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Sand temperatures at sea turtle nesting beaches at the Pacific coast of Guatemala

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This thesis is worth 60 study points

Summary

The climate is changing, bringing extremities such as increased periods of rainfall, but also draughts and warming temperatures. There are several species with presumed little capacity to adapt to climate changes, such as species who exhibit temperature dependent sex determination (TSD). Sea turtles (*Chelonioidea*), along with several other reptiles (*Reptilia*) are one of these species. Sea turtles are long lived migratory reptiles, where all seven species (*Caretta caretta, Chelonia mydas, Dermochelys coriacea, Eretmochelys imbricata, Lepidochelys kempii, Lepidochelys olivacea* and *Natator depressa*) are either vulnerable, endangered or critically endangered. The sea turtles come ashore and nest on sandy beaches all over the world. When the temperature changes, the sex ratio and hatching success for such species with TSD is affected. In this study I measured sand temperature through 2019 at two important sea turtle nesting beaches at the Pacific coast of Guatemala, El Banco and Hawaii. Temperature recorders were placed in two transects relative to the shoreline (in exposed sand and in the vegetation belt), and at two different depths (30 and 50 cm). From the measurements I examined the effects of external factors on sand temperatures and found that environmental factors such as burial depth, type of surrounding environment at surface, precipitation, wind velocity, solar radiation and year (2018 and 2019) had an effect on the sand temperatures. Beach locality and type of transect (position relative to shoreline) did not have an effect on the sand temperature. Increased sand temperatures close to concrete constructions suggests that urban development affect the sand temperatures. I also investigated mean sand temperatures compared to pivotal temperature (i.e. the constant incubation temperature that will equally distribute both male and female turtle hatchlings) and upper lethal incubation temperatures for the three nesting sea turtles species (*Dermochelys coriacea, Chelonia mydas* and *Lepidochelys olivacea*) at the Pacific coast of Guatemala. I found that the measured mean sand temperature preceded the pivotal temperature at El Banco and Hawaii. The measured mean sand temperature did not precede the lethal incubation temperature, although some months came very close.

Key words: Conservation biology, Climate changes, Temperature dependent sex determination, Pivotal temperature, Sea turtles, Upper lethal incubation temperature.

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Contents

1. Introduction

Changes in climate affects the environment on several levels. Mean temperature on the planet's surface is likely to increase by 1.5°C within 2030–2052, and sea levels are expected to rise as much as 0.6m in the next hundred years. A warming environment results in increased extremities such as heatwaves, droughts, heavy precipitation and flooding. Warming environments also changes the climate zones which influence species abundancy, ranges and activities (IPCC, 2018). Today, various other evidence of ecological response to climate changes is brought forth by several scientific studies and field biologists worldwide (Walther et al. 2002), like changes in species distribution, physiology and phenology (Hughes 2000). There is sufficient evidence of severe decline in species due to climate changes, and to predict that at least some species will undergo extinction (Hughes 2000, Walther et al. 2002, Hare 2003, Hansen et al. 2006). Species sensitive to such changes are e.g. amphibians (*Amphibia*) (Pounds 2001), corals (*Anthozoa*) (Hoegh-Guldberg 1999) and species who depend on external temperatures to incubate their eggs (Janzen 1994). Burrow- or mound nesting behaviour is found in some bird species, e.g. the megapod family (*Megapodiidae*) (Harris et al. 2014). It is also common in several species of reptiles (*Reptilians*) (Janzen 1994), such as lizards (*Lacertidae*), crocodiles (*Crocodilians*), and turtles (*Testudines*) (Lang and Andrews 1994, Tousignant and Crews 1995, Bock et al. 2020). These species` sex determination of offspring will be influenced by the surrounding temperature for their eggs (Bock et al. 2020). This trait is called temperature dependent sex determination (Bull and Vogt 1979, Lang and Andrews 1994) (hereafter TSD). Crocodiles (*Crocodylidae*) and alligators (*Alligator mississippiensis*) for example, produce mainly male hatchlings with higher incubation temperatures, while with cooler temperatures mainly females emerge their nests (Lang and Andrews 1994, González et al. 2019).

