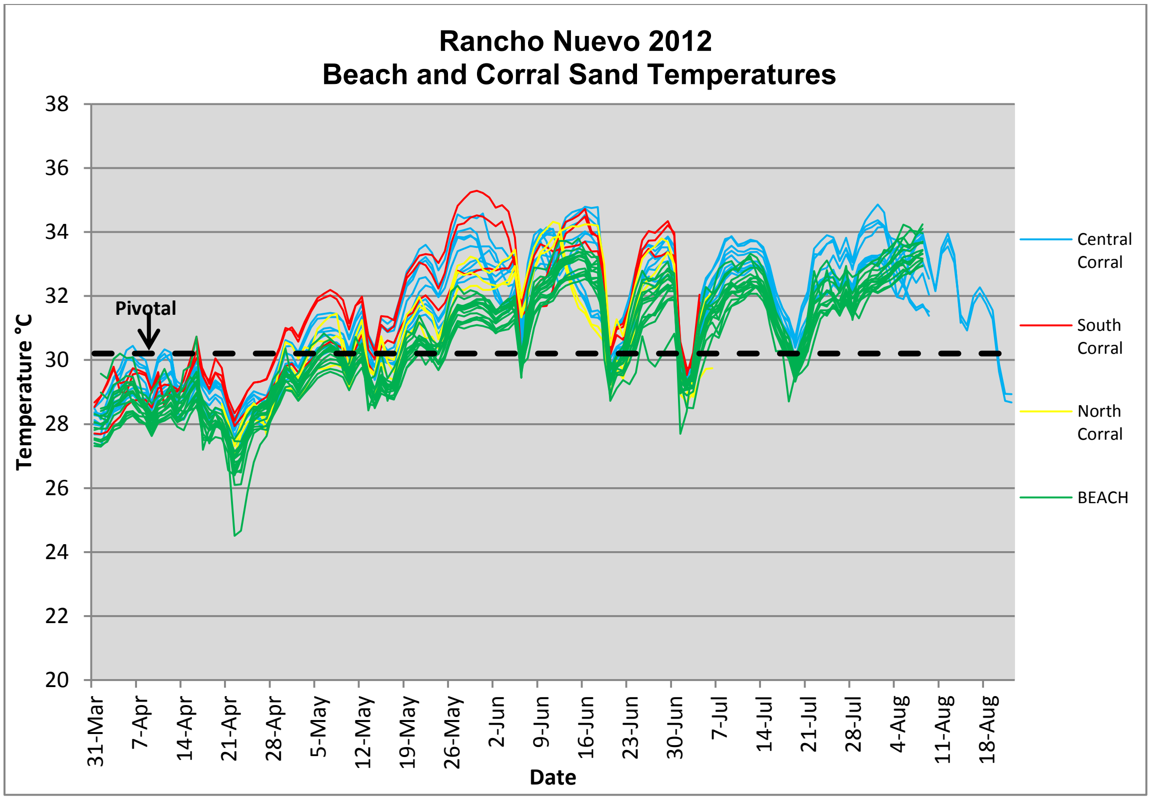


Figure 4: Sand temperatures in egg corrals at Rancho Nuevo in 2012. Blue: RN Corral; Yellow: NRN Corral; Red: SRN Corral. The dashed line at 30.2°C represents the estimated pivotal temperature based on Shaver et al., 1988.

Nest Temperatures in the Egg Corrals and on the Natural Nesting Beach

Temperatures were also monitored in subsets of nests in the egg corrals and on the natural nesting beach for each nesting season from 2009-2012 (Figures 5 to 18). Data loggers in these nests recorded temperatures that generally mimicked seasonal trends in sand temperatures. Nests laid early in the season (e.g. late March to early April) had temperatures that were initially below pivotal temperature, but gradually rose to temperatures that were at or above pivotal temperature. Nests laid in mid to late May experienced temperatures that were initially at or above pivotal and gradually rose to well above the pivotal temperature. Nests laid in late May and in June generally had temperatures that were well above pivotal temperature unless they were affected by a tropical weather system and associated rain that lowered incubation temperatures. In general, temperatures in early season nests indicated the production of mixed sex ratios with some male biases (Tables 1-4). In contrast, from mid-May through the end of the nesting season, the beach and corral temperatures suggest that female biased sex ratios predominate with the exception of times when tropical weather systems cool the nesting beach.

Table 1: Sex ratios predicted for data logger nests from egg corrals (i.e. main, north and south egg corrals) in 2009.

Month	**100% Male**	**Male Bias**	**Piv. Temp.**	**Female Bias**	**100% Female**	**Total**
MARCH	0	4	0	1	1	6
APRIL	0	1	0	2	4	7
MAY	0	1	0	0	7	8
JUNE	0	1	0	0	8	9
JULY	0	0	0	0	1	1
Total	0	7	0	3	21	31

Table 2: Sex ratios predicted for data logger nests from egg corrals (i.e. main, north and south egg corrals) in 2010.

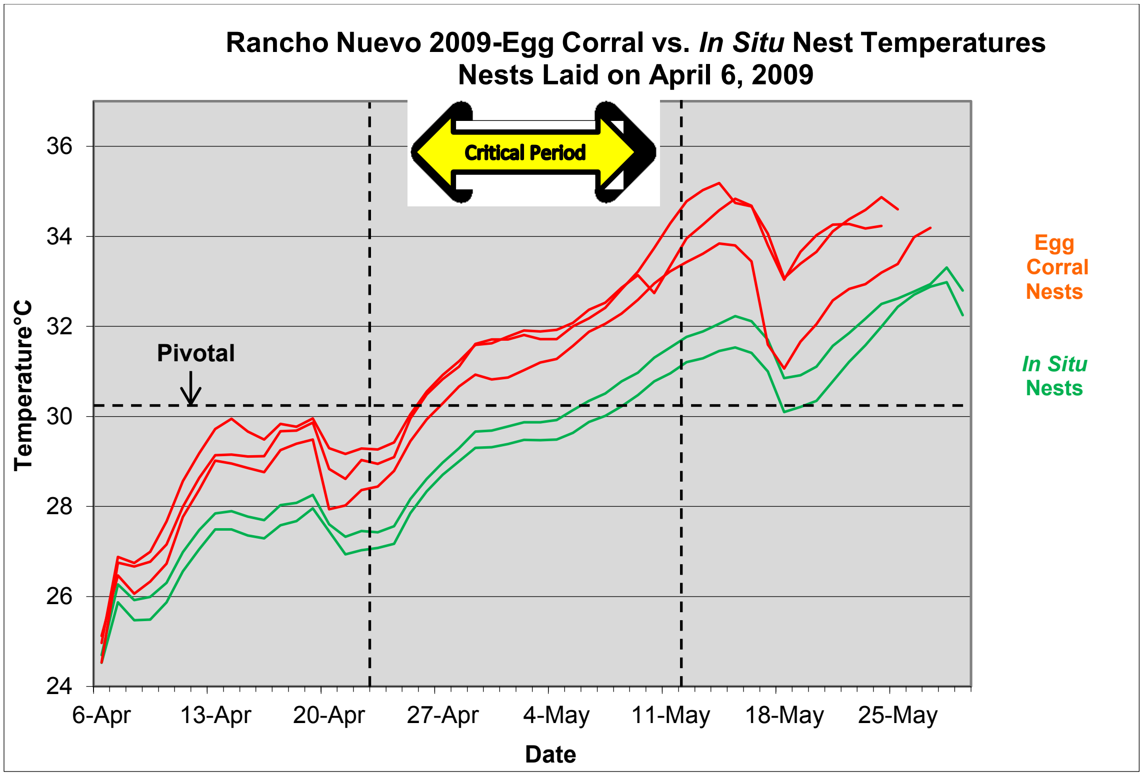
Month	**100% Male**	**Male Bias**	**Piv. Temp.**	**Female Bias**	**100% Female**	**Total**
APRIL	0	1	0	1	7	9
MAY	0	0	0	0	7	7
JUNE	0	0	0	0	3	3
JULY	0	0	0	0	1	1
Total	0	1	0	1	18	20

Table 3: Sex ratios predicted for data logger nests from egg corrals (i.e. main, north and south egg corrals) in 2011.

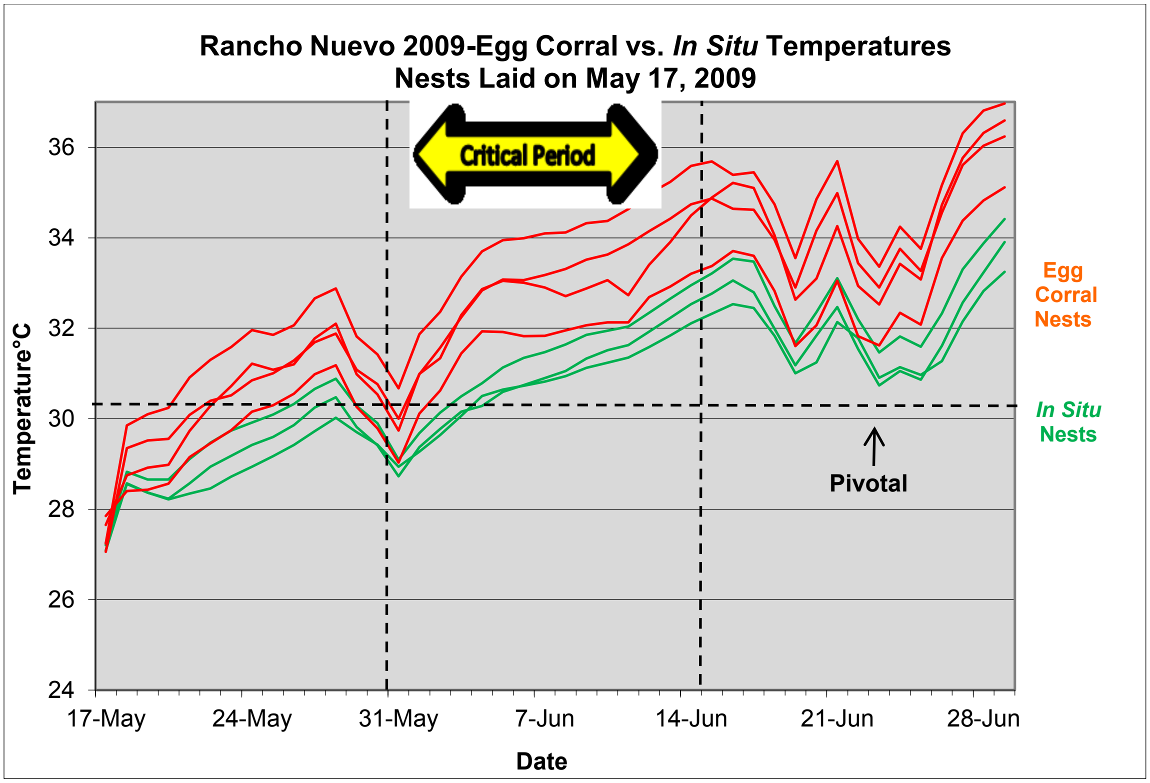
Month	**100% Male**	**Male Bias**	**Piv. Temp.**	**Female Bias**	**100% Female**	**TOTAL**
MARCH	0	1	0	0	0	1
APRIL	0	0	0	2	2	4
MAY	0	0	0	0	6	6
JUNE	0	2	0	1	3	6
JULY	0	0	0	0	0	0
AUGUST	0	0	0	0	3	3
TOTAL	0	3	0	3	14	20

Table 4: Sex ratios predicted for data logger nests from egg corrals (i.e. main, north and south egg corrals) in 2012.

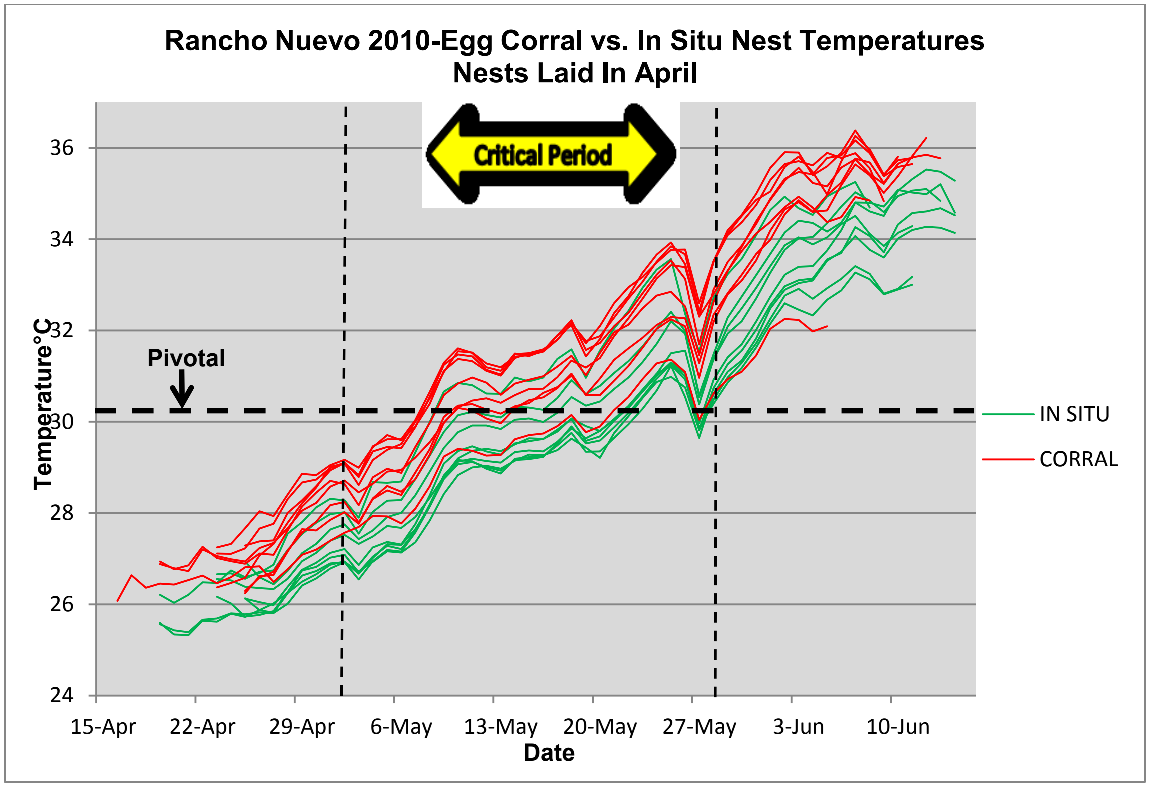
Month	**100% Male**	**Male Bias**	**Piv. Temp.**	**Female Bias**	**100% Female**	**TOTAL**
APRIL	0	2	0	4	9	15
MAY	0	0	0	0	11	11
JUNE	0	0	0	0	8	8
TOTAL	0	2	0	4	28	34



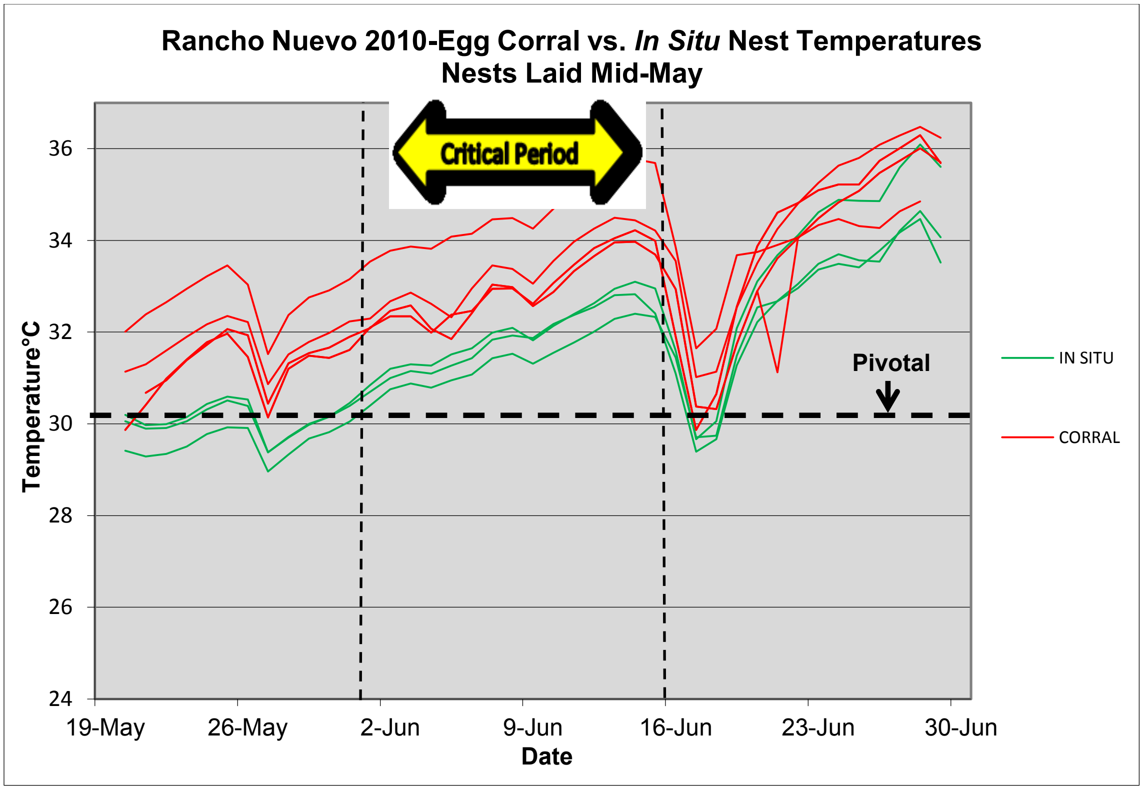
Figures 5. Examples of nests laid on April 6, 2009. Nest incubation temperatures were monitored with data loggers. The sex-determining middle third of incubation is denoted by vertical dashed lines. The approximate pivotal temperature is denoted by the horizontal dashed line at 30.2°C from Shaver et al. (1988). Red lines indicate nests relocated to egg corrals. Green lines indicate *in situ* nests left to incubate on the natural nesting beach.



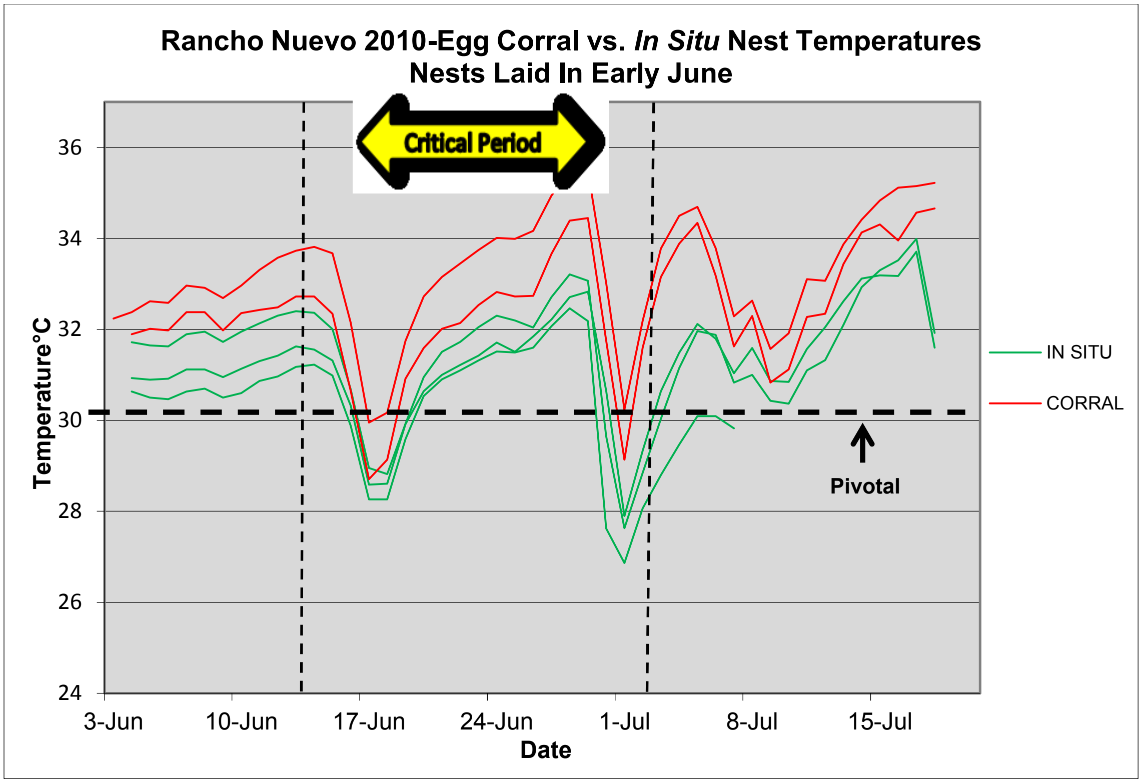
Figures 6. Examples of nests laid on May 17, 2009. Nest incubation temperatures were monitored with data loggers. The sex-determining middle third of incubation is denoted by vertical dashed lines. The approximate pivotal temperature is denoted by the horizontal dashed line at 30.2°C from Shaver et al. (1988). Red lines indicate nests relocated to egg corrals. Green lines indicate *in situ* nests left to incubate on the natural nesting beach.



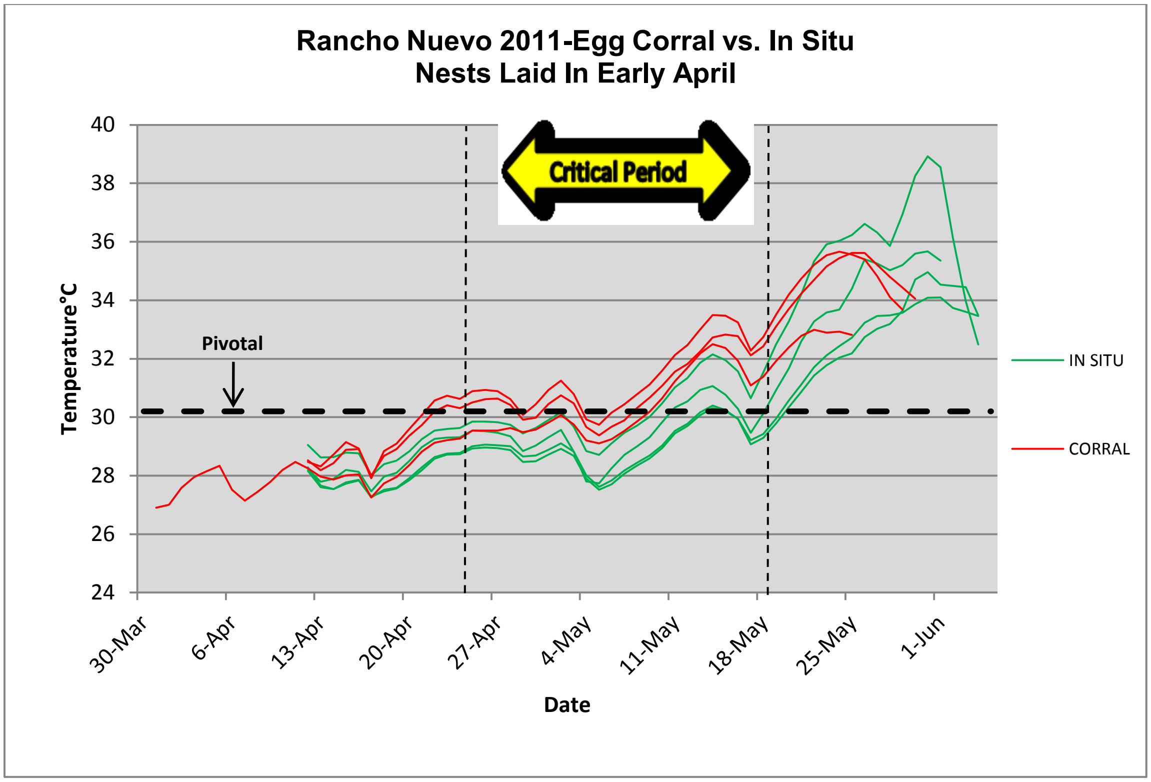
Figures 7. Examples of nests laid in mid to late April 2010. Nest incubation temperatures were monitored with data loggers. The sex-determining middle third of incubation is denoted by vertical dashed lines. The approximate pivotal temperature is denoted by the horizontal dashed line at 30.2°C from Shaver et al. (1988). Red lines indicate nests relocated to egg corrals. Green lines indicate *in situ* nests left to incubate on the natural nesting beach.



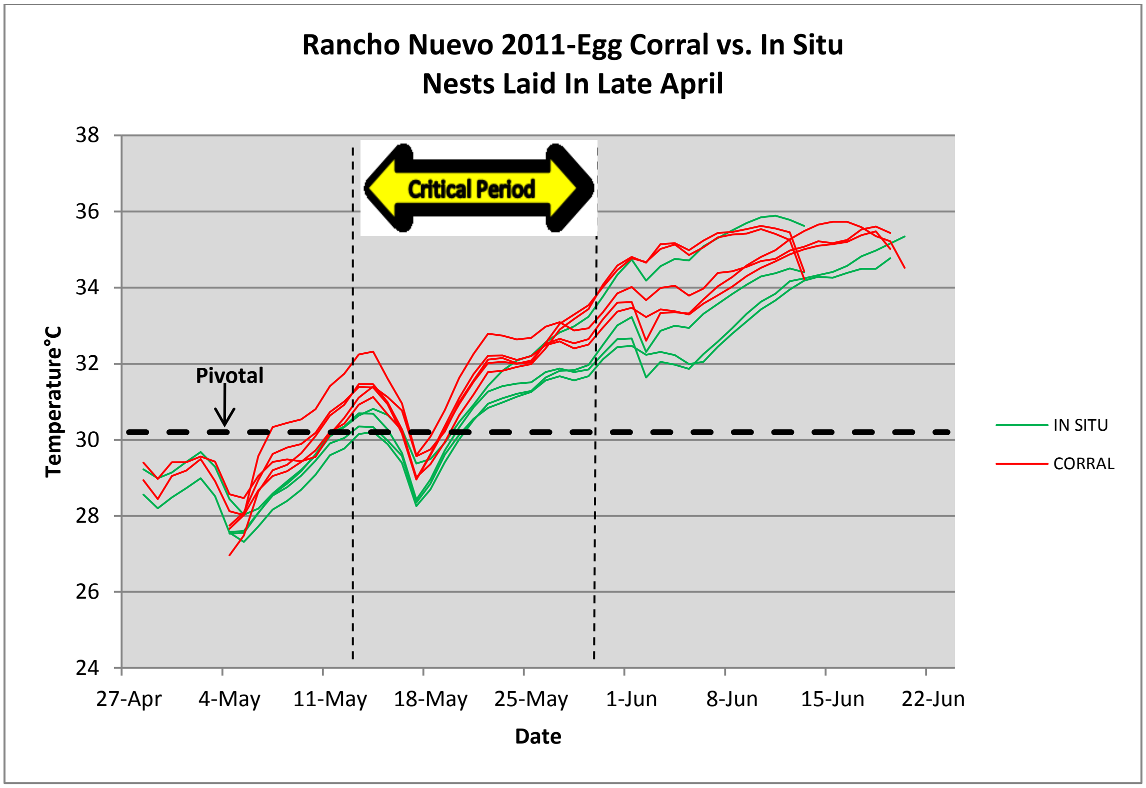
Figures 8 Examples of nests laid in mid-May 2010. Nest incubation temperatures were monitored with data loggers. The sex-determining middle third of incubation is denoted by vertical dashed lines. The approximate pivotal temperature is denoted by the horizontal dashed line at 30.2°C from Shaver et al. (1988). Red lines indicate nests relocated to egg corrals. Green lines indicate *in situ* nests left to incubate on the natural nesting beach.



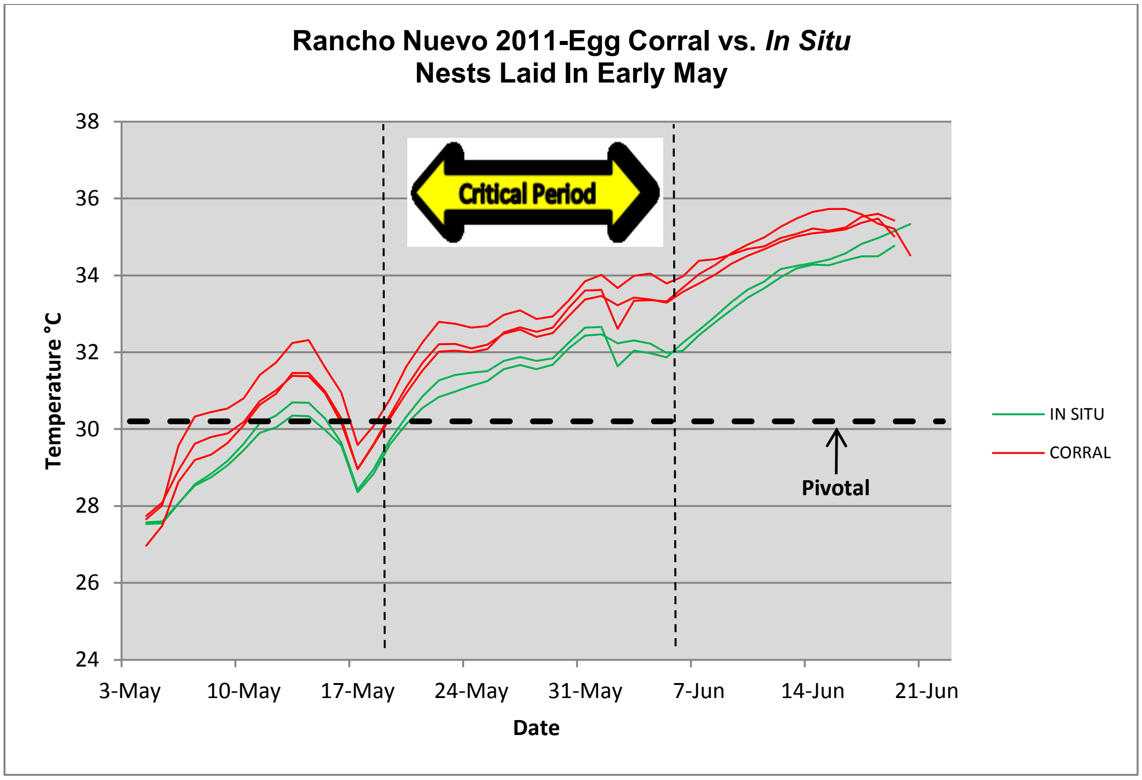
Figures 9. Examples of nests laid in early June 2010. Nest incubation temperatures were monitored with data loggers. The sex-determining middle third of incubation is denoted by vertical dashed lines. The approximate pivotal temperature is denoted by the horizontal dashed line at 30.2°C from Shaver et al. (1988). Red lines indicate nests relocated to egg corrals. Green lines indicate *in situ* nests left to incubate on the natural nesting beach.



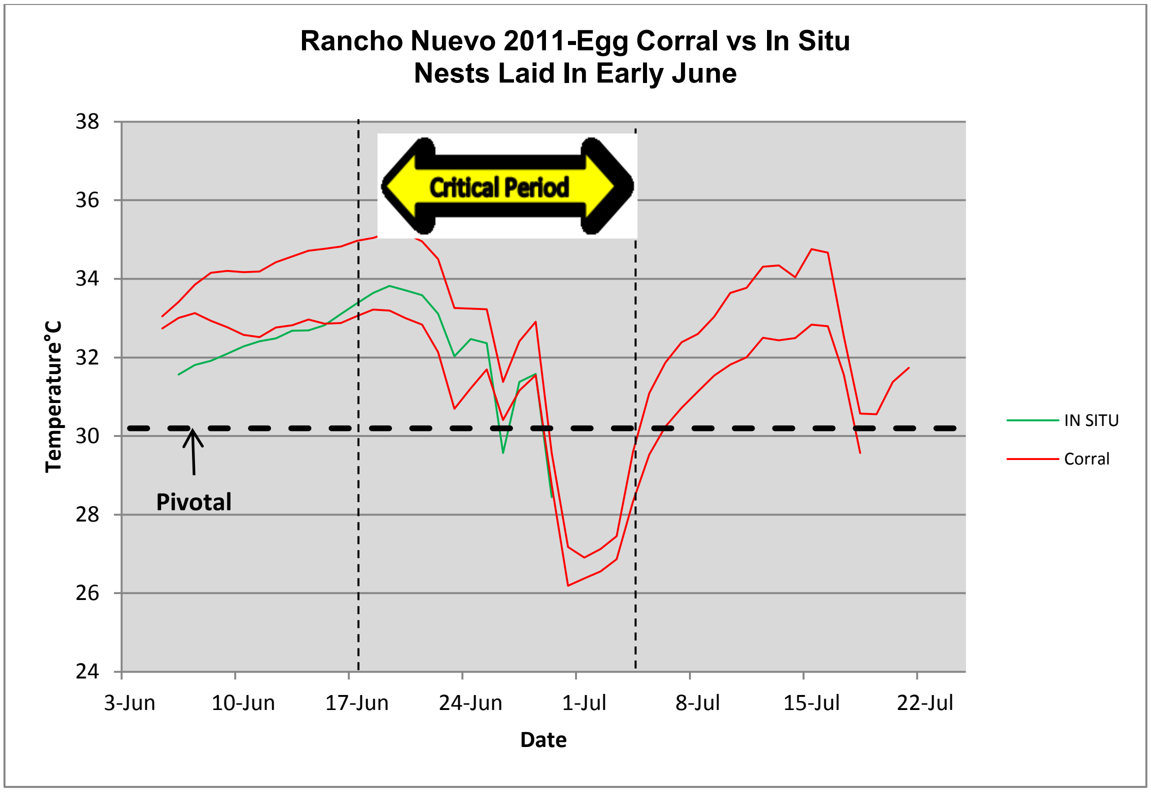
Figures 10. Examples of nests laid in early April 2011. Nest incubation temperatures were monitored with data loggers. The sex-determining middle third of incubation is denoted by vertical dashed lines. The approximate pivotal temperature is denoted by the horizontal dashed line at 30.2°C from Shaver et al. (1988). Red lines indicate nests relocated to egg corrals. Green lines indicate *in situ* nests left to incubate on the natural nesting beach.



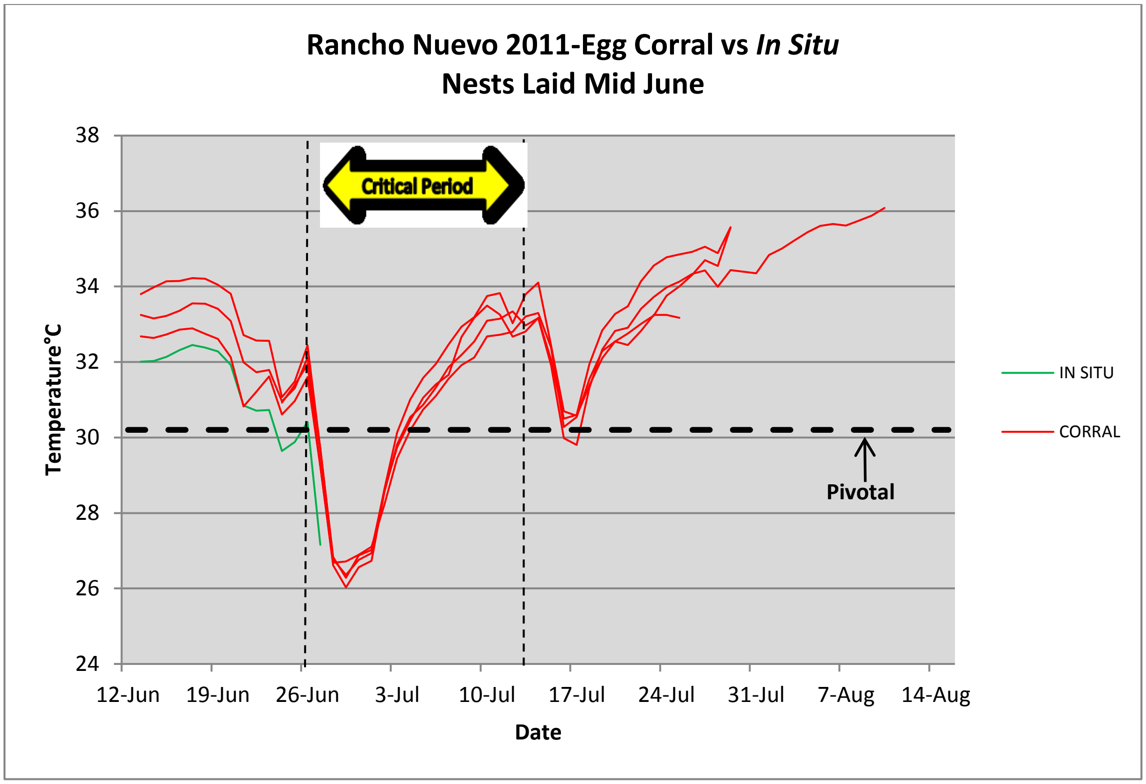
Figures 11. Examples of nests laid in late April 2011. Nest incubation temperatures were monitored with data loggers. The sex-determining middle third of incubation is denoted by vertical dashed lines. The approximate pivotal temperature is denoted by the horizontal dashed line at 30.2°C from Shaver et al. (1988). Red lines indicate nests relocated to egg corrals. Green lines indicate *in situ* nests left to incubate on the natural nesting beach.



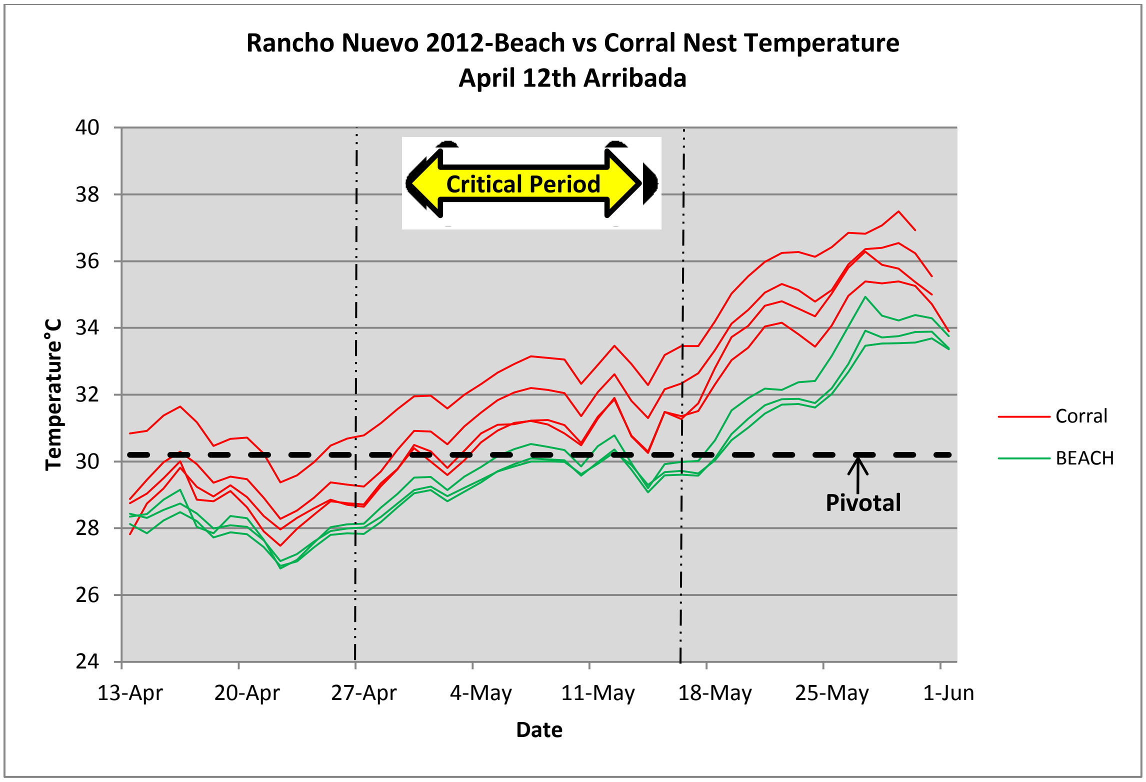
Figures 12. Examples of nests laid in early May 2011. Nest incubation temperatures were monitored with data loggers. The sex-determining middle third of incubation is denoted by vertical dashed lines. The approximate pivotal temperature is denoted by the horizontal dashed line at 30.2°C from Shaver et al. (1988). Red lines indicate nests relocated to egg corrals. Green lines indicate *in situ* nests left to incubate on the natural nesting beach.



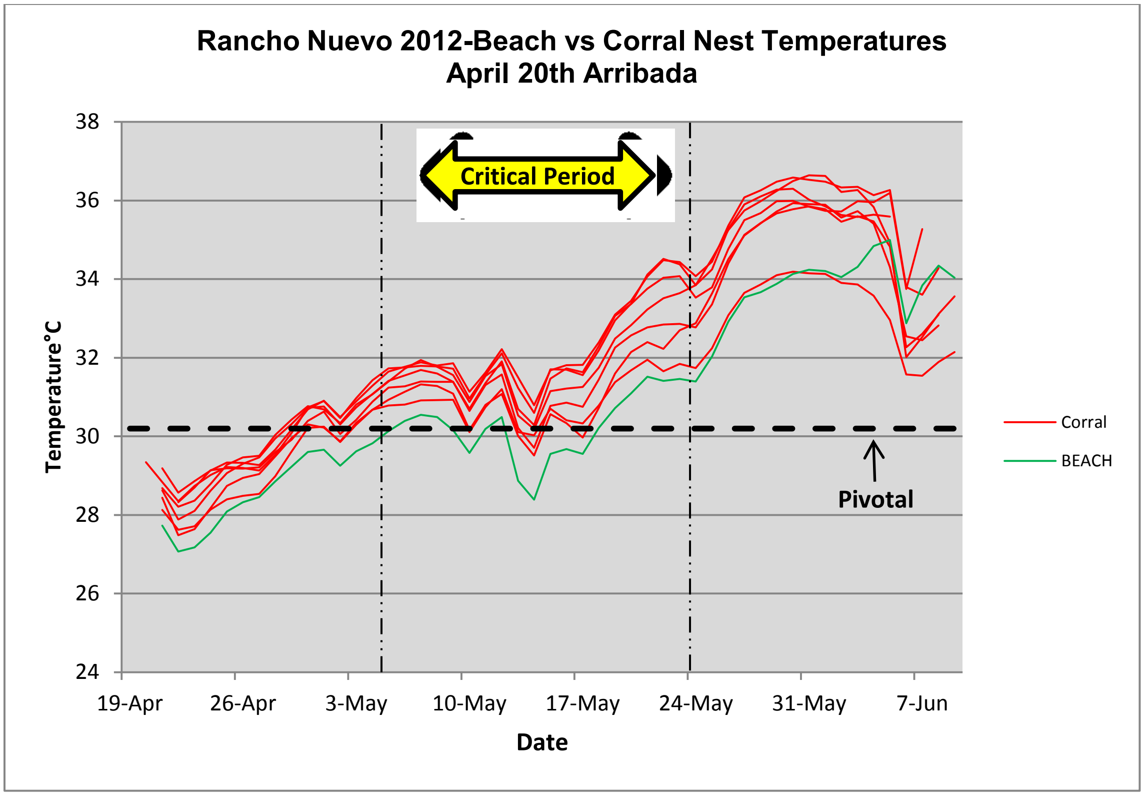
Figures 13. Examples of nests laid in early June 2011. Nest incubation temperatures were monitored with data loggers. The sex-determining middle third of incubation is denoted by vertical dashed lines. The approximate pivotal temperature is denoted by the horizontal dashed line at 30.2°C from Shaver et al. (1988). Red lines indicate nests relocated to egg corrals. Green lines indicate *in situ* nests left to incubate on the natural nesting beach.



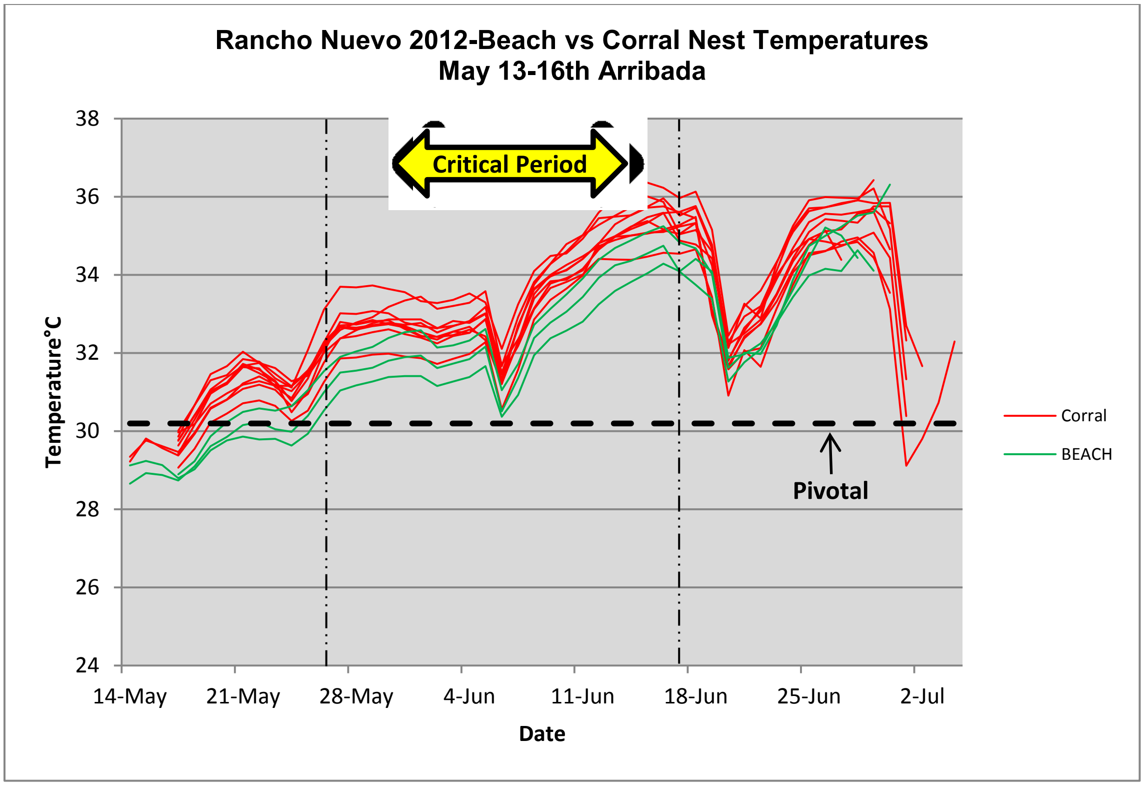
Figures 14. Examples of nests laid in mid June 2011. Nest incubation temperatures were monitored with data loggers. The sex-determining middle third of incubation is denoted by vertical dashed lines. The approximate pivotal temperature is denoted by the horizontal dashed line at 30.2°C from Shaver et al. (1988). Red lines indicate nests relocated to egg corrals. Green lines indicate *in situ* nests left to incubate on the natural nesting beach.