Sea turtles (*Chelonioidea*) exhibit TSD, and among many other reptiles, is experiencing a global decline in response to the ongoing climate change (Gibbons et al. 2000). Sea turtles are long-lived migratory reptiles (Horne et al. 2014), and all seven species (*Caretta caretta, Chelonia mydas, Dermochelys coriacea, Eretmochelys imbricata, Lepidochelys kempii, Lepidochelys olivacea and Natator depressa*) are either vulnerable, endangered or critically endangered (IUCN 2019). Changes in climate influence sea turtle nesting conditions as the female turtles come ashore to bury their eggs in the sand of their natal beaches (Brothers and Lohmann 2015). Like with crocodilians, the sex of the turtle hatchlings is decided during the embryo development at incubation in the nests (Bull and Vogt 1979). Opposite as to found with crocodilians however, with warmer incubation temperatures, sea turtle hatchlings emerge as females, and equally, with lower temperatures, hatchlings emerge as males (Lutz et al. 2002a). The constant incubation temperature that will equally distribute both male and female turtle hatchlings, is known as the pivotal temperature (hereafter PT). Higher temperatures during incubation also effect the phenotype, producing smaller sea turtle hatchlings (Horne et al. 2014). If the temperature gets too high, and precedes a certain limit, depending on species, the hatchlings will die. This is called the upper lethal incubation temperature (hereafter ULT) (Valverde et al. 2010). Even small changes in temperature can impact TSD and cause skew sex dispersal for sea turtles (Fuentes and Porter 2013). Changes that we are now experiencing in the climate seems to be happening at a speed too high for natural adaptation to take place for species with TSD (Bull et al. 1982), and available data already shows evidence of a globally female skewed sex ratio of sea turtles (Hays et al. 2014, Laloë et al. 2016). A female biased population in one nesting location is not necessarily of concern to the breeding success of the sea turtles in general. Studies shows that male sea turtles can mate with several females, and that a lower percentage of males to females not necessarily equals less mating success (Spotila 2004). In nests at Playa Grande, Costa Rica, the paternity of hatchlings has been studied to find that in 30% of the clutches, the eggs had been fathered by more than one male turtle (Spotila 2004). A female sea turtle can harvest sperm in her oviducts, and so will be able to fertilize several clutches of eggs with the sperm from just one male sea turtle (Pearse and Avise 2001). As male turtles will breed on a more frequent level than females, a female skewed population of sea turtles could possibly have little negative impact for the species (Hays et al. 2014). However, to maintain a healthy population with genetic diversity and with a healthy competitive mating behavior there need to be a certain number of males as well as females (Spotila 2004, Mitchell et al. 2010, Wright et al. 2012).

Similar to several other reptiles, sea turtles do not perform postovipositional care (Liles et al. 2015). This means that there is no parental care after the eggs has been placed in the sand (Pearse and Avise 2001). The further development of eggs is thereafter fully dependent on the surrounding environment. In addition to rising air temperatures (Bentley et al. 2020), several other external factors influence the temperature in the sand surrounding the sea turtle nest. The depth in which the nests are buried has been found to be one such factor. Preferred nesting depths will differ between species, populations and even individuals of sea turtles (Laloë et al. 2016), and temperatures has been found to decrease in deeper nests (Lutz et al. 2002).

Vegetation and shade from trees has also shown to be of great importance for cooling sea turtle nests, decreasing sand temperature as much as ~2°C compared to exposed sand (Staines et al. 2019). Sand color is another factor which has been found affect sand temperatures and albedo i.e. the sand capacity to reflect received solar radiation (Fadini et al. 2011). Darker sands tends to absorb solar radiation at a higher rate than sands of lighter color (Hays et al. 2001). Other factors that can affect sand temperatures such as winds, precipitation has been studied to a variating degree. Wind has not been investigated much in correlation with sea turtle nesting sites but has, however been investigated in several studies concerning birds. It has been found that in general, there is a greater hatching success in sites with less wind exposure (Heenan and Seymour 2012, Millones and Frere 2018). Studies on sand temperatures and precipitation shows that rainfall and tides would not contribute much to predictions of mean temperatures in the sand, but will cool the sand temperature for a short period of time (Staines et al. 2019) as rainfall is not consistent through the year (Laloë et al. 2016). Data on environmental variables such as these, are useful for future predictions of how climate will change in the decades to come.