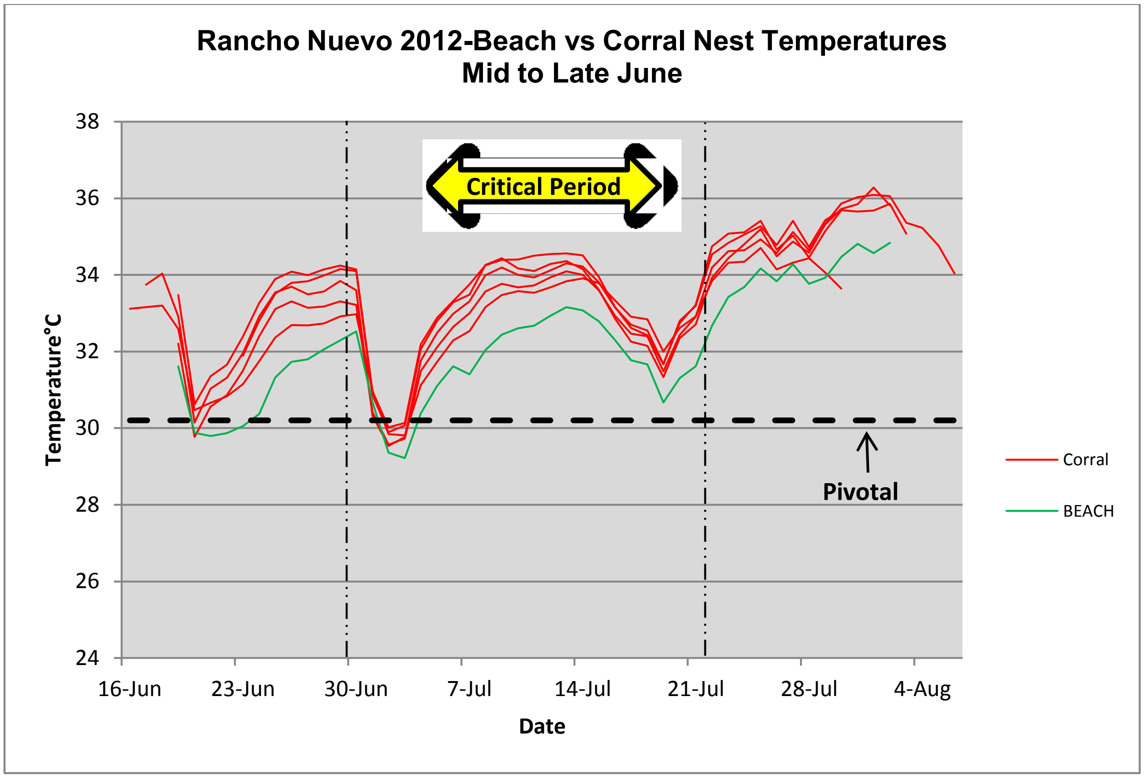
Figures 15. Examples of nests laid during arribada on April 12, 2012. Nest incubation temperatures were monitored with data loggers. The sex-determining middle third of incubation is denoted by vertical dashed lines. The approximate pivotal temperature is denoted by the horizontal dashed line at 30.2°C from Shaver et al. (1988). Red lines indicate nests relocated to egg corrals. Green lines indicate *in situ* nests left to incubate on the natural nesting beach.



Figures 16. Examples of nests laid during arribada of April 20, 2012. Nest incubation temperatures were monitored with data loggers. The sex-determining middle third of incubation is denoted by vertical dashed lines. The approximate pivotal temperature is denoted by the horizontal dashed line at 30.2°C from Shaver et al. (1988). Red lines indicate nests relocated to egg corrals. Green lines indicate *in situ* nests left to incubate on the natural nesting beach.



Figures 17. Examples of nests laid in mid May 2012. Nest incubation temperatures were monitored with data loggers. The sex-determining middle third of incubation is denoted by vertical dashed lines. The approximate pivotal temperature is denoted by the horizontal dashed line at 30.2°C from Shaver et al. (1988). Red lines indicate nests relocated to egg corrals. Green lines indicate *in situ* nests left to incubate on the natural nesting beach.



Figures 18. Examples of nests laid during mid to late June 2012. Nest incubation temperatures were monitored with data loggers. The sex-determining middle third of incubation is denoted by vertical dashed lines. The approximate pivotal temperature is denoted by the horizontal dashed line at 30.2°C from Shaver et al. (1988). Red lines indicate nests relocated to egg corrals. Green lines indicate *in situ* nests left to incubate on the natural nesting beach.

Comparison between Sand and Nest Temperatures in Egg Corrals at Rancho Nuevo

The average temperature over the middle third of incubation was determined for each nest in the egg corral (Figure 19). The sand temperatures in the egg corral were also averaged over the same time periods and were not significantly different than the nest temperatures (T-test, p=0.187). A regression analysis was used to evaluate if average sand temperature was an accurate predictor of the average nest temperature during the critical period of incubation ($R^2 = 0.862$, p=4.69E-84).

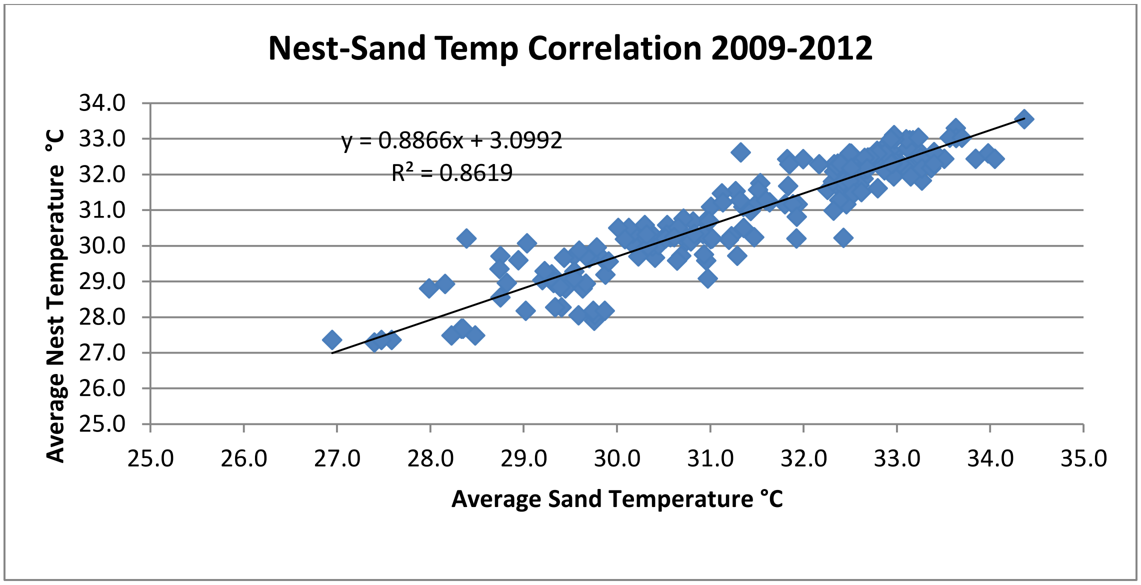


Figure 19. Correlation between average nest temperature during the middle third of incubation and average sand temperature during the same time periods.

Sex Ratio Predictions for 2009 – 2012 in the Kemp's Ridley Recovery Program

Sex ratios were predicted for each nest relocated to the egg corrals for the 2009 – 2012 nesting seasons. The seasonal nesting distribution relative to the daily average sand temperature in the egg corrals (at nest depth) for each nesting season is shown in Figures 20 - 23 (2009 – 2012 respectively). Figures 24 – 27 (2009 – 2012 respectively) show the seasonal nesting distribution relative to the average temperatures during the middle third of incubation for each lay date in each nesting season. The seasonal nesting distribution was used along with the average middle third temperature data to predict the sex for each nest relocated to egg corrals for the 2009 – 2012 nesting seasons (based on the average middle third temperature/sex ratio categories described above). The overall sex ratios predicted for all nests relocated to the egg corrals for each of the four nesting seasons are shown in Table 5.

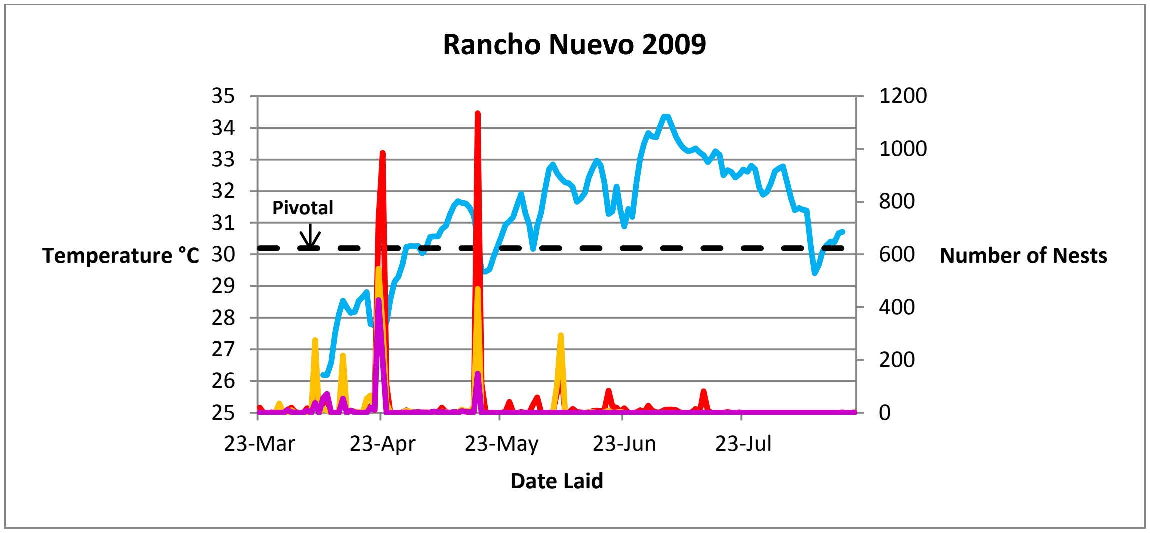


Figure 20. Blue line indicates the average daily temperature in the egg corrals. Red (main egg corral), yellow (south egg corral), and purple (north egg corral) lines indicate total nests relocated each day to the egg corrals in 2009 with the major peaks representing arribadas.

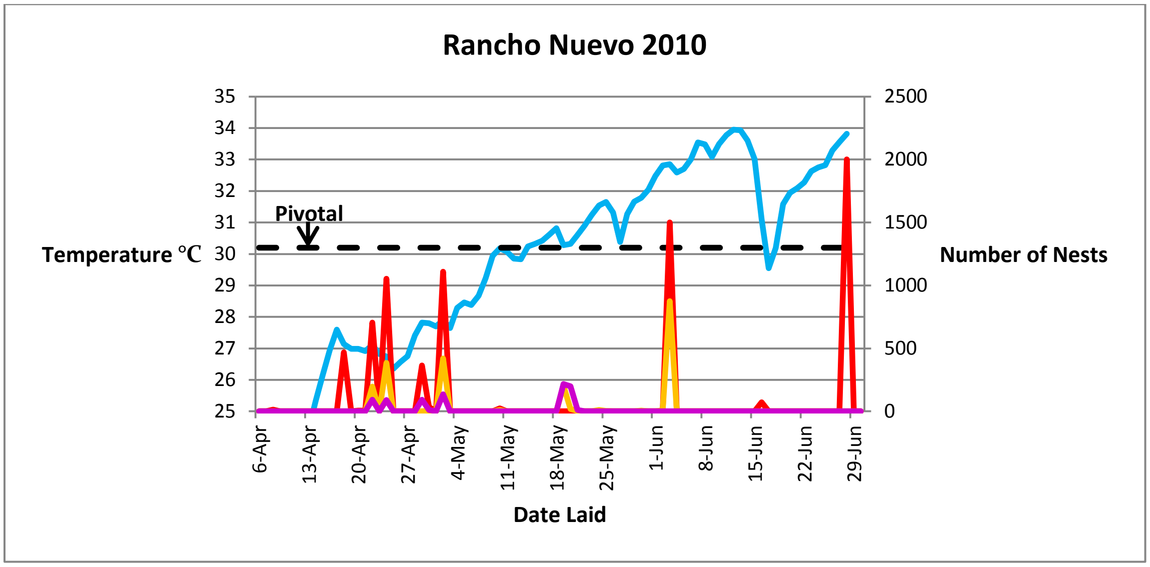


Figure 21. Blue line indicates the average daily temperature in the egg corrals. Red (main egg corral), yellow (south egg corral), and purple (north egg corral) lines indicate total nests relocated each day to the egg corrals in 2010 with the major peaks representing arribadas.

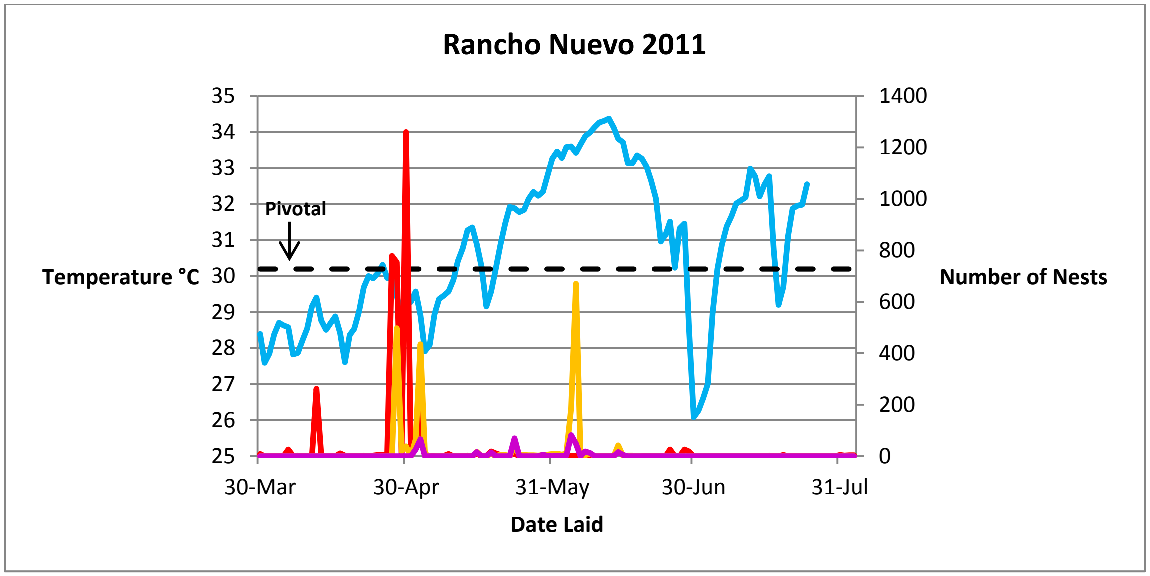
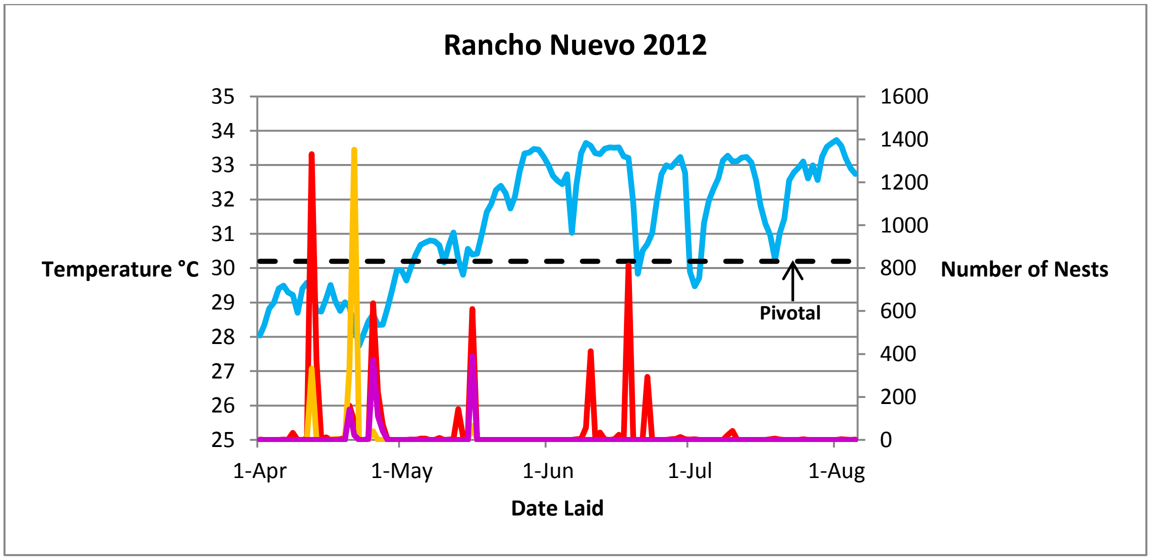


Figure 22. Blue line indicates the average daily temperature in the egg corrals. Red (main egg corral), yellow (south egg corral), and purple (north egg corral) lines indicate total nests relocated each day to the egg corrals in 2011 with the major peaks representing arribadas.



Figures 23. Blue line indicates the average daily temperature in the egg corrals. Red (main egg corral), yellow (south egg corral), and purple (north egg corral) lines indicate total nests relocated each day to the egg corrals in 2012 with the major peaks representing arribadas.

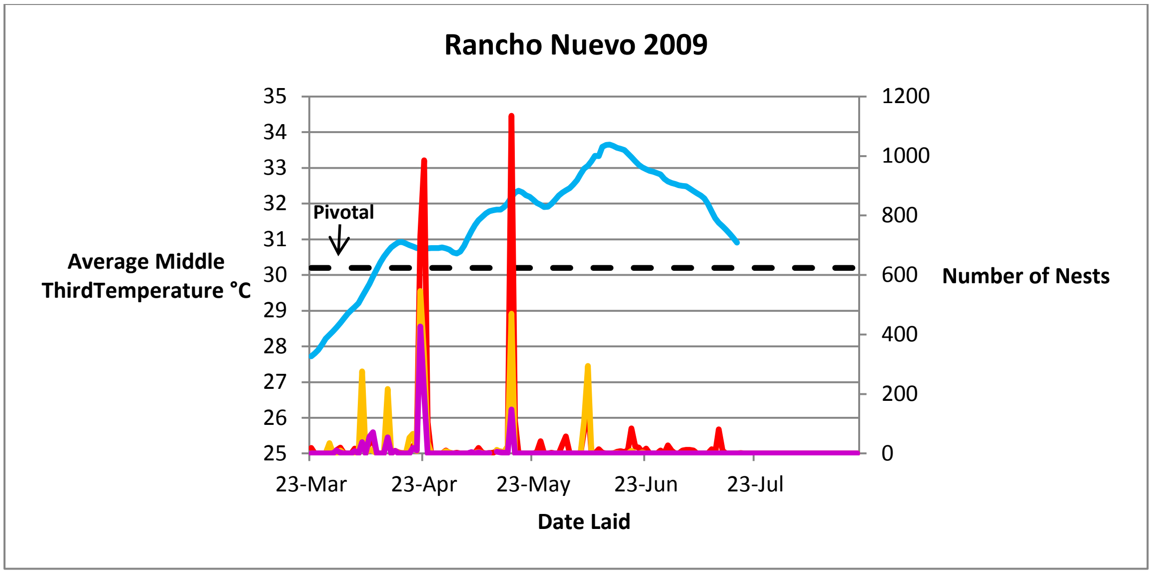


Figure 24. Blue line indicates average temperature in the main egg corral during the middle third of incubation for each lay date in the nesting season. Red (main egg corral), yellow (south egg corral), and purple (north egg corral) lines indicate total nests relocated each day to the egg corrals in 2009 with the major peaks representing arribadas.

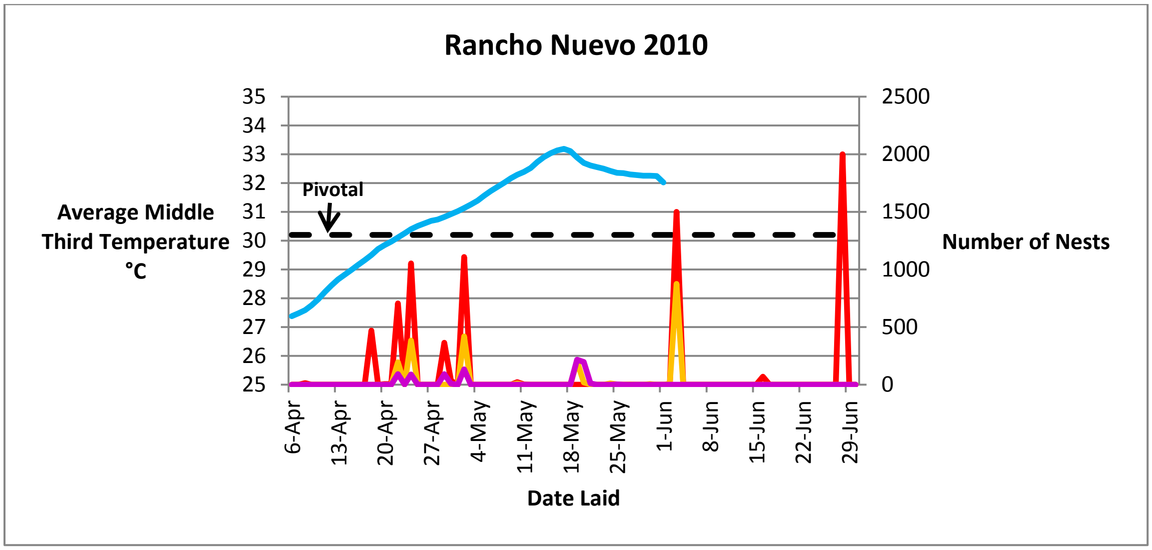


Figure 25. Blue line indicates average temperature in the main egg corral during the middle third of incubation for each lay date in the nesting season. Red (main egg corral), yellow (south egg corral), and purple (north egg corral) lines indicate total nests relocated each day to the egg corrals in 2010 with the major peaks representing arribadas.

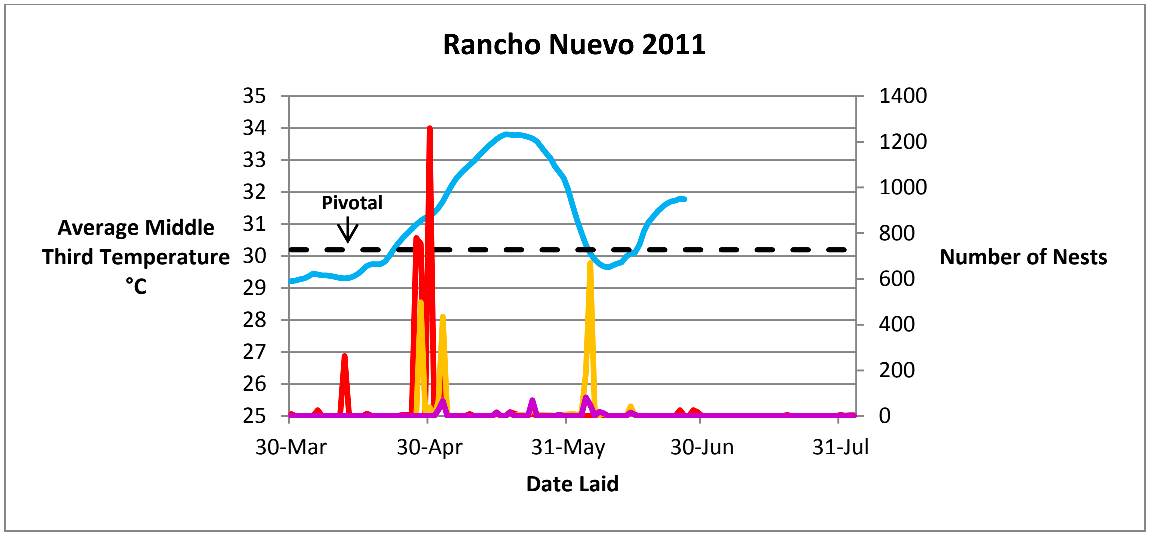


Figure 26. Blue line indicates average temperature in the main egg corral during the middle third of incubation for each lay date in the nesting season. Red (main egg corral), yellow (south egg corral), and purple (north egg corral) lines indicate total nests relocated each day to the egg corrals in 2011 with the major peaks representing arribadas.