Future scenarios for nesting sea turtles and sand temperature have been predicted in studies with climate models and projections (Fuentes and Cinner 2010, Fuentes and Porter 2013). Such studies are often based on sand temperature recordings combined with air temperature records, but mostly with only studying air temperature (Laloë et al. 2016). Actual data of the nesting environment is important to be able to successfully manage and conserve sea turtle species at population level. It also provides valuable data to use for future climate modelling to better predict future scenarios. Temperature recordings of sand has been done to some extent in rookeries and natural nesting sites (Laloë et al. 2016, 2017, Castheloge et al. 2018, Bentley et al. 2020). The study of Laloë et al. (2016) showed that a female skew has been ongoing since the late nineteenth century, and that there will be no more than 2.4% male hatchlings of the three studied sea turtle species by 2030. Calculations on sand and air temperatures indicates that this has been going on for decades on several beaches already (Wyneken et al. 2013). Such indications, however, are mostly based on expert judgement and conditions at certain populations.

This study aims to investigate the conditions of below ground temperature in the sand on two important nesting beaches for sea turtles at the pacific coast of Guatemala, El Banco and Hawaii beaches. I investigated if external factors such as burial depth, type of surrounding environment at surface, precipitation, wind velocity, solar radiation and year (2018 and 2019) influence the sand temperature in which the sea turtle bury their nests. I predict that sand temperatures measured:

1. differ with burial depth, beach locality, type of transect (position relative to shoreline), type of surrounding environment at surface, precipitation, wind velocity, solar radiation and year (2018 and 2019)

2. precede the pivotal temperatures for the three nesting sea turtle species, and will result in a female-skewed sex ratio during their nesting seasons.

3. precede the upper lethal limit of incubation temperatures for the three nesting sea turtle species, and will result hatching failure during their nesting seasons.

2. Materials and methods

2.1. Study area

This study was conducted in 2019 at the Pacific coast of Guatemala in Central America at two important nesting locations for sea turtles, El Banco and Hawaii beaches. Central America is suffering under increased warming temperatures (Aguilar et al. 2005) and other extremities, such as increasing trends of rainfall (Nakaegawa et al. 2014). It is projected that precipitation will increase in dry periods, and likewise, decrease in the rainy season (Imbach et al. 2018) Guatemala is a country considered particularly vulnerable to such climatic changes and falls within the ranks of top 20 in the Global climate risk index from 1999-2018 (Eckstein et al. 2019). The weather conditions at the Pacific coast of Guatemala vary a lot through the year, ranging from tropical storms and droughts to invasions of cold air in the winter. The warmest months measured in El Banco and Hawaii during 2019 are March and April (Supplementary Figure 1) From May until October the country can be quite moistened by the tropical storms during the rainy season (Hastenrath 1967). The country dries up in the dry season stretching from November to April (Hastenrath 1967, Horst et al. 2020) (Supplementary Figure 2). The volcanic activity in the country has made its print on the landscapes and soils, resulting in darker coloured beaches at the pacific coast of Guatemala compared to the white beaches on the Caribbean coastline. These dark beaches are often referred to as the “black beaches”. The beaches are mainly built up by red bed sedimentary rocks, cretaceous sediments and volcanic debris (Bird 2010).

El Banco and Hawaii beaches are located near the small village of Monterrico in the Santa Rosa department. The two beaches lie about 12 km apart (Figure 1). The two beaches of El Banco and Hawaii are located in an area with high biological diversity and ecological value, surrounded by marine estuarine and marine coastal ecosystems like tropical mangrove forests (García-Fuentes et al. 2014). The two beaches differ a little in topography and population density. Hawaii beach (Figure 2) is located in a more flat and open landscape than El Banco with dunes and grassy, forested vegetation (Figure 3). There are some hotels and private properties with dense planted vegetation beds on the west side of El Banco Beach. The surroundings to the east are quite different, with sand dunes, open grasslands and dried, crisp vegetation (Figure 3). In Hawaii there is quite a few private properties and hotels located on the east side of the beach. The west side of Hawaii beach is more open and has almost no buildings on the beach front, with some old and deserted concrete foundations (Figure 2). In both Hawaii and El Banco there are sea turtle hatcheries; Arcas Parque Hawaii and Tortugario El Banco. Sea turtle eggs are here collected and incubated under controlled conditions as a measure to conserve the species (Muccio 2019).

Figure 1. Location of the two sea turtle beaches studied, El Banco and Hawaii on the Pacific coast of Guatemala.

Figure 2. The open, scarcely populated west side of Hawaii Beach (left). The dense and populated east side of Hawaii Beach with hotels, houses etc. (right).