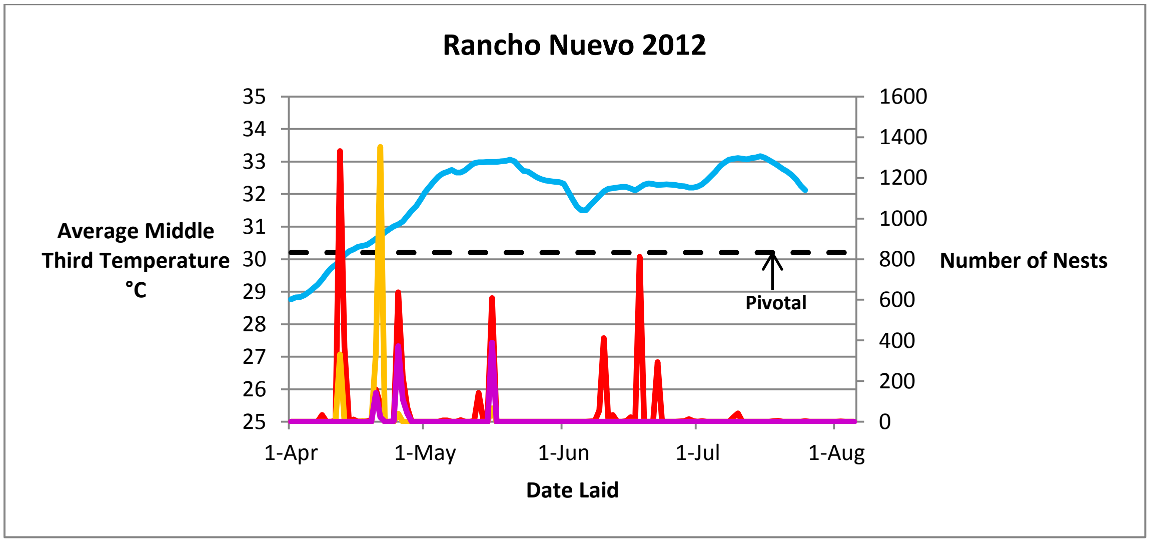


Figure 27. Blue line indicates average temperature in the main egg corral during the middle third of incubation for each lay date in the nesting season. Red (main egg corral), yellow (south egg corral), and purple (north egg corral) lines indicate total nests relocated each day to the egg corrals in 2012 with the major peaks representing arribadas.

Table 5: Predicted sex ratios for egg corral nests for the 2009 – 2012 nesting seasons. The number of nests used in sex ratio predictions for each year represents those that had temperature data available for the sex ratio calculations. *During 2010, sand temperature data loggers in the egg corrals were removed on June 28th due to Hurricane Alex, therefore an additional hypothetical range of sex ratios is included in the table that includes nests laid later in the season with sex ratios based on typical temperatures during July and August.

Year	Total Nests in Corrals	Number of Nests Used in Sex Ratio Predictions	Sex Ratio (% Female)
2009	8120	8115	79.7%
2010	10373	5926, *10373	72.4%, *73.5% - 84.2%
2011	6131	6064	80.6%
2012	8734	8730	76.1%

Hypothetical Sex Ratio Produced on the Natural Nesting Beach

In an effort to estimate a hypothetical sex ratio produced on the natural nesting beach, sex ratios were calculated for the 2009 -- 2012 nesting seasons using nesting beach temperatures instead of average egg corral temperatures for all nests relocated to the egg corral. Figures 29 – 32 (2009 – 2012 respectively) show the seasonal nesting distribution relative to both the average daily temperature on the nesting beach and the average daily temperature in the main egg corral for comparison. Figures 33 – 36 (2009 – 2012 respectively) show the seasonal nesting distribution relative to the average temperature for the middle third of incubation for both the natural nesting beach and the main egg corral for comparison. The hypothetical sex ratio for each nest was calculated based on the middle third of incubation as described above, but using beach temperatures rather than egg corral temperatures. The predicted sex ratios from the nesting beach were compared to those in the egg corrals, and were significantly less female biased than those predicted for the egg corral (Fisher's Exact Tests, p<0.0001). Beach temperature data from 2010 and 2011 did not span the entire season, because data loggers were removed mid-season due to hurricanes. Therefore, only partial season data sets were compared for those two years. Further, those two years were not included in estimating the hypothetical sex ratios for the natural nesting beach produced over the entire nesting season. Full season data sets were recorded during 2009 and 2012 for the nesting beach and the predicted sex ratios are shown in Figure 37 in comparison to the predicted egg corral sex ratios. In both years, the seasonal sex ratios predicted for the natural nesting beach were female biased.

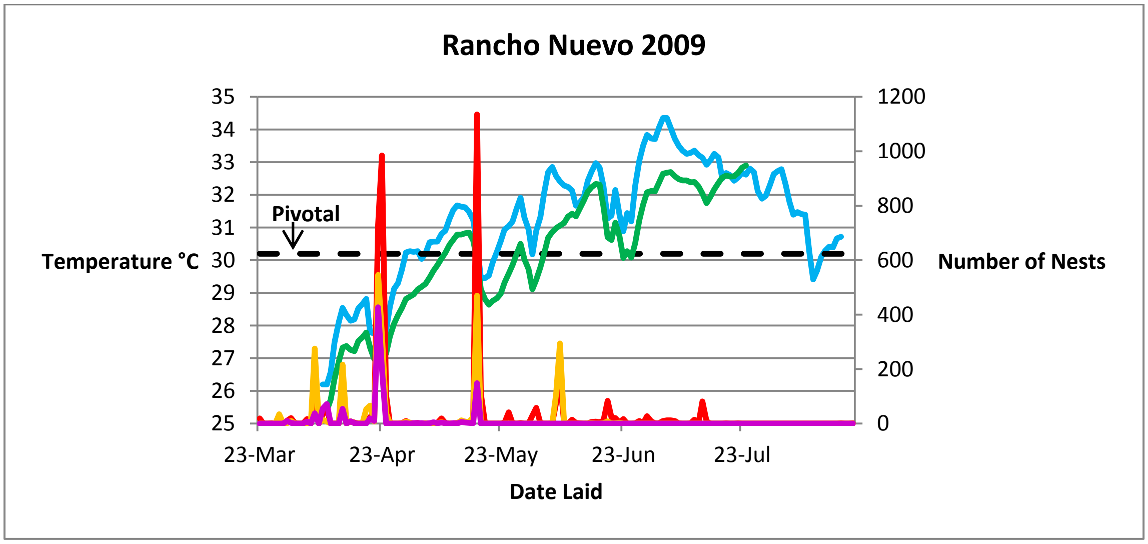


Figure 28. The green line represents the daily average temperature on the natural nesting beach, the blue line represents the daily average temperature in the main egg corral. Red (main egg corral), yellow (south egg corral), and purple (north egg corral) lines indicate total nests relocated each day to the egg corrals in 2009 with the major peaks representing arribadas.

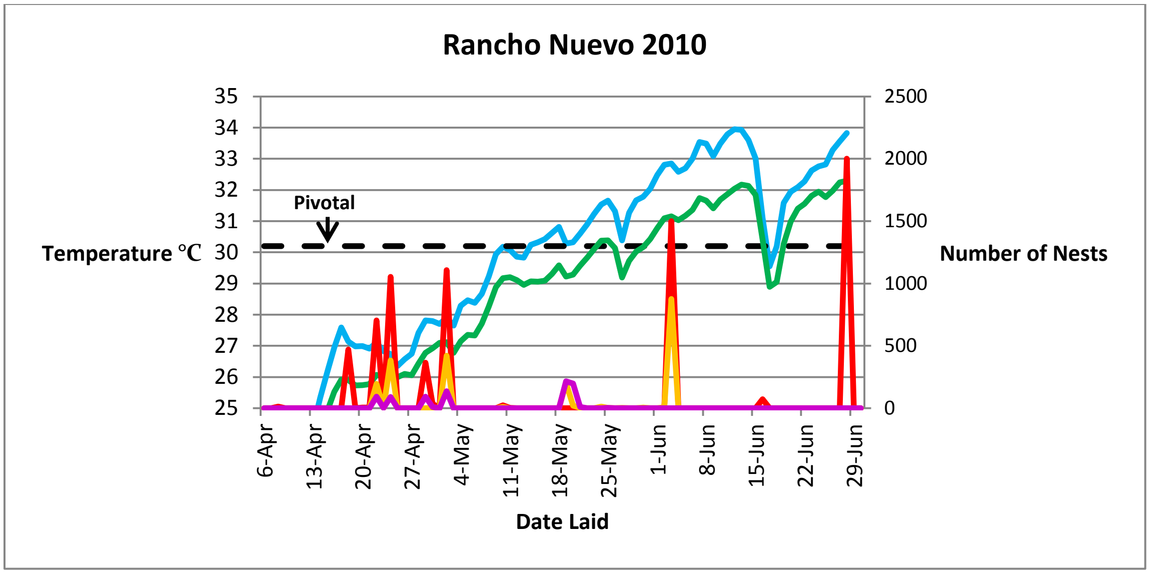


Figure 29. The green line represents the daily average temperature on the natural nesting beach, the blue line represents the daily average temperature in the main egg corral. Red (main egg corral), yellow (south egg corral), and purple (north egg corral) lines indicate total nests relocated each day to the egg corrals in 2010 with the major peaks representing arribadas.

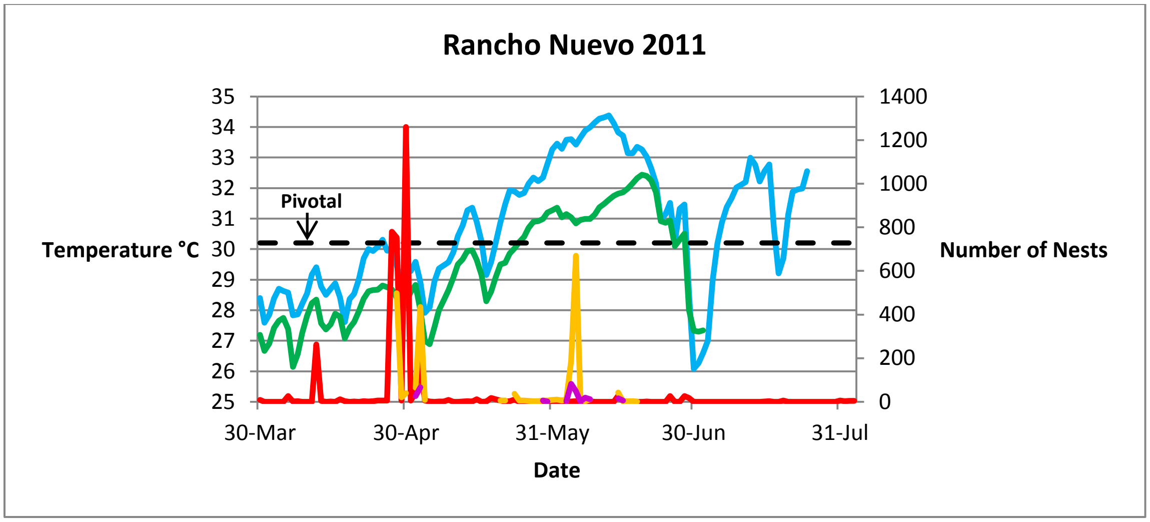


Figure 30. The green line represents the daily average temperature on the natural nesting beach, the blue line represents the daily average temperature in the main egg corral. Red (main egg corral), yellow (south egg corral), and purple (north egg corral) lines indicate total nests relocated each day to the egg corrals in 2011 with the major peaks representing arribadas.

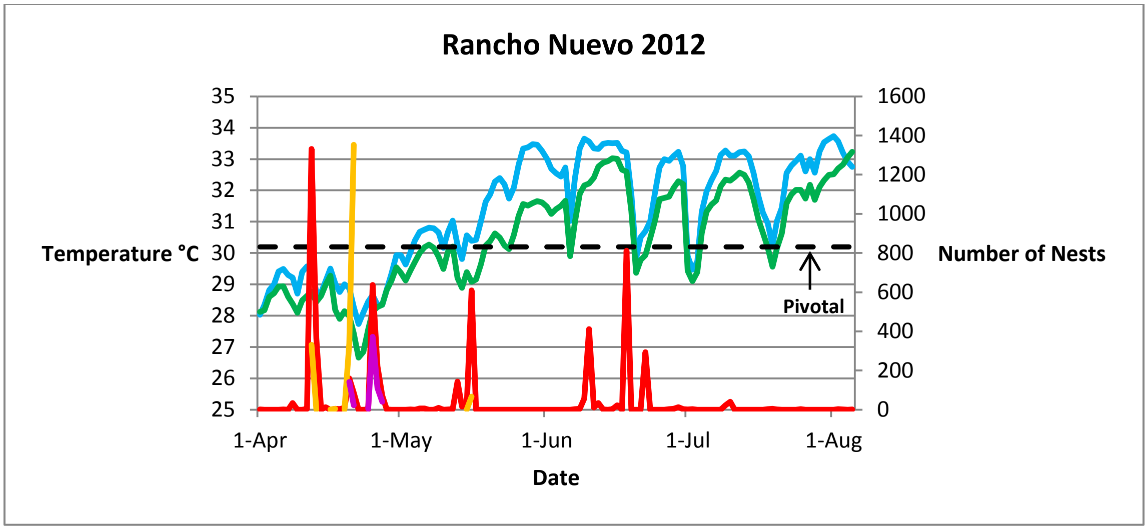


Figure 31. The green line represents the daily average temperature on the natural nesting beach, the blue line represents the daily average temperature in the main egg corral. Red (main egg corral), yellow (south egg corral), and purple (north egg corral) lines indicate total nests relocated each day to the egg corrals in 2012 with the major peaks representing arribadas.

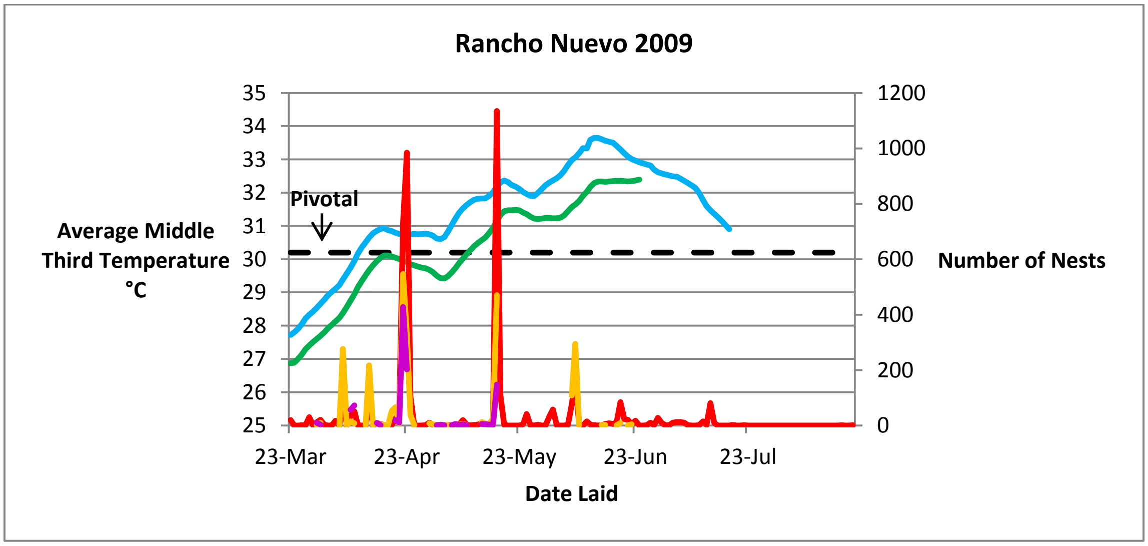


Figure 32. The green line represents the average temperature during the middle third of incubation on the natural nesting beach, the blue line represents the average temperature during the middle third of incubation in the main egg corral. Red (main egg corral), yellow (south egg corral), and purple (north egg corral) lines indicate total nests relocated each day to the egg corrals in 2009 with the major peaks representing arribadas.

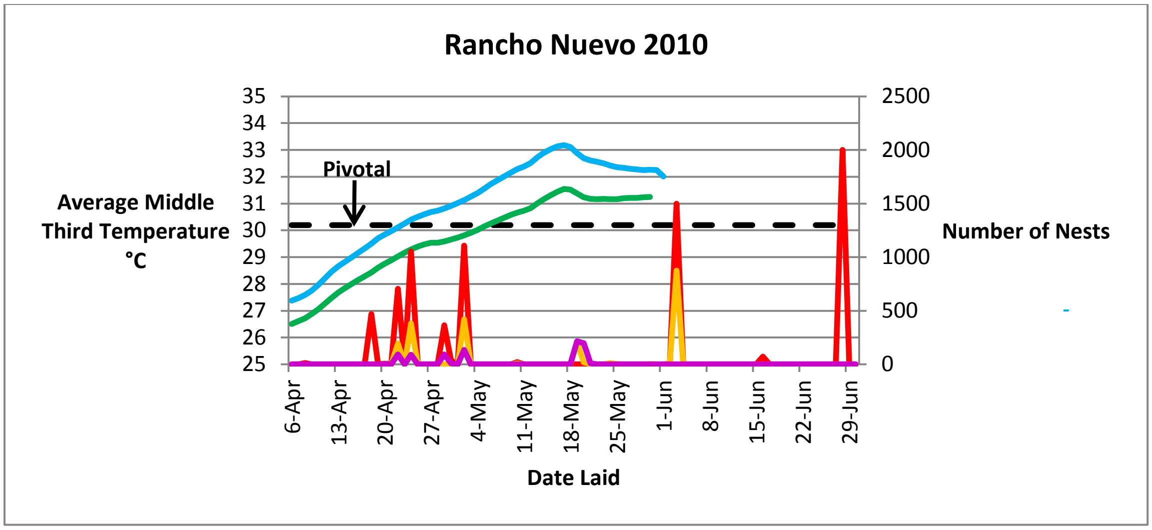


Figure 33. The green line represents the average temperature during the middle third of incubation on the natural nesting beach, the blue line represents the average temperature during the middle third of incubation in the main egg corral. Red (main egg corral), yellow (south egg corral), and purple (north egg corral) lines indicate total nests relocated each day to the egg corrals in 2010 with the major peaks representing arribadas.

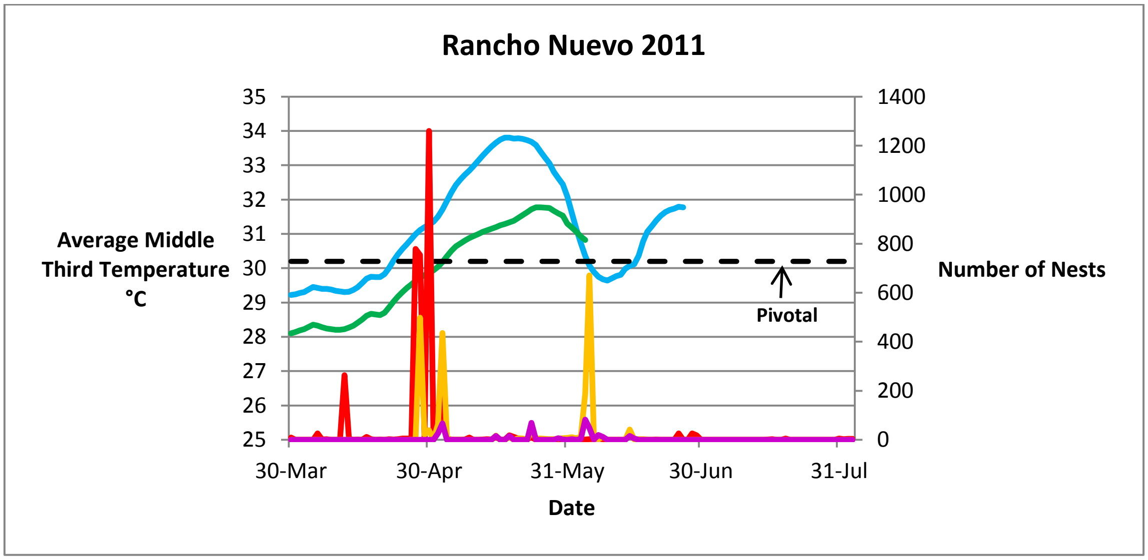


Figure 34. The green line represents the average temperature during the middle third of incubation on the natural nesting beach, the blue line represents the average temperature during the middle third of incubation in the main egg corral. Red (main egg corral), yellow (south egg corral), and purple (north egg corral) lines indicate total nests relocated each day to the egg corrals in 2011 with the major peaks representing arribadas.

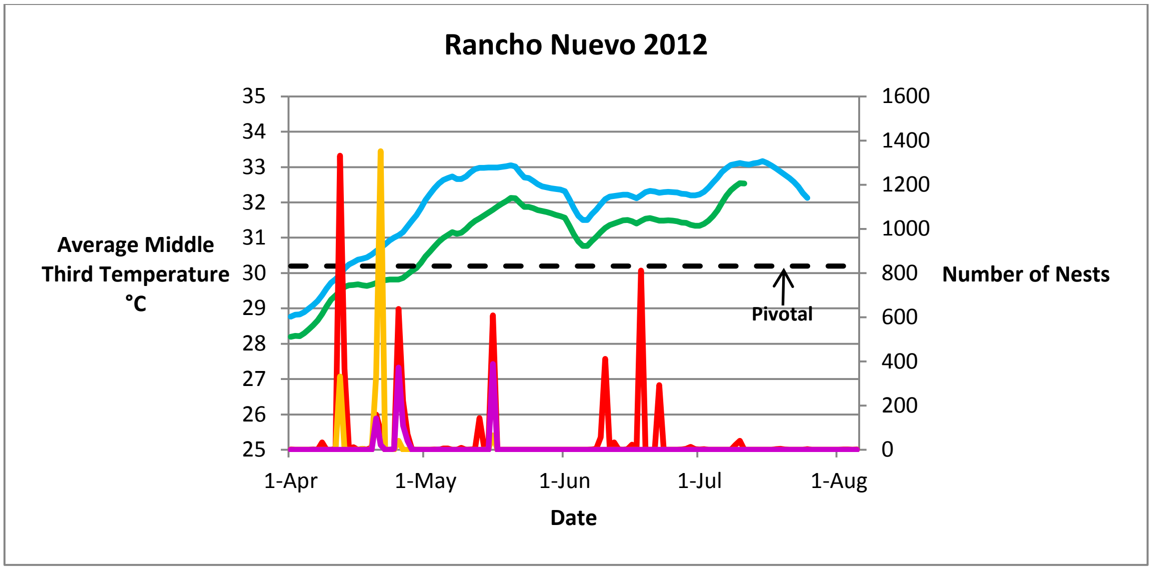


Figure 35. The green line represents the average temperature during the middle third of incubation on the natural nesting beach, the blue line represents the average temperature during the middle third of incubation in the main egg corral. Red (main egg corral), yellow (south egg corral), and purple (north egg corral) lines indicate total nests relocated each day to the egg corrals in 2012 with the major peaks representing arribadas.

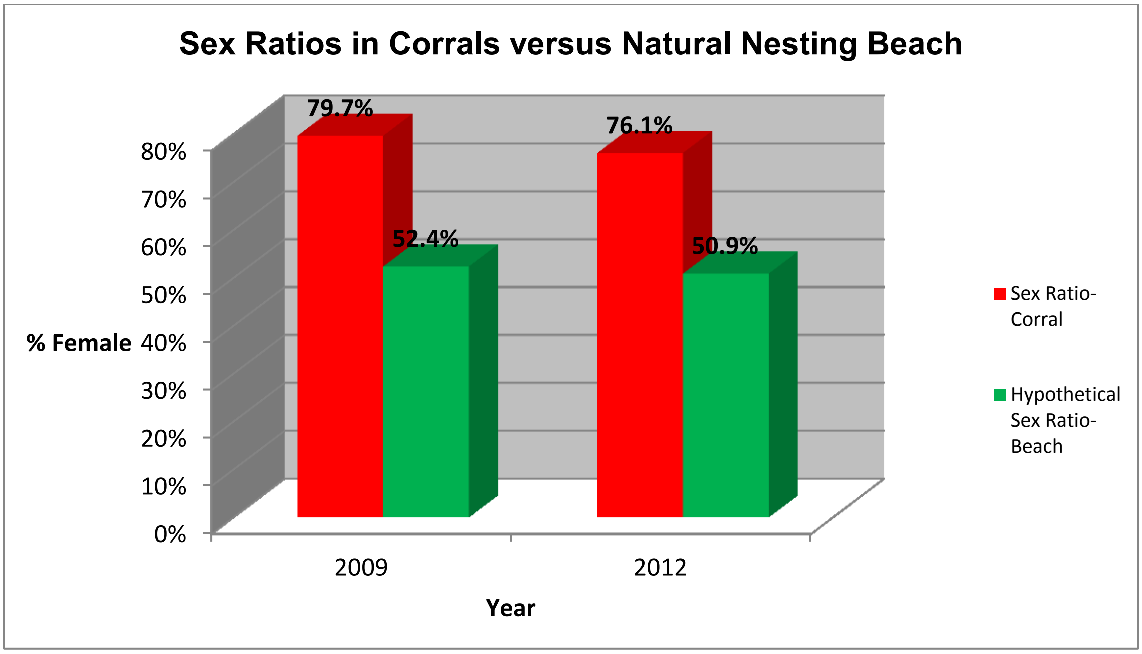


Figure 36. Yearly sex ratios in the main egg corral (red bars) and hypothetical sex ratios on the natural nesting beach (green bars). Complete seasonal data sets were available for 2009 and 2012. Data sets were omitted for the 2010 and 2011 nesting seasons since data loggers were prematurely removed from the beach in preparation for Hurricane Alex (June 30, 2010) and Hurricane Arlene (June 30, 2011) that impacted the Rancho Nuevo area. Green bars represent the hypothetical sex ratios that would have been produced if those same nests had been left to incubate *in situ* for each year.

Impact of Global Climate Change on Sex Ratios

Sex ratios for all nests in the egg corrals were calculated simulating a conservative 1°C increase in average egg corral temperatures in an effort to gain insight on the potential impact of global climate change on sex ratios. A 1°C increase in incubation temperatures in the egg corral resulted in sex ratios that were significantly more female biased than sex ratio predictions based on current incubation temperatures (Fisher's Exact Test, $p<0.0001$) (Figure 39). This model was also used to calculate hypothetical sex ratios on the natural nesting beach resulting from a 1°C increase in average beach temperatures (Figure 40). In both cases, the full seasonal data sets for 2009 and 2012 were used for the analysis.

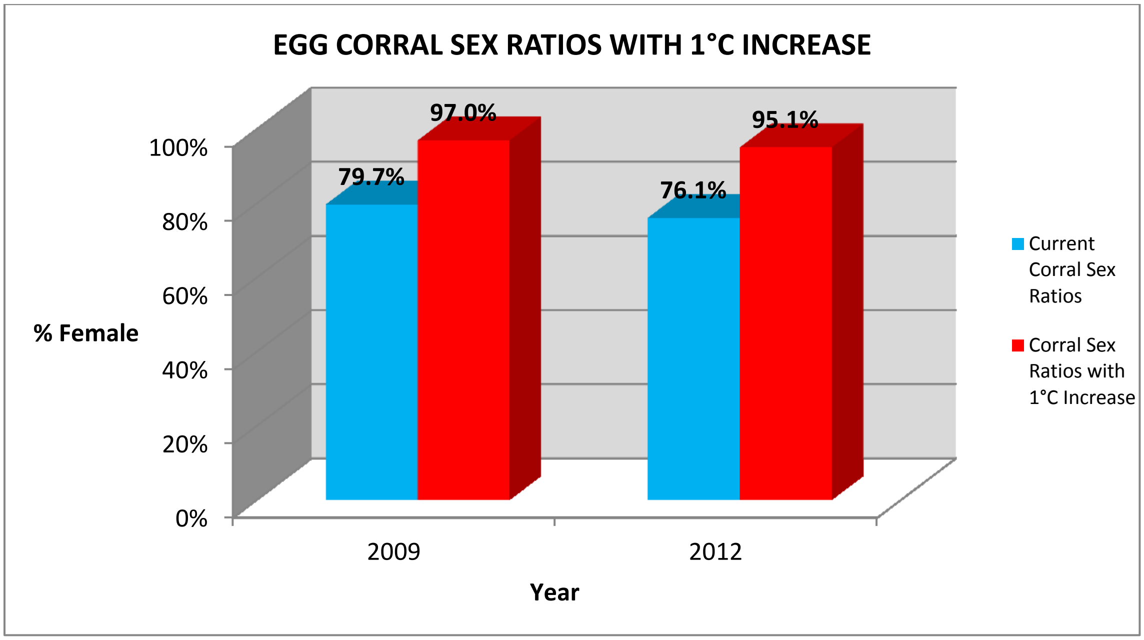


Figure 37. Sex ratios based on known incubation temperatures in the egg corrals for the 2009 and 2012 nesting seasons (blue bars) compared to sex ratios projected with a hypothetical increase of 1°C in incubation temperatures (red bars). Complete seasonal data sets were available for 2009 and 2012. Data sets were omitted for the 2010 and 2011 nesting seasons since data loggers were prematurely removed from the beach in preparation for Hurricane Alex (June 30, 2010) and Hurricane Arlene (June 30, 2011) that impacted the Rancho Nuevo area.

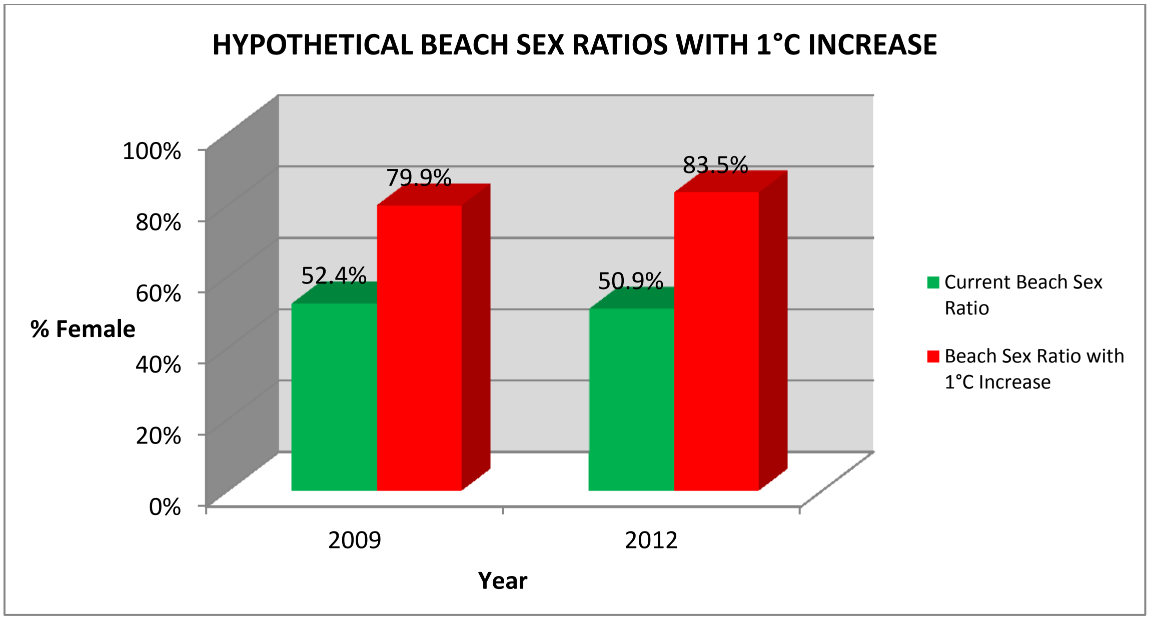


Figure 38. Yearly sex ratios for known incubation temperatures on the natural nesting beach for the last six years (green bars) compared to yearly sex ratios projected with a hypothetical increase of 1°C in incubation temperatures (red bars). Complete seasonal data sets were available for 2009 and 2012. Data sets were omitted for the 2010 and 2011 nesting seasons since data loggers were prematurely removed from the beach in preparation for Hurricane Alex (June 30, 2010) and Hurricane Arlene (June 30, 2011) that impacted the Rancho Nuevo area.

Discussion

Seasonal Trend in Sand Temperature and Sex Ratio Production

The egg corrals and the natural nesting beach showed similar seasonal trends in sand temperatures for each nesting season from 2009-2012. Temperatures increase from late March through April, but typically remain below the pivotal temperature estimated for the Kemp's ridley. Temperatures continue to increase during the early portion of the nesting season reaching the pivotal temperature (Shaver et al., 1988; LeBlanc et al., 2012) by early to mid-May. Temperatures increase to well above pivotal by early June and then remain high with the exception of cooling events associated with tropical weather systems. Based on these seasonal temperature trends, sex ratios produced in egg corral nests laid during the early portion of the nesting season (late March through mid-April) were predicted to produce mixed sex ratios with many male biases in most years. Nests laid during late April were predicted to produce female biases, and from mid-May through the remainder of the nesting season, nests were typically predicted to produce all females. Overall, the results reveal a seasonal shift in sex ratio production in which male-biases are produced early in the nesting season, followed by a shift to female biases, and then all females. The all-female trend dominates the majority of the nesting season, except in cases in which tropical weather systems lowered sand temperatures, resulting in the short-term production of female-biased or even male-biased nests. Several previous studies in sea turtles have also reported seasonal variation in sand temperatures and hatchling sex ratios (Mrosovsky et al., 1984; LeBlanc, 2004; Eich, 2009).

Data loggers placed into *in situ* nests were chosen randomly throughout the nesting season to represent a sample of the temporal variation in actual nest temperatures throughout the entire season. The results reflect the seasonal shift in predicted sex ratios. Early season nests produced a greater number of male biased nests. Predicted sex ratios in the data logger nests shifted to female biased and all female sex ratios for nests laid later in the season during the peak of nesting. These findings are consistent with those reported for *in situ* nests at Rancho Nuevo from 2005-2008 (Eich, 2009).

The seasonal shift in sex ratio production has significant conservational implications. Specifically, the results indicate that nests laid at the start of the nesting season represent an important source of males for the population and this should be considered when deciding which nests throughout the season should be moved and protected in the egg corral. Because of the seasonal shift in sex ratios, the timing of the arribadas can have a significant impact on the overall seasonal sex ratio. The timing of arribadas determines when nests will experience the thermosensitive period and can therefore have a significant effect on the sex ratio of hatchlings produced.

Temperature data loggers also captured the significant cooling effects of major tropical weather systems. Hurricanes Alex on June 30, 2010 and Arlene on June 30, 2011 moved through the Rancho Nuevo area and lowered sand temperatures to near or below pivotal temperature. The overall sex ratio for these two nesting seasons was therefore shifted due to the significant cooling of sand temperatures by tropical weather systems. Major seasonal weather events that lead to the cooling of sand temperatures could therefore also be an important source of male hatchling production. Previous studies at Rancho Nuevo have also reported a decrease in overall female bias for nesting seasons that experience major tropical weather systems (Park, 2006).

Overall Seasonal Sex Ratio in the Kemp's Ridley Recovery Program

During the current study, the peak of nesting at Rancho Nuevo occurred from approximately mid-April through mid-June. Therefore, the majority of nests were predicted to produce female biases or all females, resulting in an overall female-biased seasonal sex ratio. The egg corrals were predicted to produce a female bias for all four years included in this study, 2009-2012, ranging from 76.1% to 80.6% female. This finding is consistent with sex ratio predictions of 75.6% for 2007 and 76.1% for 2008 for Rancho Nuevo (Eich, 2009). However, the current study is a more comprehensive prediction since the predictions by Eich, (2009) were only for the main egg corral and did not include the satellite corrals.

Temperatures in all three egg corrals were generally similar in temperature and significantly warmer than the natural nesting beach. However, a significant difference in egg corral temperatures was detected in 2009 in which the north corral was cooler than the main corral. Due to its location next to one of the seasonal rivers along the coast, the north corral is frequently inundated with tidal fluctuations. Persistent tidal inundation during 2009 could have cooled temperatures in the north corral relative to the other two corrals that perhaps did not experience such severe tidal influence, thus creating a significant difference between yearly temperatures in all three corrals for this year.

The approximate 3 females: 1 male sex ratio predicted for the egg corrals could be affecting the recovery rate of the Kemp's ridley. Coyne and Landry (2007) projected the growth of the Kemp's ridley population under several different sex ratio scenarios and found the greatest rate of recovery for an approximate 3 female to 1 male sex ratio (assuming males do not become a limiting factor for the population). A 3:1 sex ratio would result in a 271% increase in the numbers of nests after 50 years, in comparison to a 1:1 sex ratio (Coyne et al., 2007). Considering the recovery rate of the Kemp's ridley over the past several decades, other sea turtle conservation programs may consider emulating the female-biased hatchling sex ratios. A female-biased sex ratio can potentially be viewed as a short-term tool that can be used to accelerate the recovery of critically endangered sea turtles.

Monitoring of sex ratios in the Kemp's Ridley Recovery Program is essential for understanding how sex ratios impact on the long-term recovery trend for this endangered species. Previous studies using subsets of nests with data loggers have produced general sex ratio estimates for Rancho Nuevo (Geis et al., 2001; Geis, 2004; Park, 2006). Additionally, a more comprehensive approach for generating high resolution, sex ratios based on all of the nests moved to the egg corral was used for the 2007 and 2008 nesting seasons (Eich, 2009). The current study extends the high resolution sex ratio predictions to include the 2009-2012 nesting seasons. This study thus represents a growing, long-term data set of high resolution hatchling sex ratio predictions that can be used to address long-term ecological and evolutionary questions pertaining to the Kemp's ridley and to sea turtle populations in general. This kind of data set is particularly important for predicting the effects of global climate change on the species in the future (see below).

Problems can arise when extrapolating sex ratio data from the egg corrals to the overall sex ratio produced at Rancho Nuevo. In some years the lack of temperature data later in the season due to hurricanes could skew the predicted sex ratio for such nesting seasons. For example, in 2010, data loggers on the beach and in the egg corral were removed on June 28th in preparation for Hurricane Alex that impacted the area on June 30. Sex ratios were therefore only predicted for nests laid up to June 1st that would have completed the middle third of incubation by June 28th. There were two late-season arribadas on June 3rd (1500 nests) and June 28th (2000 nests) that were thus not included in the sex ratio calculations since they occurred after the sand data loggers in the egg corral were removed. These two arribadas, represent a total of 3500 nests that would most likely have been at least female biased (i.e. approximately 75% female), if not 100%

female, given the typical sand temperature at the time of the season that these arribadas occurred. If these nests are included in the sex ratio calculations (using either a 75% female or all female prediction), the overall sex ratio predicted for 2010 would range from 70.6% female to 82.8% female.

Hypothetical Sex Ratio Prediction for the Natural Nesting Beach

Sand temperature data from the egg corrals and the natural nesting beach indicated that the egg corrals are significantly warmer than the natural nesting beach by an average of 1.04°C ± 0.57°C. This trend appears to be a consistent feature reported in a variety of past studies at Rancho Nuevo (Geis et al., 2001; Geis, 2004; Park 2006; Eich, 2009). Therefore, incubation temperatures in the egg corrals reach and exceed pivotal temperature earlier in the season than incubation temperatures on the natural beach. Thus, the egg corrals are predicted to produce a greater female bias than the natural beach, though the natural beach is still female biased. As examples, if all of the nests that were moved to the egg corrals from 2009 and 2012 had been left *in situ,* the resulting sex ratios would have been 57.4% female for 2009, and 59.8% female for 2012 (full-season data sets for 2010 and 2011 were not available due to hurricanes). The difference in sex ratios produced on the natural nesting beach and the main egg corral is most likely because of where the egg corrals at Rancho Nuevo are located. The egg corrals are constructed high on the open beach adjacent to the dune that borders the beach. This location helps prevent significant tidal inundation or loss of nests due to erosion when weather systems move through the area. Due to the elevation, which is well above the water table, and lack of vegetation, the corrals are relatively warm compared to most natural nesting locations on the beach that are closer to the surf.

The sex ratios predicted for the natural beach represent the sex ratio that can be expected as the Kemp's Ridley Recovery Program transitions to leaving the majority of nests *in situ.* It is plausible, that this shift to a lower female-biased sex ratio could slow the recovery rate for this species. However, this sex ratio may represent a natural sex ratio for the Kemp's ridley. This point can be considered as part of the ultimate goals of the recovery plan as the species gradually returns to an ecologically stable and natural state.

Additionally, the results indicate that a female bias may be a natural sex ratio for the Kemp's ridley. Evolutionary theory would suggest an equal 1:1 sex ratio if there is equal parental investment in both sexes. However, a wide variety of sex ratios have been reported for species with TSD, and many hypotheses have been suggested to account for these biases (Shine, 1999). In particular, female biases have been reported for many sea turtle populations and may be the result of evolutionary selection (Wibbels, 2003; Shaver and Wibbels, 2007). Therefore, the Kemp's ridley, like many other sea turtle populations, may naturally have a female-biased sex ratio.

Impact of Global Climate Change on Sex Ratios

The IPCC has projected an increase in surface temperatures of 1-4 °C by the year 2100 using various models based on different levels of carbon emissions (Solomon et al., 2007). The current study hypothetically simulated a conservative scenario by projecting a

1°C increase in temperatures for nests in the egg corrals for the 2009 and 2012 nesting seasons (these were the seasons with complete temperature data sets). Although the resulting sex ratios of 97.0% and 95.1% (respectively) seem extreme, they represent a very conservative estimate of the projected rise in global temperature. Considering that the current warming trend has been tracking higher than the 4°C projection (Solomon et al., 2007), the actual impact could be significantly greater than that estimated in the current study. While a moderate female bias could be beneficial to the recovery of an endangered sea turtle (Wibbels, 2003; Shaver and Wibbels, 2007), extreme female biases could be detrimental. Such biases could reduce the number of males to the point that they could limit the reproductive output of a population. The increased incubation temperatures used in the current simulation would also lead to prolonged periods of time spent at lethal temperatures that would reduce hatching success and hatchling fitness (Limpus et al., 1979; Mickelson and Downie, 2010, Maulany et al., 2012).

Assuming that a greater portion of nests will be left *in situ* as the Kemp's ridley gradually recovers, the conservative 1°C increase in average temperatures was also simulated for natural beach temperatures. The results also indicate an increase in female bias, though to a lesser extreme than in the egg corrals (i.e. 79.9% and 83.5% for 2009 and 2012 nesting seasons, respectively). The natural beach may therefore offer a small buffer to increasing temperatures and extreme female biases. However, other options such as the continued use of corrals with added shading to lower incubation temperatures may have to be considered in decisions regarding the management and conservation of the species in the future.

It is plausible that the biology and ecology of the Kemp's ridley may adapt to global climate change. For example, the seasonal timing of nesting may shift in response to warmer temperatures. Such changes have been reported in freshwater species of turtles (Schwanz and Janzen, 2008). If turtles start nesting earlier, that could definitely impact average incubation temperatures. However, in the case of the Kemp's ridley that nests multiple times throughout a nesting season (Márquez et al., 2001; Rostal and Plotkin, 2007), the temperatures during the second or third nesting of a season may have reached well above pivotal if not into lethal ranges. It is also plausible that the sex determining mechanism could potentially adapt by shifting the transitional range of temperatures and pivotal temperature. However, the molecular and physiological mechanisms underlying TSD in sea turtles are not clearly understood (Wibbels, 2003), so it is difficult to assess the ability of this system to adapt to temperature change. Further, considering the relatively long age to maturity in the Kemp's ridley, there would be a limited number of generations to allow for genetic changes, especially given the projected rate of climate change (Solomon et al., 2007). Regardless, the results of the current study clearly show that global climate change represents a major threat to the future survival of the Kemp's ridley.

Finally, the Kemp's ridley may represent a model system for examining the effects of climate change on a temperature-sensitive species. The life history of the Kemp's ridley makes it particularly vulnerable to changes in environmental temperature. It has a limited distribution, primarily inhabiting the Gulf of Mexico, and it has one primary nesting beach where the majority of nesting occurs for the entire species. Further, its sex determination, resulting sex ratios, and hatching success are temperature-sensitive. The timing of its seasonal reproductive cycle may also be temperature sensitive. As such, the Kemp's ridley may represent an optimal sentinel species for evaluating the impact of global climate change. Thus, it is imperative that the Kemp's ridley be closely monitored in the future to assess potential changes in its biology and conservation status.

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NEST AND HATCHLING SURVIVAL AT RANCHO NUEVO, THE PRIMARY NESTING BEACH OF THE KEMP'S RIDLEY SEA TURTLE

by

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Abstract

The Kemp's ridley was historically the most endangered sea turtle in world and was on the brink of extinction during the mid-1980's. Due to over four decades of intense conservation efforts, this species is now showing a gradual recovery. Part of these conservation efforts include the relocation of almost all nests to protected egg hatcheries (i.e. egg corrals) at the primary nesting beach at Rancho Nuevo, Mexico. In fact, the species has recovered to the point that the annual nesting is now exceeding the capacity of the egg corrals. Thus, the Kemp's Ridley Recovery Program is now transitioning away from protecting nests in egg corrals to leaving nests out on the natural nesting beach. Therefore, the survival rate of the *in situ* nests and resulting hatchlings is of prime interest to the conservation and management of the Kemp's ridley. It is imperative from a management perspective to evaluate the abundance of predators and their impacts on *in situ* nest survival, hatching success, and hatchling survival during seafinding. The current study evaluated predator abundance during 2011 and 2012 nesting seasons at Rancho Nuevo. Additionally, the study addressed *in situ* nest and hatchling survival during the 2009 -2012 nesting seasons using nests from arribadas. The results indicate a limited group of diurnal and nocturnal predators frequent the beach of Rancho Nuevo and that the abundance of these predators is generally low, but variable, depending on location and timing. The results also reveal that predator impact on the natural nesting beach is relatively low, resulting in high nest survival of arribada nests. Additionally, predation on hatchlings following emergence is also relatively low with most of the hatchlings successfully reaching the surf. The results support the use of the arribada nesting strategy for maximizing the production of hatchlings from nests on the

natural nesting beach as the Kemp's Ridley Recovery Program gradually shifts away from the use of egg corrals as this species continues to recover. The results also provide insight on the evolutionary advantage of arribada nesting, resulting in predator satiation.

Introduction

The Kemp's ridley sea turtle was historically an abundant species found throughout the Gulf of Mexico, but its nesting location was unknown to the scientific community. In 1963, Henry Hildebrand solved the "riddle" of where the Kemp's ridley sea turtle nested through the discovery the 1947 Herrera film (Hildebrand, 1963). From this film, he estimated 40,000 turtles nested in a single mass nesting event, or arribada, at Rancho Nuevo, Mexico. The Kemp's ridley is one of only two species of sea turtle known to nest in these arribadas, yet the number of turtles involved in these mass nesting events had severely declined by the time the Herrera film was discovered in 1961. Intense exploitation of eggs and incidental capture in fishing trawls initially led to the decline of the Kemp's ridley and by the mid 1980's the species had diminished to fewer than 300 nesting females annually (Marquez, 1994). Due to the continued decline of nesting at Rancho Nuevo, Mexico, a binational plan was initiated in 1978 (Pritchard et al., 1983; Marquez, 1994; Klima and McVey, 1982; Woody, 1989) to prevent the extinction of the Kemp's ridley, and it called for the protection of nesting females and the relocation of all nests to protected egg hatcheries (i.e. egg corrals).

Fortunately, the species has responded to intense conservation efforts. There has been a gradual increase in nesting numbers, and in recent years, the number of nests each year now exceeds the capacities of the egg corrals. The Kemp's Ridley Recovery Program is now forced to leave a growing percentage of nests from each year on the natural nesting beach to incubate *in situ* as the egg corrals fill. It is therefore of conservational interest to determine the natural predation rate out on the nesting beach and how that will affect nest and hatchling survival. The purpose of this study is to evaluate the fate of these *in situ* nests and their potential impact on the recovery of the Kemp's ridley as a whole. The study also evaluates the abundance and distribution of predators on the nesting beach. A previous study indicated a variety of nocturnal and diurnal predators could affect nests (Eich, 2009), and the current study evaluates and extends the results of that study. These data are a prerequisite for the development of effective management strategies for selecting the locations, timing, and number of nests that are left on the natural nesting beach. Leaving a portion of the Kemp's ridley nests to incubate *in situ* also provides an opportunity to evaluate the evolutionary significance of the arribada nesting behavior. Nesting en masse could provide certain advantages over scattered nesting such as reduced predation rate through predator satiation.