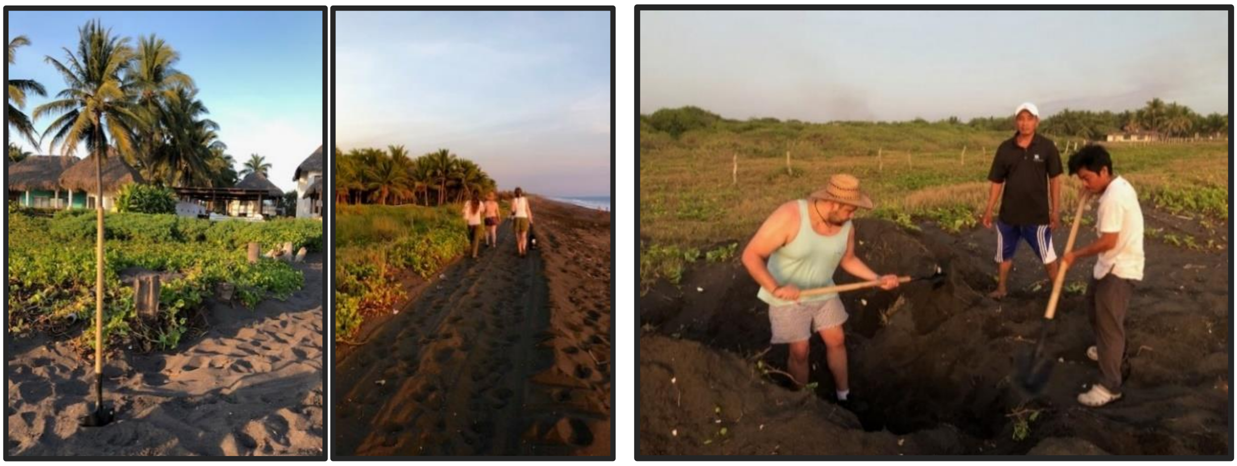


Figure 3. The constructed, planted and populated landscape on the west side of El Banco Beach (left). The dark sand and more open landscape with dunes and dry grass on the east side of El Banco Beach (right).

2.2. Study species

This study focuses on the nesting conditions for the three sea turtle species that nests in El Banco and Hawaii beaches. The beaches are visited by four of the seven species of sea turtles. The four ranging from large to small, with the largest of all seven species being the leatherback (*Dermochelys coriacea*), the eastern Pacific green (*Chelonia mydas*), the hawksbill (*Eretmochelys imbricata*) and the smallest of the four and most abundant, the olive ridley (*Lepidochelys olivacea*). Of these four species, there has been documented nesting's at the

Guatemalan pacific coast from all but the hawksbill turtle (Brittain et al. 2007, Muccio 2019). The nesting season for the olive ridley in the pacific coast stretches mainly from July to October (CONAP 2015, Muccio 2019). At the pacific coast of Guatemala however, the season seem to span mainly from August to September, with the most abundance in September month (Montes 2004). The green turtle nests from May until August, and the leatherback nests from December until February (CONAP 2015, Muccio 2019).

The adult, reproductive age of a sea turtle is around 20-30 years, depending on species and population (Spotila 2004). The number of eggs produced during a season differs between species, populations and countries. A summary from Spotila (2004), shows that there is somewhere between 50–130 eggs per clutch, and between 1.5–7 clutches each season. Incubation time for sea turtles, depending on temperature, is usually around 6-13 weeks (Lutz et al. 2002a), and in one study average being reported being 52.7 days (Hirth 1980). The defining period of embryo sex development generally occurs during the middle third of the incubation period (Spotila 2004, Wyneken et al. 2013). From the time the eggs have been deposited in the sand until adulthood, the sea turtle faces several challenges. Egg-loss by predators or egg-gatherers, habitat loss, destroyed nests, fishing, boat-strikes, pollution and marine debris are some of the threats to sea turtle survival (Klein et al. 2017). In addition to this, the temperature is increasing in the sand where sea turtles lay their eggs. The PT for sea turtles, depending on species, is mainly perceived to lie somewhere between 27°C and 31°C, the majority between 29.0–30.0°C (Lutz et al. 2002, Wyneken et al. 2013). There are no published data about PT of the nesting sea turtle populations in the pacific coast of Guatemala available. As PT is reported to vary between locations, species and populations, the most accurate for this study would be to use data from neighbouring countries. Pivotal temperature for the leatherback in the neighbouring country Costa Rica, has been reported to be 29.4°C and the green turtle 28.5–30.3°C (Lutz et al. 2002a). Studies from Brazil and Costa Rica shows that the PT of olive ridley is perceived to lie at approximately 30.5°C, and thereby one of the highest PT of the seven species (Wibbels et al. 1998, Lutz et al. 2002b, 2002a). The upper lethal incubation temperature (ULT) for sea turtle embryos has been found to be 35°C (Valverde et al. 2010 and Howard et al. 2014). This ULT at 35°C and the PT of 30.5°C was used to compare with measured mean sand temperatures in this study.

2.3. Study design and data collection

In early December of 2018, 80 LogTag Trix-8 temperature recorders were placed in the sands of the two beaches of Hawaii and El banco. The recorders have a measurement range of -40°C to +85°C and a rated temperature reading accuracy at ±0.5°C for -20°C to +40°C. The recorders were programmed to measure temperature at hourly time intervals. The temperature recordings were set up to all measure from December 2018 until November 2019. In this study, I also looked at temperature recordings collected in 2018, from May until December. The difference between the two years is that in 2018 the loggers were only placed in one transect, in the sand. In 2019 I added another transect, in the vegetation line as well. In both studies it has been recorded temperatures at two different depths in each location (30 and 50 cm). Between each location in the transect there was approximately 100 meters ±5 m, and between the vegetation and sand transect approximately 1.5-4 m (Figure 4, A and B). In each location, two temperature recorders were buried. One was buried at 50 cm which is a typical depth for sea turtles to bury their eggs (Limpus 2009), and the other at 30 cm directly above. Detailed drawings with three cross point measurements for each of the locations were drawn up, and the loggers were buried with fish string to ease the excavation after one year buried in the sand. The coordinates for all the locations were taken with a handheld GPS (Supplementary Table 1).

Figure 4. Locations of temperature recordings at EL Banco beach (A) and Hawaii Beach (B) (red and green pinpoints).

The temperature recorders were collected during 4-9th of December in 2019. The recorders were located and excavated from the locations, recovering 78 of 80. Of the 78 recorders retrieved, 25 still had functioning battery and intact data when found. After the remaining recorders were examined at USN, I managed to retrieve data from 34 recorders. The data from the recorders that could be retrieved was downloaded by using a LogTag interface. It was necessary to exclude five recorders from the further analysis, due to failing data. This left me with a total of 29 temperature recorders to analyse for this study (Supplementary Table 2). There was some difference in the set up and length of measured temperatures for each temperature recorder. The start and stop were hence set to the same for all, starting at 13.12.2018 at 06:00 AM and stopping at 03.11.2019 kl. 00:00 PM when preparing for the data analysis.

Historical weather data of air temperature, precipitation, solar radiation and wind velocity was collected from Instituto Privado de Cambio Climático (ICC 2020). The nearest weather stations to both sites were used; La Canadelaria for the El Banco transect, and La Maquina for the Hawaii transect (Supplementary Figure 1, 2, 3 and 4).

2.4. Data analysis

I tested the effects of burial depth, beach locality, type of transect (position relative to shoreline), type of surrounding environment at surface, precipitation, wind velocity, solar radiation and year (2018 and 2019) on the sand temperatures at the Pacific coast of Guatemala by using linear mixed models (LMM). A list of ten candidate models was created to represent the main working hypothesis of the effects of physical position, weather variables, location and year on sand temperatures. Burial depth, beach locality, type of transect (position relative to shoreline), type of surrounding environment, precipitation, wind velocity, solar radiation and year were considered as fixed effects and individual temperature recorder ID was considered as random effect, using year as random slope in some models. Year was treated as fixed effect because there are only two levels, making it impossible to use as a random effect (Harrison 2015). Relevant interactions were not included to avoid unnecessary increase in the complexity of the models evaluated. None of the fixed effects used in all models were correlated (Pearson r coefficient <0.5), and variance inflation factor values were <3 (Zuur et al. 2010).