Methods

Nest Predation

Approximately 300 to 500 nests from one arribada each year were left on the natural nesting beach to incubate *in situ* during the 2010 – 2012 nesting seasons. These *in situ* nest study sites were used to evaluate nest and hatchling survival on the natural nesting beach. If possible, a high density nesting area (approximately 300 to 500 nests per

300 meters of beach) and a low density nesting area (approximately 50 nests or less per 300 meters of beach) of nests from an arribada were established to compare the survival rates of nests and hatchlings relative to nest density. The high and low density nesting areas on the Rancho Nuevo beach varied depending on the location of the arribada. The location of each nest was recorded by GPS and was marked with either a labeled stake (2010 and 2011) or with a labeled rock (2012). All *in situ* nests involved in this predation study were monitored daily for signs of predation to quantify the predation rate. A nest was marked as "semi-depredated" if a portion of the eggs in a clutch were destroyed by predators, leaving some eggs untouched and intact. Likewise, a nest was marked as "completely depredated" if all the eggs in a nest were totally destroyed, leaving no viable eggs intact for that nest.

Hatching Success

Following hatchling emergence, the contents of each *in situ* nest in 2011 and 2012 were removed and inventoried to determine average hatching success. Eggshells, unhatched eggs and dead hatchlings were used to calculate the average hatching success for each *in situ* nest.

Hatchling Survival from Nest to Surf

Hatchling survival during their movement to the sea was evaluated for all *in situ* nests in the high and low density nesting study areas during the 2012 nesting season. Following emergence, the hatchling tracks leading away from the nest were evaluated based on the estimated percentage of the tracks that successfully reached the high tide line. Seafinding success was assessed for each nest using five general categories, either all (100%), most (75%), half (50%), few (25%) or none (0%) of the hatchlings made it to the water. The goal for this portion of the study was to quantify the level of predation on hatchlings during their seafinding behavior.

Predator Abundance

The identity and abundance of predators on the beach at Rancho Nuevo was evaluated for the 2011 and 2012 nesting seasons. For each year, 4 to 5 different study areas from Barra Corrizo (18 km north of the main turtle camp) to Barra del Tordo (12 km south of the main turtle camp) along the beach were established as a part of this study. In each section, 10 one-meter squares of sand, or "predator plots" were created and evenly-spaced approximately every three meters on the beach flat adjacent to the dune where the majority of nesting occurs. The predator plots were evaluated 1 – 3 days per week throughout the nesting season. During an evaluation day, the plots were checked twice daily. The plots were checked once in the morning to document nocturnal predators that walked through the area during the previous night, and once later in the afternoon to document diurnal predators that walked through each plot during the day. Predator tracks were identified using standard field guides to animal tracks. The plots were smoothed after each observation to ensure only new tracks were recorded. Periodically, motion-triggered wildlife cameras were positioned amidst the predator plots in each study area to record predators that visited the plots. The pictures provide visual verification of the identity and abundance of predators that visit specific locations of the beach.

In 2011, there were three predator-plot study sites established to the north of the main camp at Rancho Nuevo. Two of the three sites were located 8.1 km to the north of the main camp and the third site was located 5.7 km to the north of the main camp.

Predator plots were also established in two locations to the south of the main camp, one 0.6 km south and the other 5.4 km south of the main camp. In 2012, three predator-plot study sites were established to the north of the main camp at Rancho Nuevo. Two sites were located at 5.7 km to the north of the main camp, and one at 4.2 km north of the main camp. Two predator plot study sites were established at 1.2 km and 5.7 km to the south of the main turtle camp.

Results

Nest Predation

During the 2010 nesting season, 288 *in situ* nests were left in a high density area (over 300 m of beach) from a June 5th arribada that occurred 9.0 km to the south of the main camp. Nests were monitored on a daily basis from June 5 to July 20. Out of 288 nests, 1.4% of nests (n=4) were completely destroyed by predators. An additional 3.5% of nests (n=10) were semi-depredated by predators, leaving the remaining 95.1% (n=274) of nests in the high density study site undisturbed by predators. Additionally, 66 nests were left *in situ* in a relatively low density nesting zone (over 300 m of beach) also approximately 9.0 km to the south of the main camp. In the low density nesting area, 66 nests were left *in situ* with 1.5% (n=1) of nests completely depredated by predators. The remaining 98.5% (n=65) of nests in the low density study site remained undisturbed by predators (Figures 1 and 2).

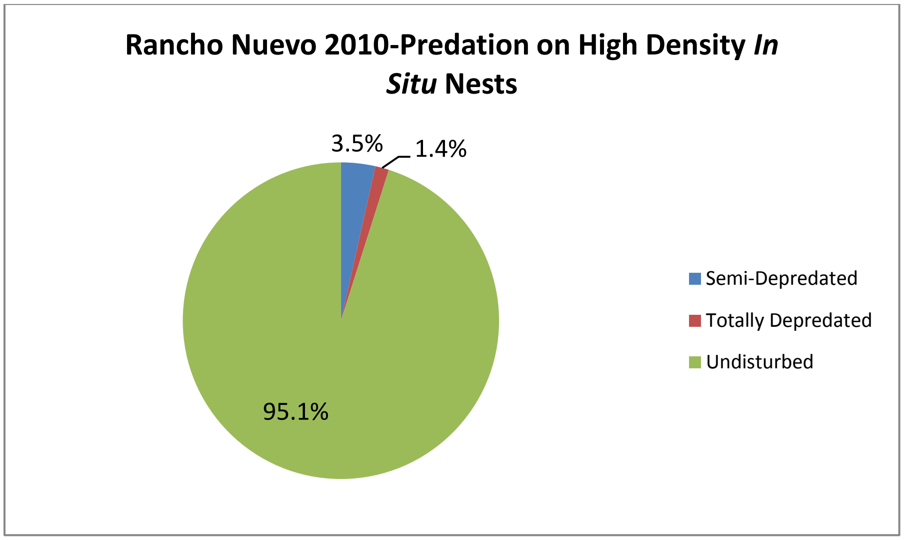
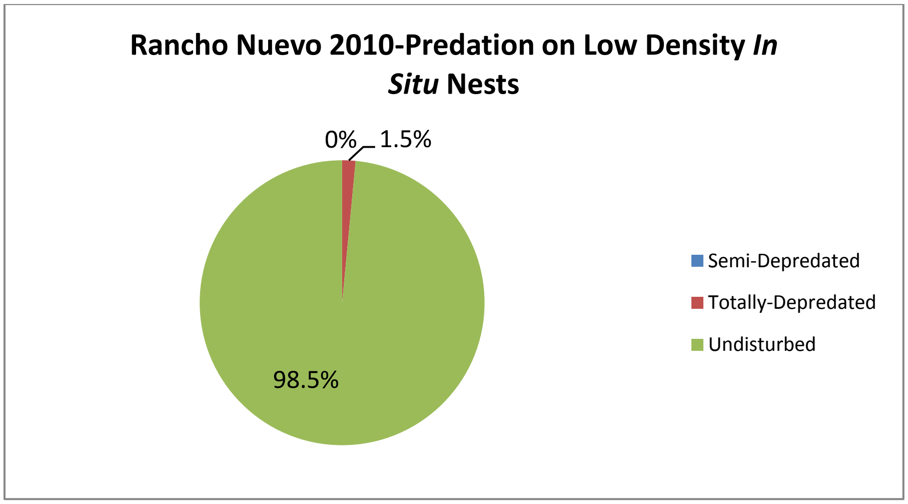


Figure 1. The percentage of *in situ* nests that were depredated throughout incubation in the high density study site during 2010.



Figures 2. The percentage of *in situ* nests that were depredated throughout incubation in the low density study site during 2010.

In 2011, high and low density nesting areas were left *in situ* from an April 28th arribada that occurred at approximately 8.4 – 8.1 km to the south of the main camp.

However, nests in the low density nesting area were lost due to high tides associated with a tropical weather system. Thus only data for the high density nesting area were evaluated for 2011. A total of 398 nests were left out on the natural nesting beach in the high density nesting area and were monitored from April 28 to June 17. Nine nests (2.3%) were completely destroyed by predators, 20.1% (n=80) were partially depredated, leaving 77.6% (n=309) of nests undisturbed by predators (Figure 3).

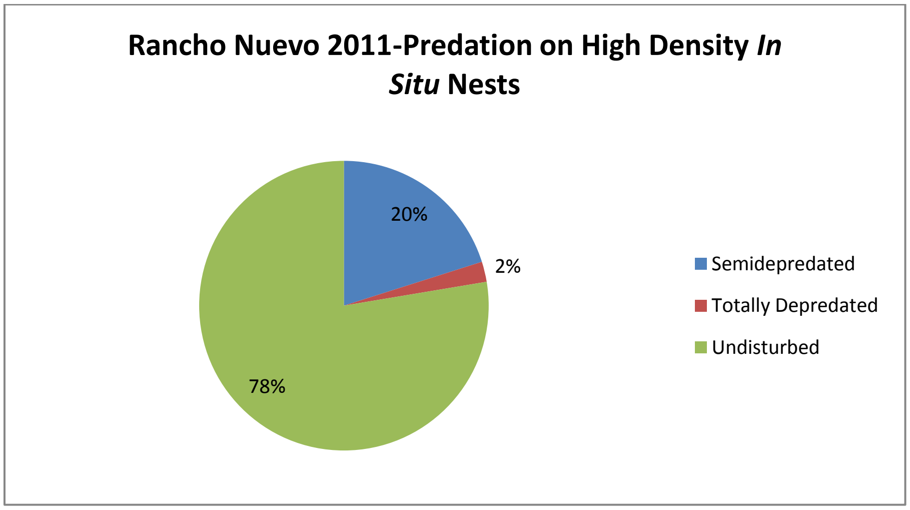


Figure 3. The percentage of *in situ* nests that were depredated throughout incubation in the high density study site during 2011.

In 2012, a total of 269 nests from the May 16th arribada were left *in situ* in a high density nesting area located approximately 12.0 – 12.3 km to the south of the main camp. Ninety-two of these nests were “lost” or unable to be located when their identifying marker was washed away with extreme high tides associated with storms. Of the 177 remaining nests, 2.8% (n=6) of nests were completely destroyed by predators, 14.1% (n=25) of nests were partially depredated, leaving the remaining 85.5% (n=146) of nests undisturbed by predators.

In the low density nesting area, 81 nests were left to incubate *in situ* at approximately 0.9 – 1.2 km to the south of the main camp. However, 17 of those nests were lost when their identifying markers were washed away by extreme high tides. Of the 64 remaining nests, 1.6% (n=1) of nests were completely depredated, 12.5% (n=8) of nests were partially depredated and the remaining 85.9% (n=55) of nests were not impacted by predators (Figure 4 and 5).

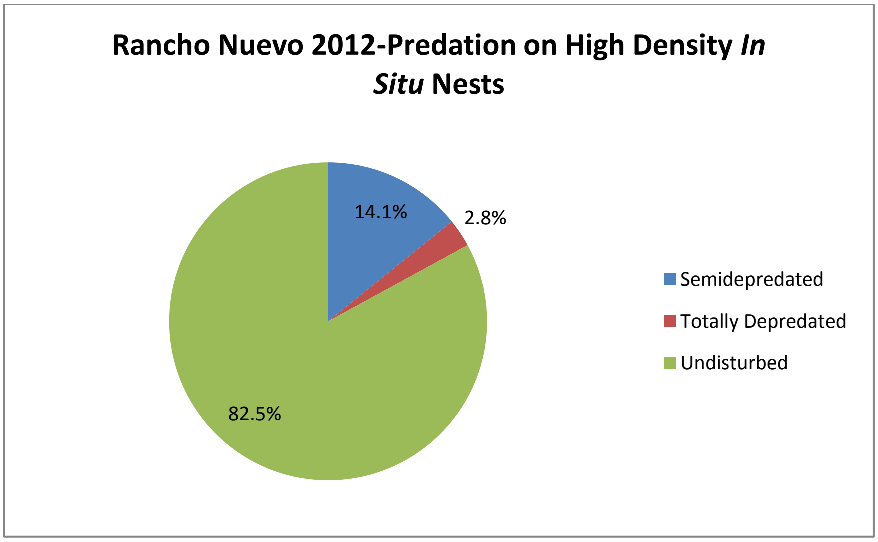
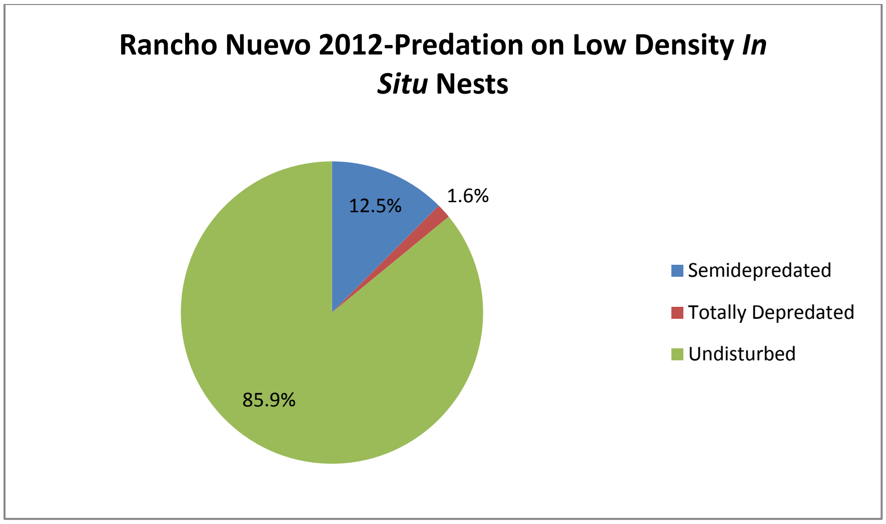


Figure 4. Percentage of *in situ* nests that were depredated in the high density nesting site in 2012.



Figures 5. Percentage of *in situ* nests that were depredated low density nesting site in 2012.

Hatching Success

The average hatching success for each *in situ* nest in 2011 and 2012 was calculated based on the remaining contents of each nest, as described in the methods above. In 2011, there were initially 398 nests left *in situ* from the April 28th arribada that were marked and monitored on a daily basis as a part of the high density nesting area. At the end of the nesting season, an additional 145 nests were found in the study site that had not been previously discovered until hatchling emergence was observed. These additional *in situ* nests were included in the analysis of hatching and emergence success for a total of 543 nests recorded. A portion of the *in situ* nests (n=118) were lost or washed out due to beach erosion associated with high tides and were unable to be assessed after emergence. These 118 nests did not have sufficient data to be included in calculations of nest success and were therefore excluded. The remaining 425 nests were used in the calculation for average hatching success. The average nest success for the high density nesting area was 79.4% for all *in situ* nests combined (Figure 6). As previously stated, the low density nesting area for this nesting season was completely washed out by high tides.

In 2012, 269 nests from the May 16th arribada were left to incubate *in situ* in a high density nesting area. Of these 269 nests, 66 nests were lost due to high tides associated with storms. Therefore, those 66 nests were excluded from this analysis. The overall hatching success for the remaining 203 *in situ* nests in the high density nesting area was 64.3%.

For the low density nesting area 81 nests were left to incubate *in situ* during the 2012 nesting season. Two of these nests did not have sufficient data to be included in calculations of nest success and were excluded. Average hatching success for the remaining 79 nests in the low density nesting area was 72.5%. Combining the data from the 2011 and 2012 nesting seasons, the average hatching success for *in situ* nests at Rancho Nuevo is currently 74.4% (Table 1).

Table 1. Hatching success for all *in situ* nests in the high and low density nesting areas during the 2011 and 2012 nesting seasons.

Year	**High Density**	**Low Density**	**Combined**
2011	79.5%		79.5%
2012	64.3%	72.5%	66.6%
Combined			**74.4%**

Hatchling Survival from Nest to Surf

In 2012, hatchlings from *in situ* nests were not directly observed crawling from the nest to the surf. Therefore, hatchling seafinding success was based on examining all hatchling tracks originating from a nest. This value represents an estimation of hatchling survival to the surf. A total of 185 *in situ* nests produced hatchlings. Assuming that an average of 100 hatchlings emerged from each nest, this means that approximately 18,500 hatchlings could have potentially reached the water. Each nest was placed into one of five categories based on the estimated percentage of hatchling tracks that successfully led all the way to the high tide line (100%, 75%, 50%, 25%, or 0% survival to the surf). Estimated hatchling survival to the water was then calculated in the following manner:

<u>Survival to the water</u>

57 nests x 100% hatchling survival to the water = 5,700 hatchlings

115 nests x 75% hatchling survival to the water = 8,625 hatchlings

13 nests x 25% hatchling survival to the water = 325 hatchlings

Total number of hatchlings that made it to the water = 14,650

The results indicate that the majority of hatchlings make it to the surf. Overall, a total of 14, 650 hatchlings successfully reached the surf out of an approximate 18,500 potential total number of hatchlings, yielding an average success rate of 79.2% for hatchlings during seafinding. Almost all hatchling tracks (approximately 100% of tracks) successfully reached the high tide line for 23.7% of nests (n=57), the tracks from 47.7% (n=115) of nests indicated that 75% of the hatchlings survived, followed by 5.4% of nests (n=13) from which approximately 25% of the hatchlings survived. For the remaining

23.2% of nests (n=56) no tracks were seen emerging from nests and therefore were not used in these calculations (Figure 6).

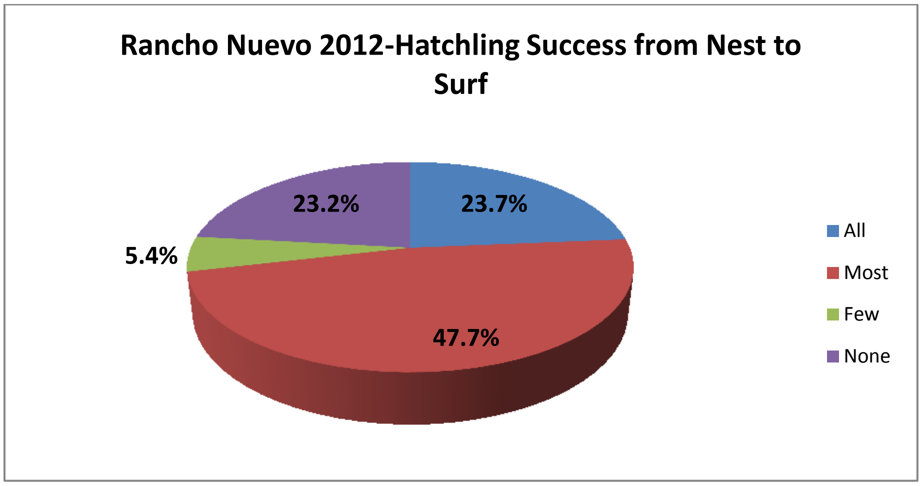


Figure 6. Percentage of nests from which approximately all (100%), most (75%), few (25%) or none (0%) of the hatchlings made it to the surf in 2012.

Predator Abundance

The results from the predator plot studies during 2011 and 2012 indicate that ghost crabs were the most prevalent predator during morning and evening observations for all locations in 2011 and 2012 (Figures 7 – 10). In addition to ghost crabs, several species of birds were the main diurnal predators on the beach (Figures 8 and 10). The primary nocturnal mammalian predators were raccoons, skunks and coyotes (Figures 7 and 9).

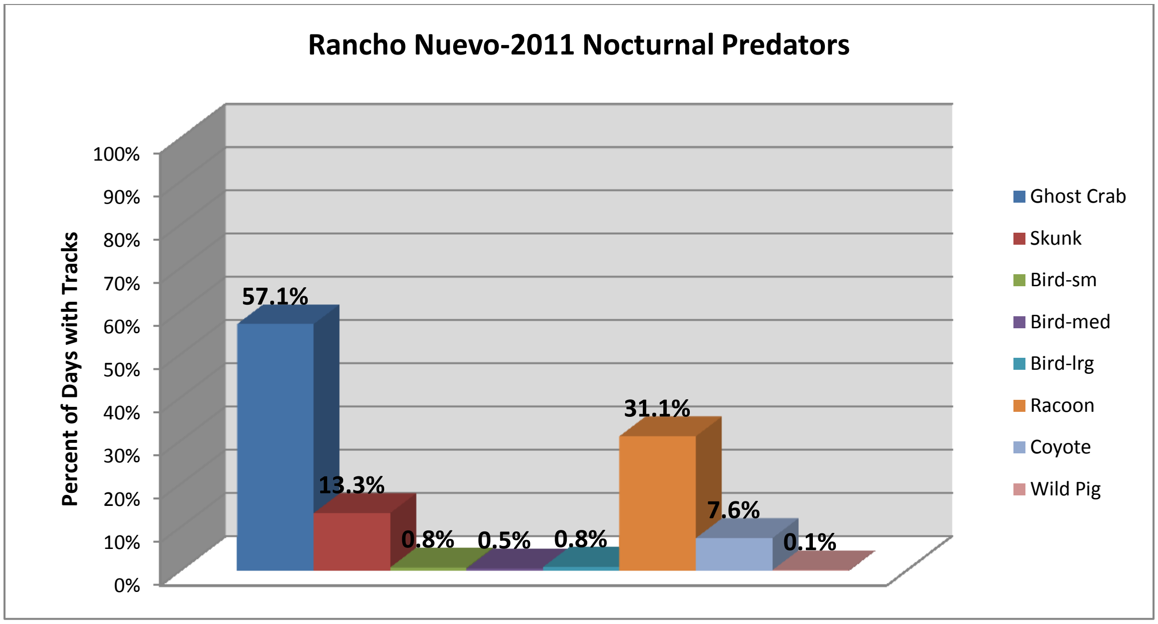


Figure 7. The percentage of days for which each type of nocturnal predator track from the previous night was recorded. Each bar corresponds to the percent of mornings averaged over all beach locations for which each type of predator was recorded in 2011.

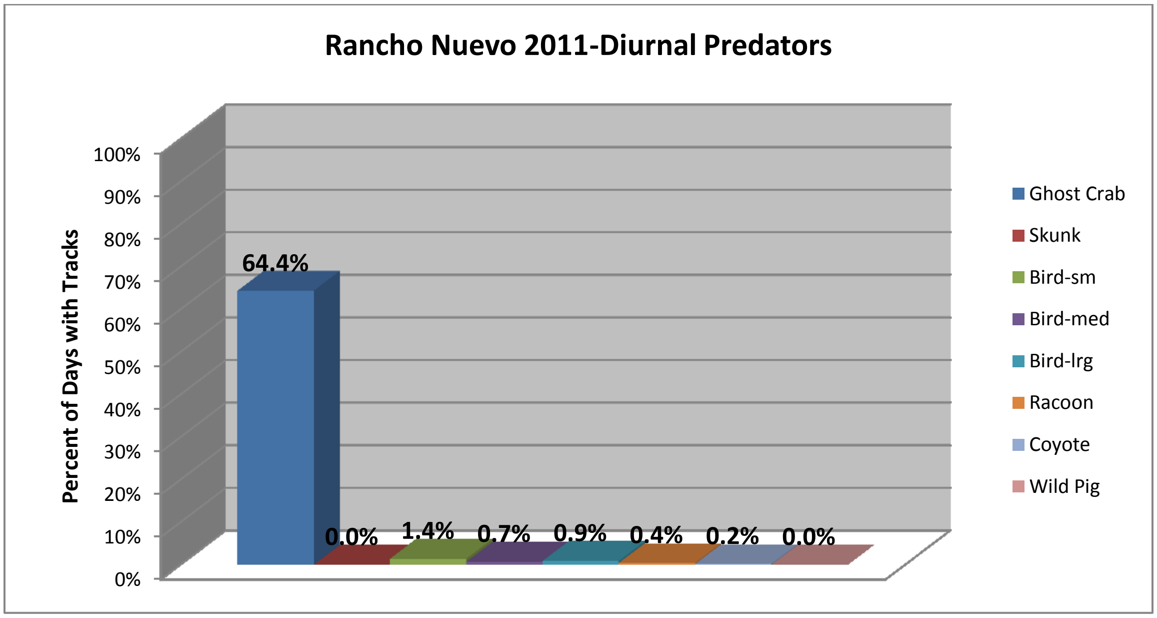


Figure 8. The percentage of days for which diurnal predator tracks were recorded. Each bar corresponds to the percent of days averaged over all beach locations that each type of predator was recorded in 2011.