Model selection was based on Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002, Leroux 2019) using the R package MuMIn (Bartoń 2020) There was no need for model averaging as ΔAICc was >2 in all the other models compared to the most parsimonious one (Burnham and Anderson 2002, Arnold 2010, Leroux 2019). Parameters that included zero within their 95% confidence interval (CI) were considered as uninformative (Arnold 2010). All analyses were conducted in R 3.5.1 (R Core Team 2018). I used residual and quantile-quantile plots to check the validity of our model (Zuur et al. 2010). Mean values are given with standard deviation (±).

3. Results

The best model was the full model that includes all the fixed effects with year/ID as random slope (Table 1).

Table 1. Model selection results using Akaike Information Criterion (AIC) and AICc weight. Response variable was temperature of sand (T) and predictors were burial depth (BD), beach locality (B), position relative to shoreline (P), type of surrounding environment (SE), precipitation (PR), wind velocity (WV), solar radiation (SR) and year (Y) with individual temperature recorder identity (ID) as random intercept and year as random slope.

Model	df	loglik	AICc	Delta AICc	weight
T ~ BD + P + SE + B + PR + WV + SR + Y + (Y | ID)	**14**	**-738639.0**	**1477306**	**0.00**	**0.994**
T ~ B + PR + WV + SR + Y + (1| ID)	10	-738648.7	1477317	11.46	0.003
T ~ PR + WV + SR + Y + (Y | ID)	9	-738649.7	1477317	11.47	0.003
T ~ BD + P + SE + B + Y+ (Y | ID)	11	-738909.5	1477841	535.04	0.000
T ~ Y + (Y|ID)	6	-738920.2	1477852	546.49	0.000
T ~ BD + P + SE + B + PR + WV + SR + Y + (1 | ID)	12	-739326.4	1478677	1370.91	0.000
T ~ PR + WV + SR + Y + (1| ID)	7	-739333.6	1478681	1375.35	0.000
T ~ B + PR + WV + SR + Y + (1| ID)	8	-739332.9	1478682	1375.91	0.000
T ~ BD + P + SE + B + Y + (1| ID)	9	-739596.3	1479211	1904.63	0.000
T ~ Y + (1|ID)	4	-739603.5	1479215	1909.06	0.000

Burial depth, type of surrounding environment at surface, precipitation, wind velocity, solar radiation and year (2018 and 2019) had an effect on the sand temperatures. Beach locality and type of transect (position relative to shoreline) did not have an effect on the sand temperature (Table 2).

Table 2. Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95 % confidence interval of explanatory variables effects on the temperatures of sand at the Pacific coast of Guatemala. Informative parameters are given in bold.

Variables	**Estimate**	**SE**	**LCI**	**UCI**
Intercept	34.4163	0.43725	33.5855	35.23381
Depth (50 cm)	**-0.5502**	**0.24321**	**-1.0054**	**-0.0971**
Beach (Hawaii)	-0.3398	0.25459	-0.8285	0.1713
Position relative to shoreline (Vegetation)	-0.1175	0.37736	-0.8211	0.5851
Type of surrounding environment (Sand)	**-1.0918**	**0.44895**	**-1.9301**	**-0.2445**
Type of surrounding environment (Vegetation)	**-1.5881**	**0.52853**	**-2.5749**	**-0.6003**
Precipitation	**-0.1922**	**0.01076**	**-0.2133**	**-0.1711**
Wind velocity	**-0.0021**	**0.00092**	**-0.0039**	**-0.0003**
Solar radiation	**-0.0002**	**0.00002**	**-0.0002**	**-0.0001**
Year (2019)	**0.3295**	**0.16808**	**0.0051**	**0.7021**

3.1. Impact of environmental factors on sand temperatures

Burial depth at 30 cm showed higher measured sand temperatures than at 50 cm (Table 2). In the measurements done in 2019 the temperatures at 30 cm was slightly higher than in 2018 (Figure 5).

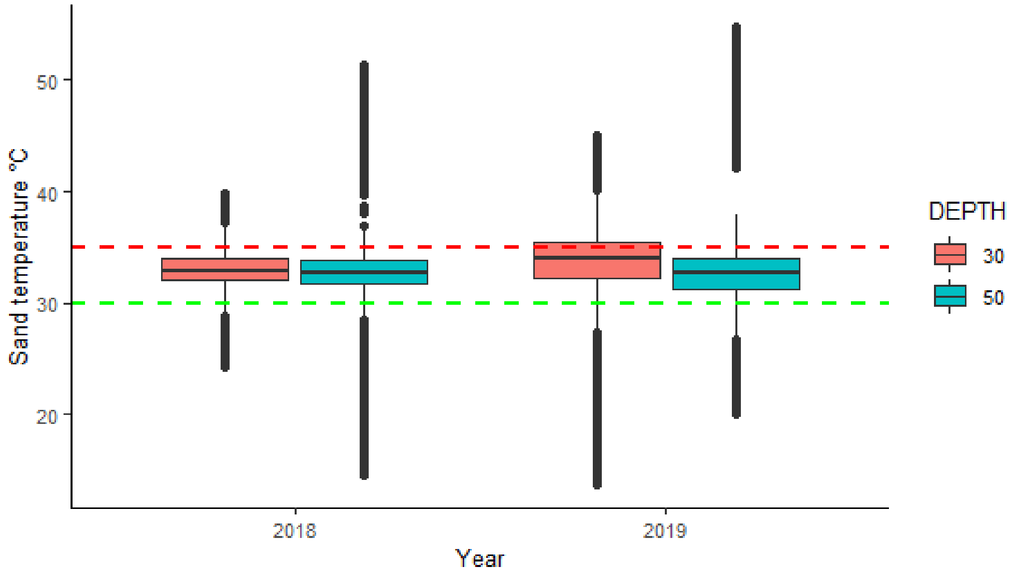


Figure 5. Boxplot showing measured sand temperatures according to burial depth (30 and 50 cm) and year (2018 and 2019) in El Banco and Hawaii. The box plot shows median values (black horizontal line), 25th and 75th percentile. Pivotal temperature (PT) marked by dashed green line. Upper lethal incubation temperature (ULT) marked with red dashed line.

For surrounding environment, the measured sand temperatures differed if the recorder was buried near concrete, in exposed sand or under vegetation cover (Table 2). Temperatures in exposed sand and under vegetation were lower than sand near concrete constructions (Figure 6).