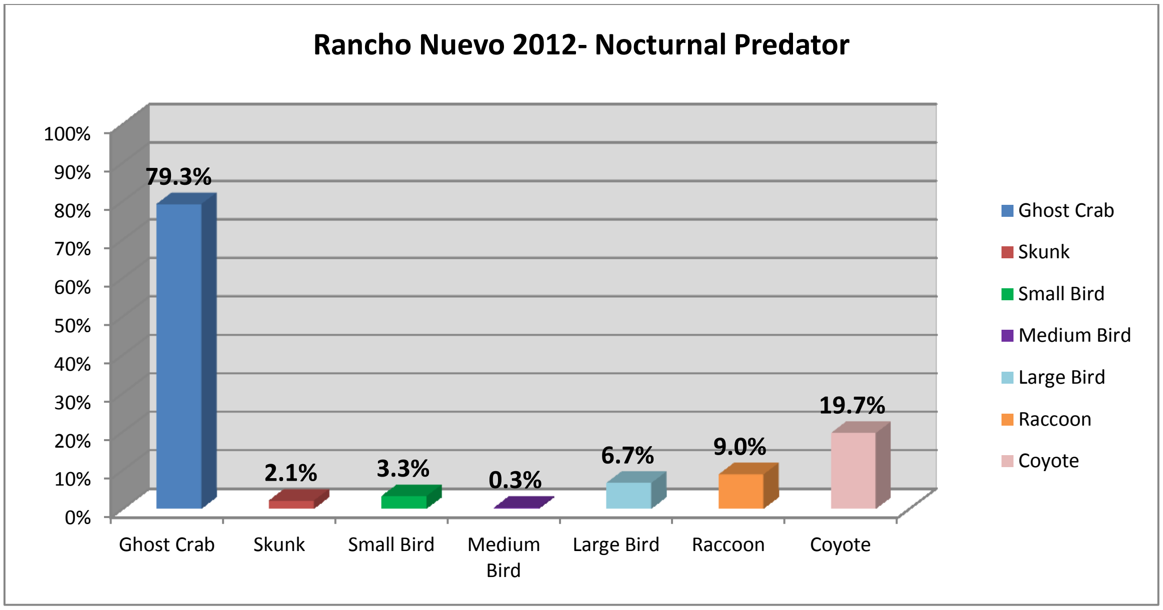


Figure 9. The percentage of days for which each type of nocturnal predator track from the previous night was recorded. Each bar corresponds to the percent of mornings averaged over all beach locations for which each type of predator was recorded in 2012.

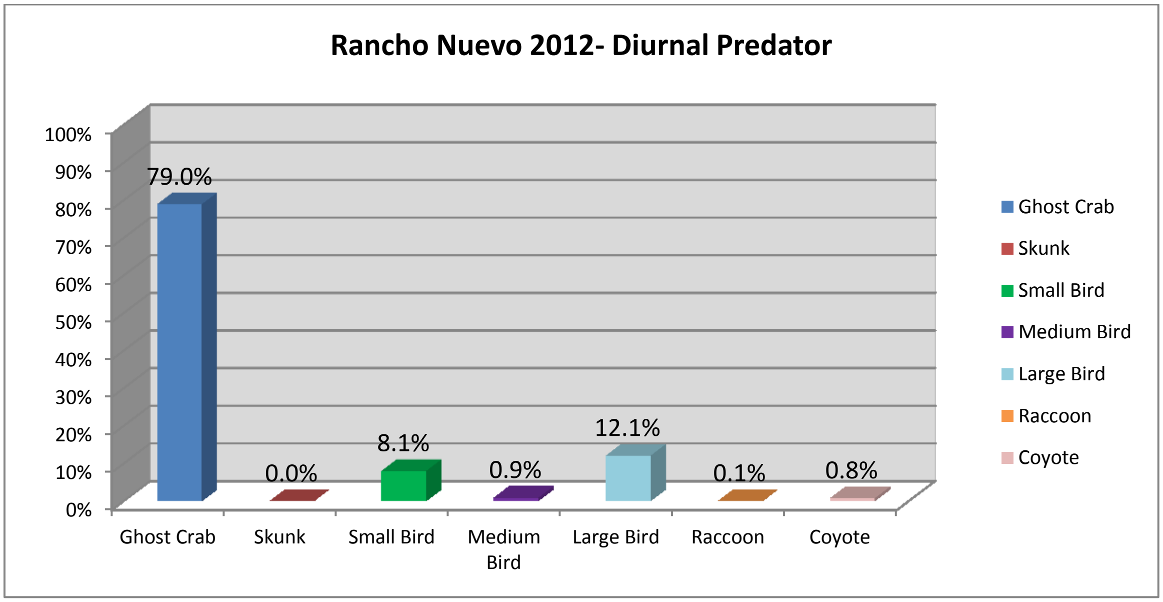


Figure 10. The percentage of days for which diurnal predator tracks were recorded. Each bar corresponds to the percent of days averaged over all beach locations that each type of predator was recorded in 2012.

Track frequencies for each location on the beach were evaluated during the 2011 and 2012 nesting seasons for the three primary nocturnal mammalian predators documented in this study, coyotes, skunks, and raccoons. In 2011, raccoons, skunks, and coyotes were not distributed equally among all beach locations over the entire nesting season and were more prevalent in certain locations (Kruskal-Wallis: raccoons, $K= 33.506$, $df = 4$, $p<0.0001$; skunks, $K=41.840$, $df = 4$, $p<0.0001$; coyotes, $K=36.654$, $df=4$, $p<0.0001$) (Figures 11 - 14). As examples, there was a greater chance of seeing a raccoon to the north of the main camp than at either of the sites to the south of the main camp (Mann-Whitney: $U=-5.223$, $p<0.0001$). There was a greater chance of seeing a skunk at the study area 5.7 km to the north of the main camp than at either of the two 8.1 km north locations or either site to the south of the main camp (*Kruskal-Wallis:* $K=25.271$, $df=2$, $p<0.0001$). Coyotes were more prevalent at all sites to the south of the main camp than at any of the sites to the north of the main camp (Mann-Whitney: $U=5.959$, $p<0.0001$).

Predator tracks were analyzed one week before and one week following all major arribadas for the 2011 nesting season to determine if these nesting events significantly affected the abundance of predators on the beach in the vicinity of an arribada. In 2011, the April 12th arribada significantly influenced the abundance of predators, as did location, and the interaction between these two factors (2-way ANOVA: *arribada,* $p<0.0001$, *location,* $p=0.010$, *and location*arribada,* $p=0.009$). The abundance of predators increased at the two 8.1 km sites to the north of the main camp following the April 12th arribada (t-test: *8.1 km N,* $p=4.12942E-5$). The April 28th arribada did not have a significant effect on the abundance of predators following the arribada, but location site did have a significant influence on the abundance of predators following the April 28th arribada, and there was no interaction between these factors (2-way ANOVA: *arribada, 0.376*, *location, p=0.003, and location *arribada, p=0.428*). Predator abundance was not significantly affected by the June 5th arribada, location, or any interaction between these two factors (2-way ANOVA: *arribada, p=0.325, location, p=0.362, and location *arribada, p=0.873*).

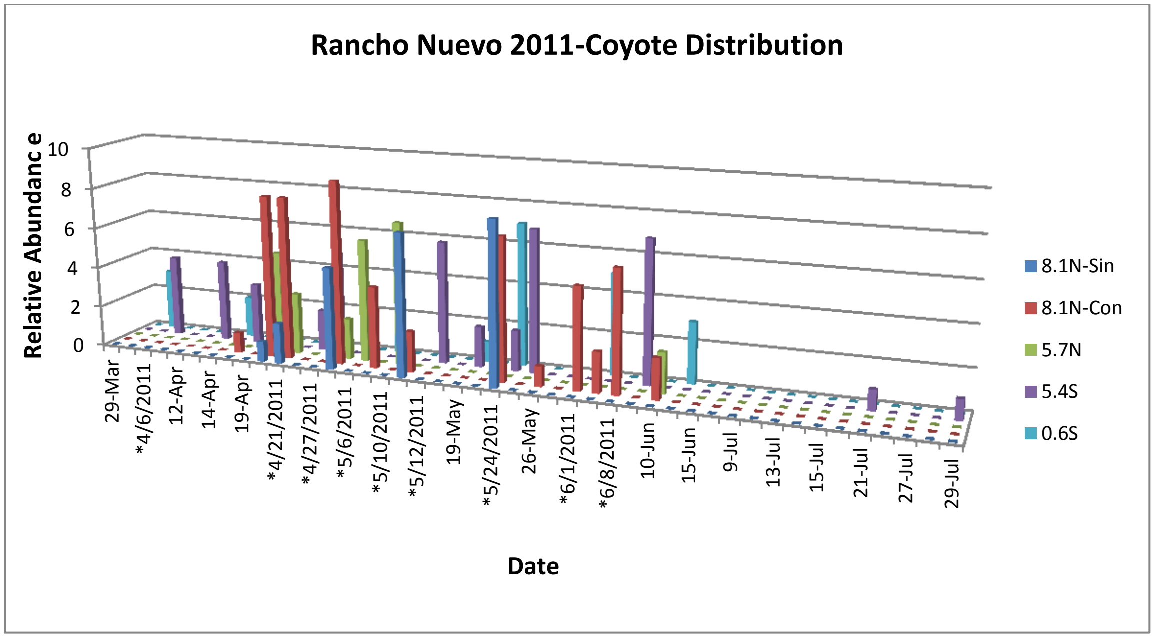


Figure 11. The abundance of coyotes in each section of beach for each day that the predator plots were monitored throughout the 2011 nesting season. Asterisks indicate days for which significant differences in predator distribution across all beach sections was detected.

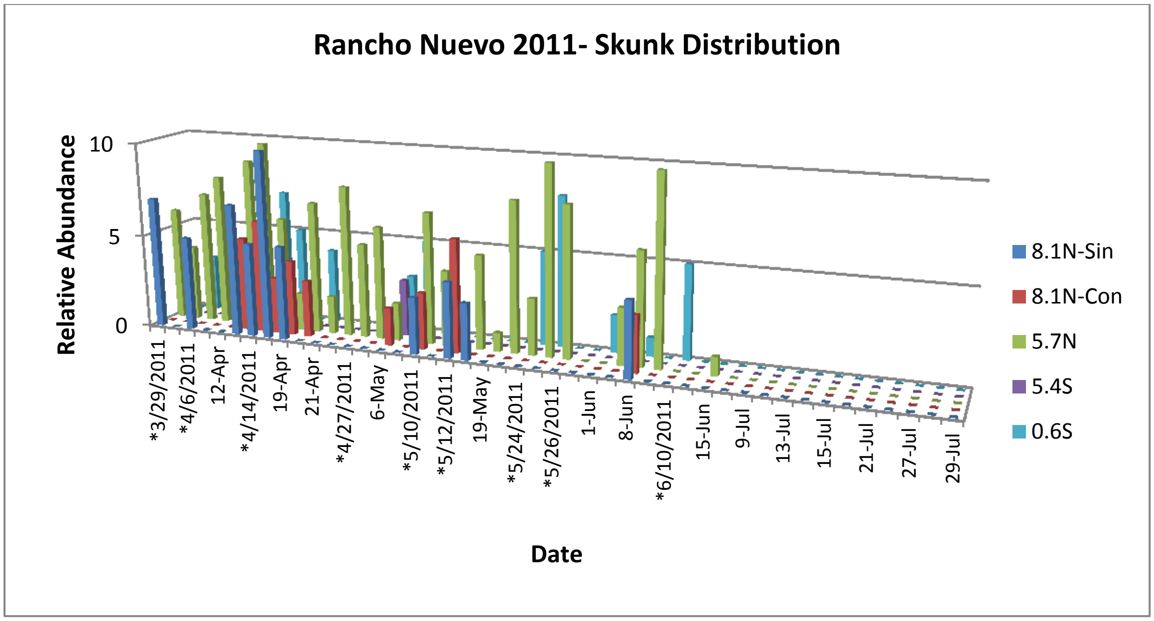


Figure 12. The abundance of skunks in each section of beach for each day that the predator plots were monitored throughout the 2011 nesting season. Asterisks indicate days for which significant differences in predator distribution across all beach sections was detected.

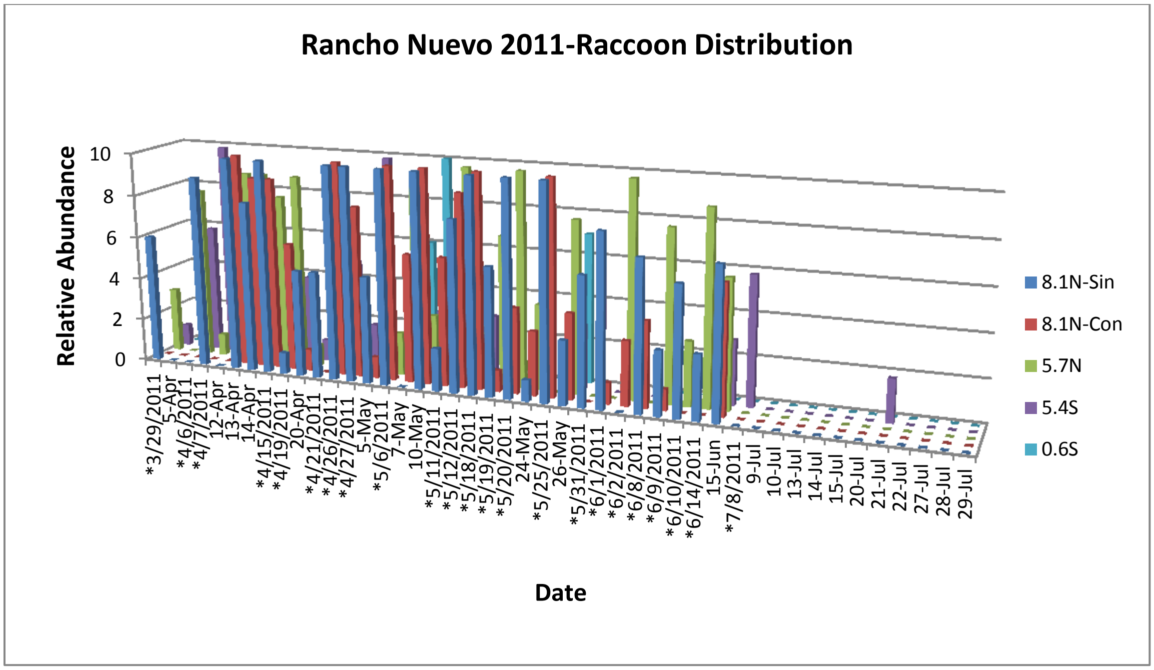


Figure 13. The abundance of raccoons in each section of beach for each day that the predator plots were monitored throughout the 2011 nesting season. Asterisks indicate days for which significant differences in predator distribution across all beach sections was detected.

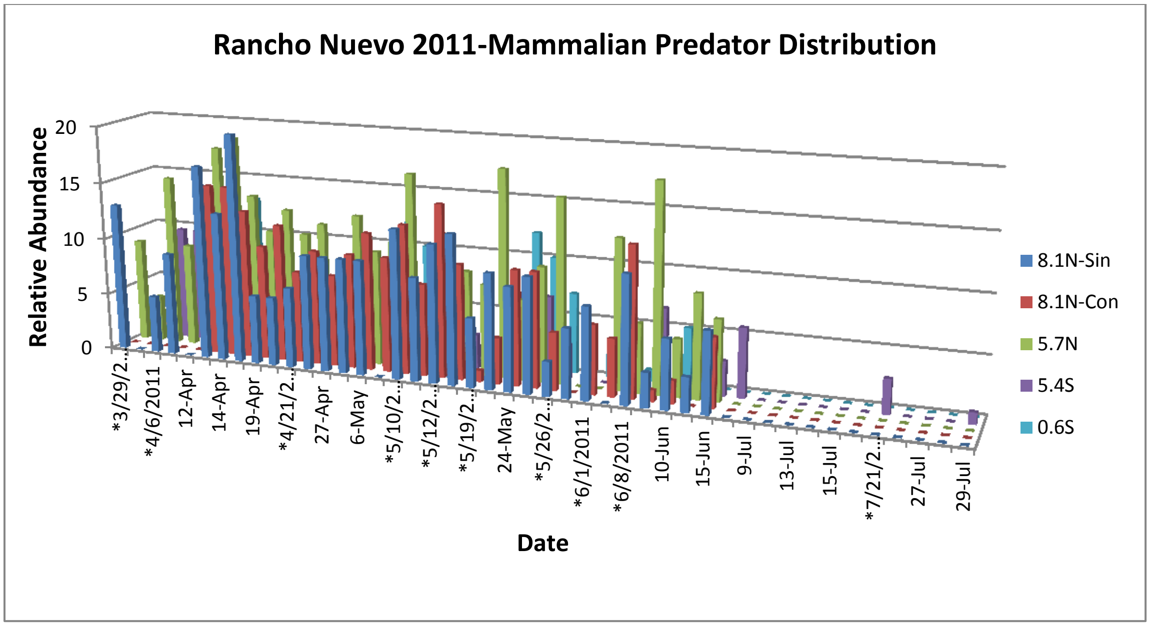


Figure 14. The abundance of mammalian predators (i.e. coyotes, raccoons, and skunks) combined for each section of beach for each day that the predator plots were monitored throughout the 2011 nesting season. Asterisks indicate days for which significant differences in predator distribution across all beach sections was detected.

In 2012, raccoons, skunks, and coyotes were not distributed equally among all beach locations and were more prevalent in certain locations (Kruskal-Wallis: raccoons, *K=38950, df=4, p<0.0001;* skunks, *K=28.755, df=4, p<0.0001*; coyotes, *K=11.433, df=4, p=0.022*) (Figures 15-18). As examples, there was a greater chance of seeing a raccoon at the site 1.2 km south of the main camp than at any other study area on the beach (Mann-Witney U: *U=-4.945, p=0.01947E-10*). There was also a greater chance of seeing a skunk at the site 5.7 km to the north than at any of the sites to the south of the main camp or the site 4.2 km to the north of the main camp (Kruskal-Wallis: *K=3.967 and -4.707 respectively, p<0.0001*). Coyotes were more prevalent at the site 5.7 km to the south of the main camp than at any other study area on the beach (Mann-Whitney: *U=-2.881, p=0.003*).

Predator tracks were analyzed one week before and one week following all major arribadas for the 2012 nesting season to determine if these nesting events significantly affected the abundance of predators on the beach in the vicinity of an arribada. In 2012, none of the major arribadas for the season had a significant effect on the presence of predators on any section of the beach. Predator abundance was not significantly affected by the late April arribada (April 21st - 25th), location, or any interaction between these two factors (2-way ANOVA: *arribada, p=0.204, location, p=0.600, and location *arribada, p=0.321*). The May 16th arribada, location, and the two factors combined did not significantly influence the abundance of predators following the arribada (2-way ANOVA: *arribada, p=0.099, location, p=0.615, location *arribada, p=0.695*). The June 10th arribada had a significant effect on predator abundance, with fewer predators on the beach in the week following the arribada, but location did not have an effect and there was no interaction between these two factors (2-way ANOVA: *arribada, p=0.035, location, p=0.059, location *arribada, p=0.680*). The late June arribada (June 8th – 22nd) also had an effect on the predator abundance, with fewer predators on the beach following the arribada, but location did not have an effect and there was no interaction between these two factors (2-way ANOVA: *arribada, p=0.023, location, p=0.344, location *arribada, p=0.930*).

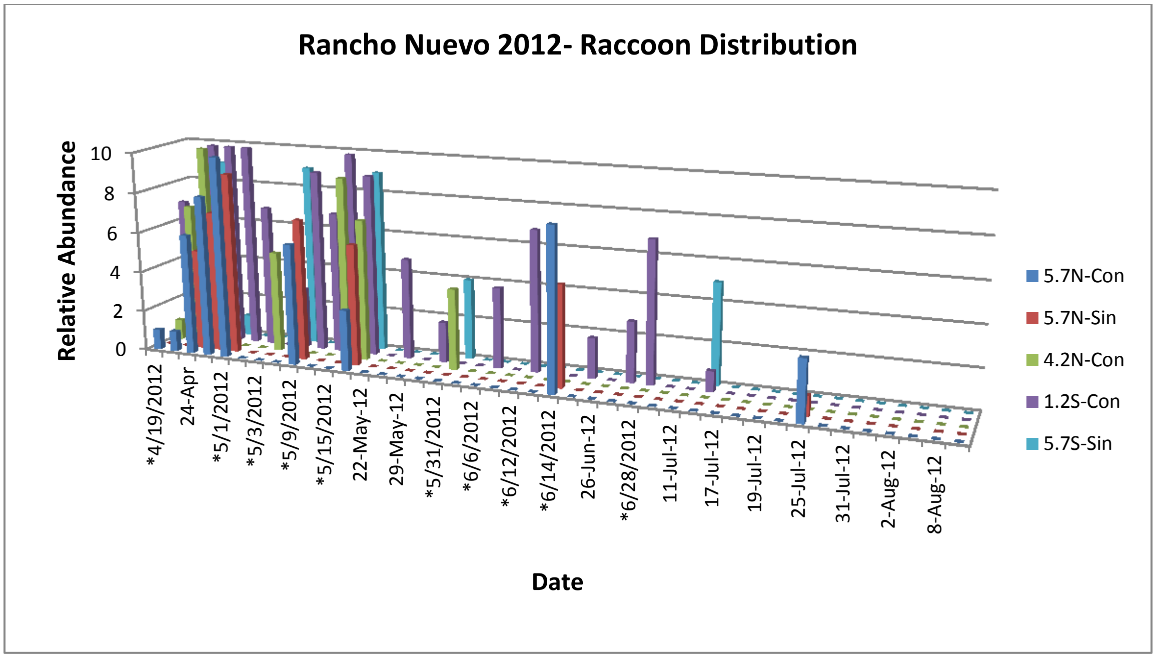


Figure 15. The abundance of raccoons in each section of beach for each day that the predator plots monitored throughout the 2012 nesting season. Asterisks indicate days for which significant differences in predator distribution across all beach sections was detected.

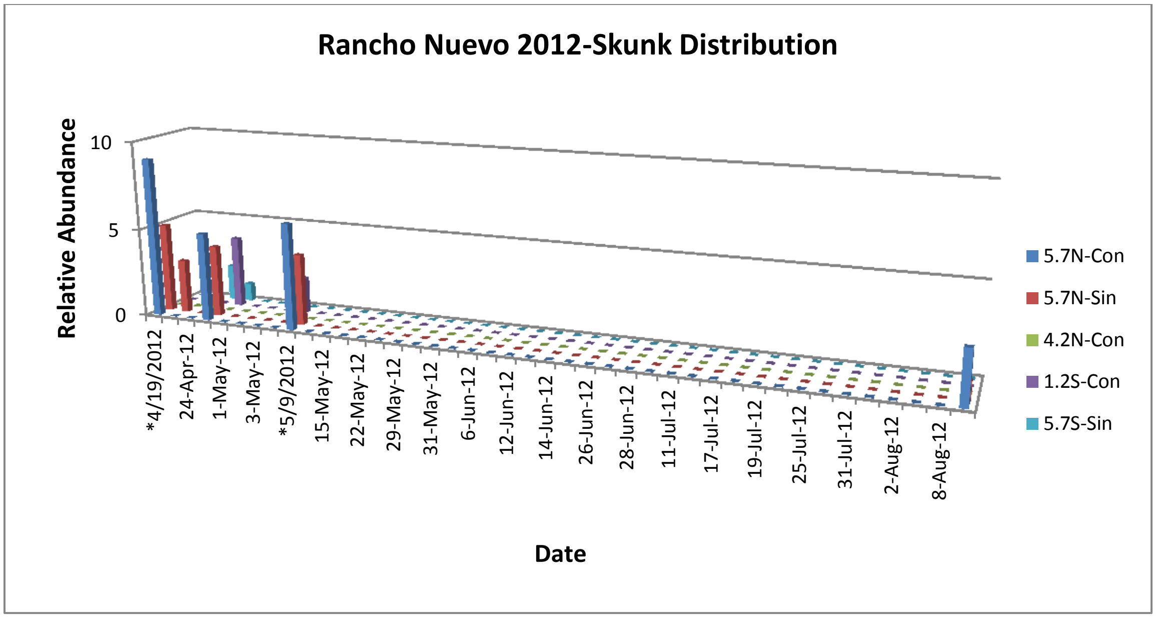


Figure 16. The abundance of skunks in each section of beach for each day that the predator plots were monitored during the 2012 nesting season. Asterisks indicate days for which significant differences in predator distribution across all beach sections was detected.

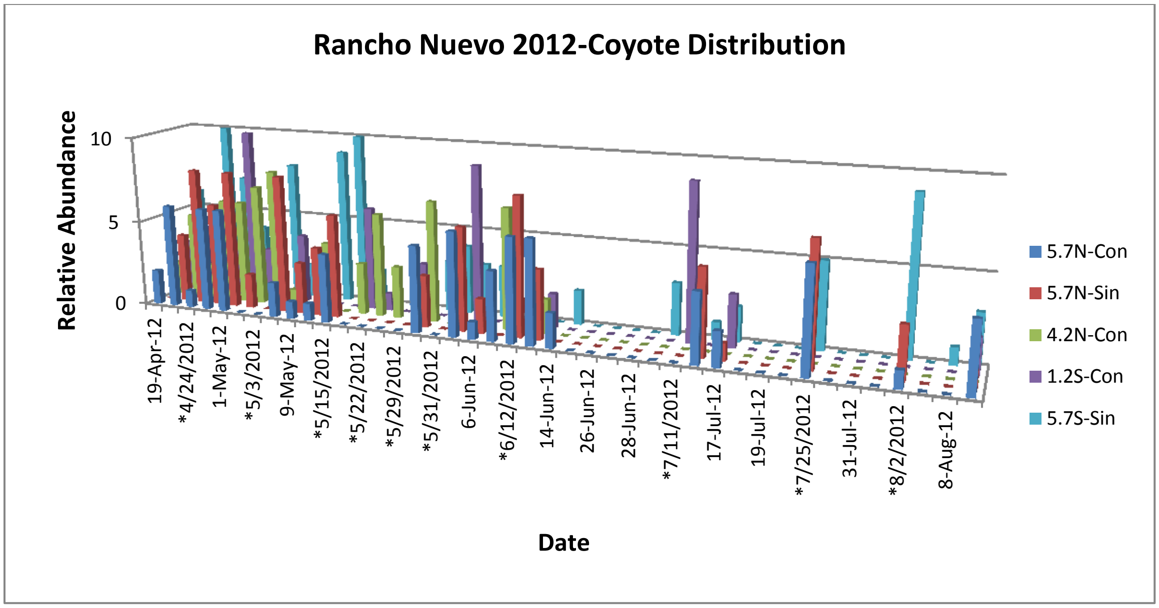


Figure 17. The abundance of coyotes in each section of beach for each day that the predator plots were monitored during the 2012 nesting season. Asterisks indicate days for which significant differences in predator distribution across all beach sections was detected.

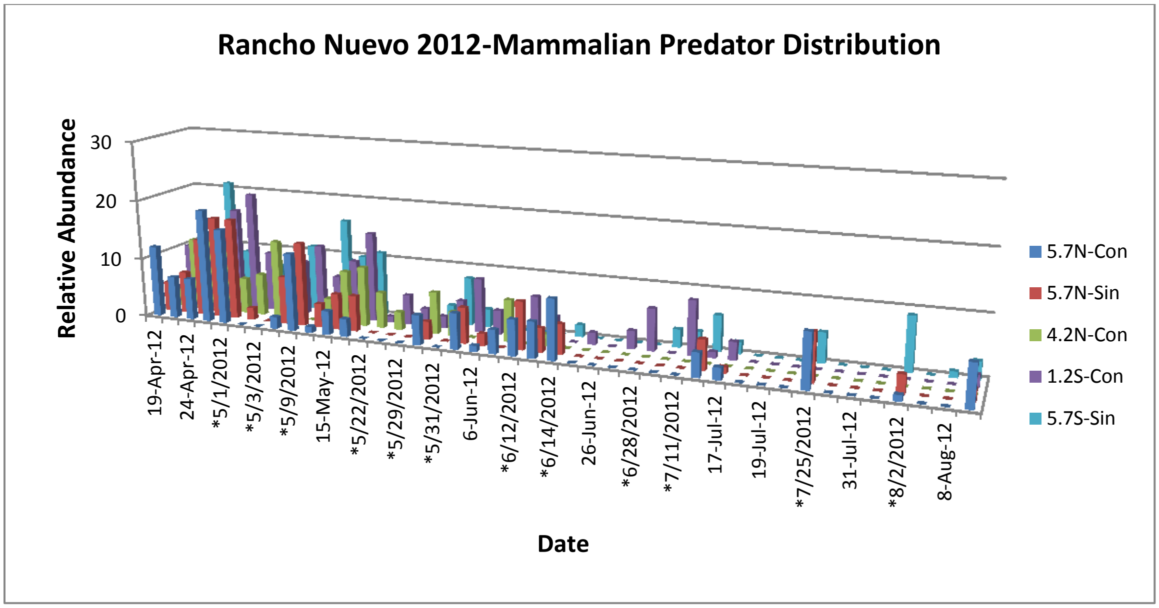


Figure 18. The abundance of mammalian predators (i.e. coyotes, raccoons, and skunks) combined for each section of beach for each day that the predator plots were monitored throughout the 2012 nesting season. Asterisks indicate days for which significant differences in predator distribution across all beach sections was detected.

Discussion

In Situ Nest Predation

Nest predation during the 2010 – 2012 nesting seasons was relatively low for nests that were allowed to incubate in their original location on the nesting beach. Seventy-eight to ninety-six percent of *in situ* nests remained undisturbed by predators in all three years included in this analysis. Though a varying portion of *in situ* nests are depredated in each year, the percentage of nests that are completely destroyed is relatively small (approximately 1 - 3%). The results of the current study indicate that selectively leaving nests *in situ* from major arribadas represents an effective management strategy and supports the hypothesis that arribada nesting provides a means to increase overall hatchling survival by predator satiation (Eckrich and Owens, 1995). It is plausible that predator abundance could change over time as an increasing number of nests are left *in situ* at Rancho Nuevo therefore continued predation studies are required to monitor any potential changes in predation level on the nesting beach as the Kemp's ridley continues to recover. Regardless, the results support the use of arribada *in situ* nests as a management strategy as the Kemp's Ridley Recovery Program transitions from primarily placing all nests into egg corrals.

The "low density" nesting areas in the current study had similar predation levels to the "high density" nesting areas. However, these "low density" nesting areas may still be more densely grouped in a given area compared to the density of nests laid by solitary females and thus may not be a true representation of scattered nesting. For example, these "low density" nesting areas examined in recent years may have as many as 60 nests per 300 m of beach. Therefore, these nesting areas may still have a density great enough to effectively reduce the percentage of egg and hatchling predation by overwhelming and satiating predators with available prey (Eckrich and Owens, 1995). In the current study, "low density" areas were chosen during an arribada to control for the time of nesting when compared to "high density" nesting areas. It may be insightful for future studies to examine true "scattered" nesting areas that are laid between arribada events. This could possibly allow for more accurate evaluation of the benefits provided by arribada nesting over solitary nesting.

In Situ Hatching Success

The estimated hatching success for *in situ* nests during the 2011 and 2012 nesting seasons of 74.4% is comparable to previous studies that estimated an average hatching success of 64.7% - 70% in egg corrals at Rancho Nuevo (Geis et al., 2002; Márquez et al., 2001). This suggests that even with predation as a factor, the hatching success for *in situ* nests is still relatively high. Thus the nest predation and hatching success evaluations from this study indicate that leaving nests *in situ* could be considered a viable management option that does not drastically affect the overall hatching success of *in situ* nests. Other Kemp's ridley nesting beaches (i.e. Padre Island National Seashore) report a higher hatching success of 83.7%. That program also relocates all nests to protective hatcheries and includes a much smaller number of nests overall (LeBlanc et al., 2012).

Loss of nests due to natural causes is a factor that must be considered when making decisions regarding the use of *in situ* nests as a management strategy for an endangered sea turtle species. For example, only work done in 2012 generated data for comparison between high and low density nesting areas. Nests in the low density nesting area were lost in 2011 due to extreme high tides, leaving only a high density nesting area for evaluation. From a comparative perspective, loss of nests represents loss of data that makes it difficult to gain a more thorough understanding of the effects of nesting density on the survival of *in situ* nests. It also represents a loss of hatchlings that would have been produced had nests been relocated to egg corrals (Whitmore and Dutton, 1985). Excluding the nests lost due to tropical weather systems inflates the survival rates estimated for nests and hatchlings. The *in situ* hatching success of 74.4% reported in this study does not include the 118 nests lost in 2011 and the 68 nests in 2012 that were lost due to high tides associated with tropical weather systems. If these *in situ* nests had been included in the calculations for this study, the hatching success would have decreased to approximately 58.9%. Thus nests lost due to tidal inundation and weather events should be considered when evaluating the use of *in situ* arribada nests as a management strategy.

However, the loss of *in situ* nests also represents a natural cause of mortality that has previously been a natural and sustainable part of the species' life history. *In situ* nests that are laid closer to the high tide are more vulnerable to tidal inundation and would thus reduce the fitness of individual female sea turtles (Wood et al., 2000; Congdon et al., 2001). If nest-site selection is a heritable trait, then loss of these vulnerable nests would eliminate traits for poor nest-site selection from the gene pool (Mrosovsky, 1983; Mrosovsky, 2006; Kamel and Mrosovsky, 2004; Kamel and Mrosovsky, 2005). Natural loss of nests would therefore be a natural selection pressure that could lead to the evolution of optimal nest-site selection in the Kemp's ridley. Relocating vulnerable *in situ* nests to the protection of egg corrals could artificially reduce the strength of this selection pressure and prevent the further evolution of nest-site choice in this species (Kamel and Mrosovsky, 2004; Mrosovsky, 1983; Mrosovsky, 2006; Mrosovsky, 2008). When working with an endangered species, the maximal production of hatchlings may be the priority, however, as the population recovers, the long-term fitness of the species should be considered and may be enhanced by allowing nature to select for maximum hatchling fitness.

Hatchling Success from Nest to Surf

The hatchling tracks from the nest to the water during 2012 indicated 79.2 % of the hatchlings emerging on the beaches of Rancho Nuevo successfully make it to the high tide line. A previous study at Rancho Nuevo estimated the survival of hatchlings from *in situ* nests to the surf to be 66.4% (Eich, 2009). These survival rates from *in situ* nests are low compared to the egg corrals that ensure 100% of the hatchlings reach the high tide line. However, the current results indicate that 79.2% represents a natural survival rate for hatchlings at Rancho Nuevo. It is possible that predation on hatchlings during their crawl to the sea may be a selecting factor in ensuring only the most robust hatchlings survive past this stage in the population (see discussion below).

Several problems were encountered in the evaluation of hatchling survival from nest to surf. For one, categorizing nests based on hatchling tracks leading away from the nest should be considered an estimation since it is using general categories of success (100%, 75%, 25%, and 0%), and could be subject to individual bias and potential bias in methodology. Another complication in determining hatchling survival from nest to surf is tidal influence on hatchling and predator tracks. High tides can erase hatchling tracks and evidence of predation that could change the overall hatchling survival for a nest. Seaweed washed in by the high tide can also obscure or prevent hatchlings from leaving tracks that beach personnel would need to evaluate the nest. Ideally, future studies may be able to incorporate field cameras or other techniques that can be used to record and verify the movements of individual hatchlings as they emerge from the nest. Such techniques can also be used as validation for current observational methodologies. However, such studies are technically and logically challenging, not to mention quite costly to monitor hatchlings emerging from hundreds of *in situ* nests.

Predator Abundance

Predator plots from the 2011 and 2012 nesting seasons show a distinct difference in nocturnal and diurnal predator composition. During the day, the main predators present on the beach were ghost crabs and birds. This is similar to previous studies that also reported birds and ghost crabs as the main diurnal predators present on the beach at Rancho Nuevo (Eich, 2009). In both years, ghost crabs were the most prevalent diurnal and nocturnal predator present on all sections of beach. The predominance of ghost crabs for all beach locations has also been previously reported at Rancho Nuevo (Eich, 2009). Although ghost crabs have been reported to burrow into nests, they generally vacate the nest after consuming a few eggs (Eckrich and Owens, 1995). Birds have typically been observed scavenging previously depredated nests and emerging hatchlings, but have not been seen to dig up the nests themselves (Fowler, 1979). A previous study at Rancho Nuevo has also reported that birds did not appear to eat as much as mammalian predators and therefore had less of an overall impact on nests (Eich, 2009). Thus the mammalian predators are of particular concern to *in situ* nest management and were the focus of the analysis in the current study. Considering the mammalian predators were generally absent from the daytime predator plot observations, track frequency analyses were only done for morning predator plot observations that represented tracks from nocturnal predators. The primary nocturnal predators on the beach in 2011 and 2012 were raccoons, coyotes, and skunks, but birds were usually scarce during the nighttime hours. This suite of nocturnal predators has been described by previous studies at Rancho Nuevo (Eich, 2009).

Predator tracks indicated that mammalian predators showed specific preferences for certain areas of the beach over others in both years included in this study. However, the specific study area most frequented by a particular predator varied between 2011 and 2012. Thus the abundance and distribution of each specific predator varied between these two years. Abundance and distribution of each predator was also significantly different among all beach locations on a daily basis, again indicating that each type of predator is frequenting certain areas of the beach more than others and that the preferred beach section changes throughout the nesting season. This could represent a response to environmental or biotic factors specific to each year (e.g. rainfall, humidity, temperature, other predators, etc.) or prey availability.

Interestingly, in the 2011 nesting season, a drastic reduction in the presence of all predators (i.e. ghost crabs, birds and mammalian predators alike) was observed for all study sites after approximately mid-June. It is possible that the predators were driven away from the beach by major environmental factors that can influence all predators in a similar manner, such as changes in seasonal rainfall, extreme temperatures and humidity, and hurricanes. Indeed, the Rancho Nuevo area experienced Hurricane Arlene shortly after this period of reduced predator presence on June 30th. Perhaps severe tropical weather systems (e.g. hurricanes, tropical storms, etc.) may flush predators off of the nesting beach and into surrounding habitat or may make foraging in surrounding habitat more profitable. In 2012, Rancho Nuevo did not experience a hurricane and the abrupt disappearance of almost all predators was not reflected in the predator plot observations. However, a gradual reduction in predators present on the beach did occur towards the end of the season and may represent a natural waning of predator abundance on the nesting beach, as has been noted for certain predators on other beaches (Eckrich and Owens, 1995). Additionally, dry periods could affect the abundance and distribution of predators due to availability of water or prey.

Further, analysis of predator abundance one week before and one week after the major arribadas that occurred during 2011 and 2012 indicated that the majority of arribadas do not have a significant effect on predator abundance. Furthermore, most arribadas did not have a significant effect on the abundance of predators at the specific study sites located closest to where each arribada occurred. These results suggest that mammalian predators may not cue in on an arribada to congregate in the vicinity of a major nesting event. Instead, these predators may be canvasing the beach in search of food and may not shift their distribution solely in response to the onset of an arribada. This agrees with the hypothesis that the nesting beach supports a basal number of predators in any one specific area of the beach, as opposed to a pulse of predators that are attracted to the location on the beach when a major arribada occurs (Eich, 2009).

One early season arribada on April 12th of 2012 was not included in this analysis since the predator plot observations did not start until April 19th. The two later season arribadas in June of 2012 appear to have an effect on the presence of predators, but there were fewer predators on the beach during the week following the arribada than during the week prior to the arribada event. It is possible that the predators may simply vacate the beach towards the end of the nesting season. It would be interesting for future studies to monitor the long-term movements of a subset of the predator species identified in the current study.

These preliminary results support the hypothesis that arribada nesting is supporting predator satiation. Despite the growing number of nests laid each year, the predation on *in situ* nests and hatchlings recorded in the current study are low compared to predation levels on other beaches (Bernardo and Plotkin, 2007; Eckrich and Owens, 1995). The low predation on *in situ* nests at Rancho Nuevo could be due to a variety of factors (Eckrich and Owens, 1995). Cues emitted by thousands of nesting females during an arribada could make it more difficult for predators to identify a single nest. After incubation, emergence from hundreds of nests would produce an overwhelming source of prey for the limited number of predators present on any given night at Rancho Nuevo. After reaching the sea, an overwhelming abundance of hatchlings would be available to satiate nearshore predators and result in a relatively smaller portion of hatchlings consumed by predators out of the total emerging at one time.

The results of the current study suggest that selectively leaving nests *in situ* from major arribadas represents an effective management strategy and means to increase overall hatchling survival from *in situ* nests through predator satiation (Eckrich and Owens, 1995). These data suggest that Rancho Nuevo has a regular community of a few predator species and that their numbers are limited at any one section of beach. It is plausible that predator abundance could change over time as an increasing number of nests are left *in situ,* therefore continued predation studies should be continued to monitor potential changes in predation on the nesting beach as the Kemp's ridley continues to recover. Together, the results support leaving nests *in situ* from arribadas as an effective management strategy that provides an alternative to moving all nests to egg corrals in the Kemp's Ridley Recovery Program.

Lastly, the current study provides insight on the ecological and evolutionary implications of the arribada. Several hypotheses have been proposed explaining the evolution of the arribada (Bernardo and Plotkin, 2007). For example, the arribada may be a mechanism of social facilitation that may enhance mating success, allowing adult Kemp's ridleys to gather in a common place for the purpose of reproduction. This could coordinate the timing of reproduction with potentially favorable environmental factors, such as currents, beach and water temperatures or other conditions, including those that may aid in hatchling dispersal throughout the Gulf of Mexico. Dispersing the hatchlings as a group may provide benefits that could also have driven the evolution of the arribada. Social facilitation associated with the arribada phenomenon could also play a role in the beach selection, including factors that allow for optimal hatchling developmental rates and sex ratios. Although a variety of these factors could be selecting for the evolution of the arribada, the current study supports the hypothesis that predator satiation could be one of the factors that may have selected for the evolution of the arribada nesting behavior. The high nest survival, hatchling production, and seafinding success in the current study represent one of the most comprehensive studies to date supporting the predator satiation hypothesis as a factor that could be selecting for the evolution and maintenance of the arribada nesting behavior. However, the current predator load could be significantly different than historic levels that may have selected for the arribada phenomenon.

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GENERAL CONCLUSIONS

This thesis addressed several major topics related to the biology and conservation of the Kemp's ridley sea turtle. The first chapter evaluated the hatchling sex ratio being produced at the primary nesting beach for the Kemp's ridley at Rancho Nuevo, Mexico. Sand and nest temperatures from the egg corrals and natural nesting beach were monitored over four nesting seasons from 2009 - 2012. These data were used to predict sex ratios produced in the Kemp's Ridley Recovery Program. Further, this chapter compared the temperatures of the egg corrals and the natural nesting beach to evaluate the effects that leaving nests to incubate *in situ* has on hatchling sex ratios. These data provide insight on long-term effects of incubation temperatures on hatchling sex ratios in the Kemp's Ridley Recovery Program at Rancho Nuevo and ultimately the recovery rate of this species. An overall female bias was predicted for each nesting season in the egg corrals (i.e. ranging from 76.1 – 80.6% female bias), though nests laid early in the season or those affected by tropical weather systems during incubation were predicted to produce males. Thus, a seasonal shift in sex ratios was observed over each nesting season, with males being produced early in the season, followed by predominantly female-biased sex ratios for the remainder of the season. The natural nesting beach was consistently cooler than the egg corrals by comparison, but was still predicted to produce an overall female-biased sex ratio for each nesting season (i.e. hypothetically ranging from 57.4 – 59.8% female bias). A female bias has been reported for many other sea turtle species as well (Wibbels, 2003) and could be the result of evolutionary selection

(Shine, 1999). A female biased sex ratio could maximize population growth, provided males do not become a limiting factor, and could therefore be accelerating the recovery rate of the Kemp's ridley (Wibbels, 2003; Coyne et al., 2007; Shaver and Wibbels, 2007).

Additionally, a hypothetical model was developed to simulate the effects of global climate change on the sex ratios produced in the Recovery Program. A 1°C increase in egg corral temperatures was predicted to produce an extreme female bias of 97.0% to 95.1% female for the 2009 and 2012 nesting seasons, respectively. Likewise, a 1°C increase in nesting beach temperatures would also have produced a greater female bias of 79.9% and 83.5% female for the 2009 and 2012 nesting seasons, respectively. Leaving nests *in situ* could therefore offer a short-term buffer to increasing temperatures associated with global climate change, but other, longer-term solutions should be considered in the future management of the Kemp's ridley. This model could prove paramount for upcoming decisions regarding the conservation of this endangered species. It is important to note that the 1°C increase in temperature used in the current model represents a conservative estimate, with some climate models predicting increases as great as 4°C.

The second chapter of this thesis evaluated the survival of nests and hatchlings on the natural nesting beach. A subset of *in situ* nests from arribadas during the 2011 and 2012 nesting seasons were monitored daily for signs of predation to evaluate natural predation rates on nests throughout the period of incubation. Hatching success and hatchling survival from the nest to the surf were also assessed for these *in situ* nests. Further, these data were also evaluated in relation to arribada nesting as a reproductive adaptation for enhancing hatchling survival through predator satiation. Predator impact on nests during incubation was relatively low with 77.6 – 98.5% of nests remaining undisturbed by predators. Between 64.3 and 79.4% of hatchlings from *in situ* nests successfully emerged in the 2011 and 2012 nesting seasons, and in 2012 approximately 79.2% of emergent hatchlings made it to the surf. Collectively, these results suggest that predator impact on nests and hatchlings is relatively minimal in comparison to predation rates reported for other sea turtle populations. This supports the hypothesis that the arribada nesting behavior may have evolved as a mechanism for maximizing hatchling production and survival. The concept of predator satiation was also supported by results from the predator track study. Predator track evaluations indicate that there is a narrow range of predator species that frequent Rancho Nuevo in limited numbers. Additionally, the distribution of predators on the beach was highly variable and was not significantly influenced by the occurrence of arribada nesting events. These results support the hypothesis that the limited number of predators at Rancho Nuevo may indeed be satiated by available prey from an arribada. This study supports the use of the arribada nesting strategy as an effective means to manage the growing number of Kemp's ridley nests as this species continues to recover. Again, the results suggest that the arribada nesting behavior may have evolved as a reproductive adaptation for maximizing hatchling production and survival through predator satiation.

The data presented in this thesis provide insight on topics regarding the biology and ecology of the Kemp's ridley. This information will be used to optimize the management strategy for the Kemp's ridley and thus enhance the recovery of this critically endangered sea turtle. Additionally, these data provide information regarding the ecology and evolution of arribada nesting in the Kemp's ridley. Multiple factors also make the Kemp's ridley a model organism for long-term studies concerning the response of sea turtles and other temperature-sensitive species to global climate change. Continued studies of the reproductive ecology of the Kemp's ridley at its primary nesting beach are paramount to evaluating long-term changes in the ecological and conservational status of the Kemp's ridley sea turtle.

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