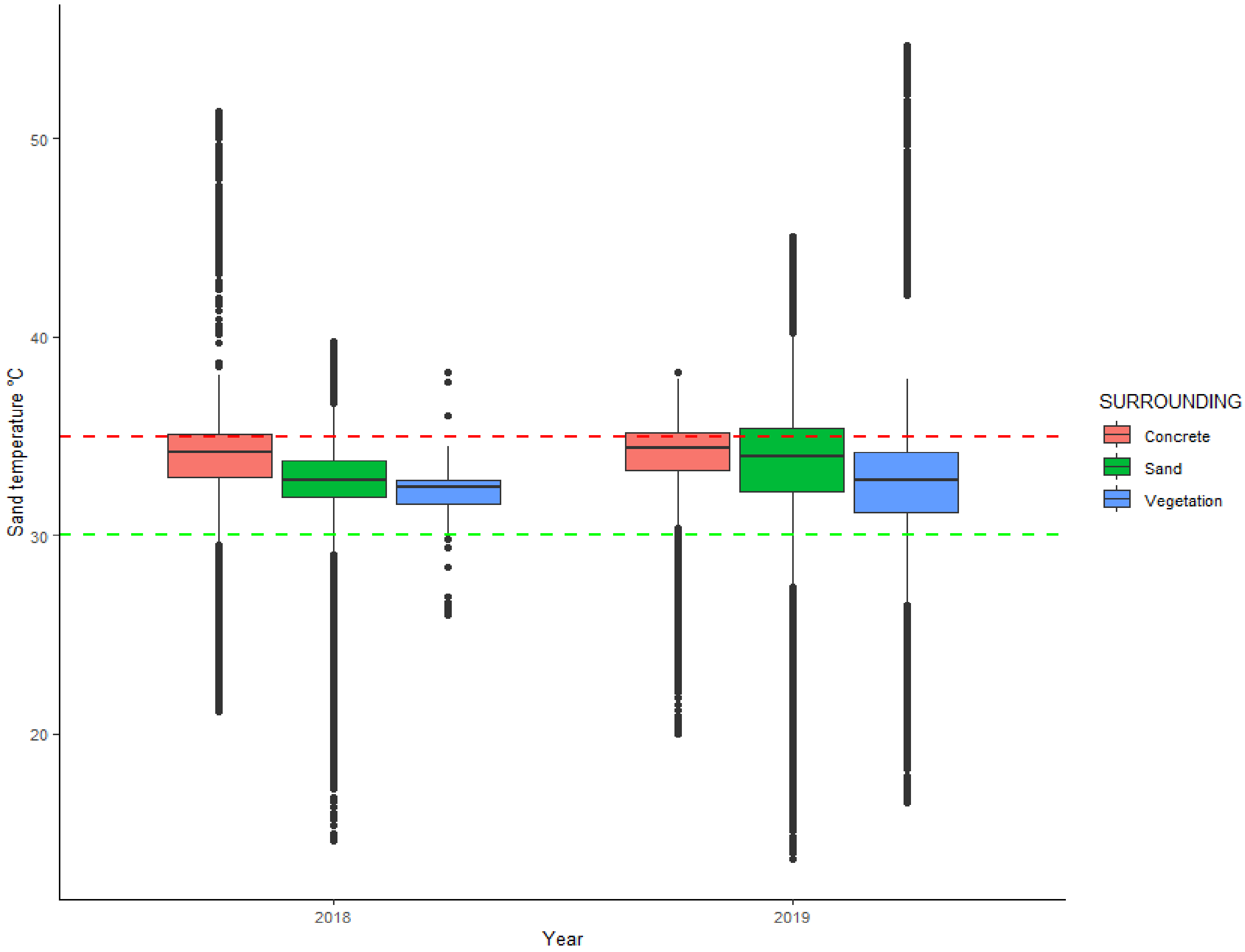


Figure 6. Box plot showing differences in measured sand temperatures according to surrounding environment on surface (near concrete, in exposed sand or sand under vegetation cover) and year. The box plot shows median values (black horizontal line), 25th and 75th percentile. Pivotal temperature (PT) marked by dashed green line. Upper lethal incubation temperature (ULT) marked with red dashed line.

With increased precipitation, the sand temperature decreased (Table 2). This was also true for temperature measurements in sand with all three types of surrounding environments (concrete/ sand/ vegetation) (Figure 7).

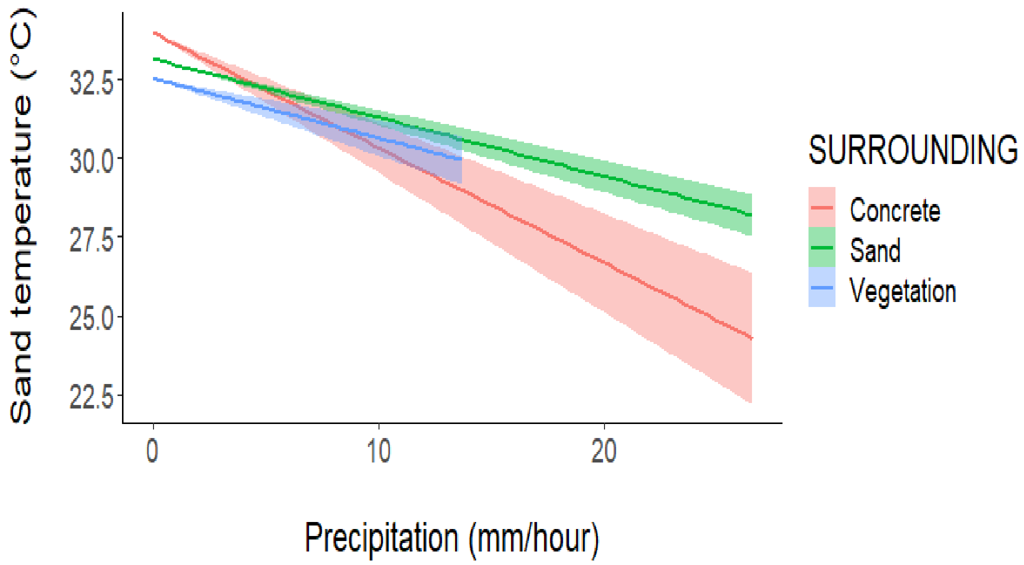


Figure 7. Relation between measured sand temperatures, surrounding environment (concrete/ sand/ vegetation) and precipitation for El Banco and Hawaii.

With increased wind velocity, the sand temperature decreased (Table 2). This was true for measured sand temperatures with all three types of surrounding environment (concrete/ sand and vegetation). The effect of wind on the sand temperature was stronger on the sand close to concrete constructions (Figure 8). The beach in Hawaii seems to be more exposed to wind than El Banco (Supplementary Figure 4).

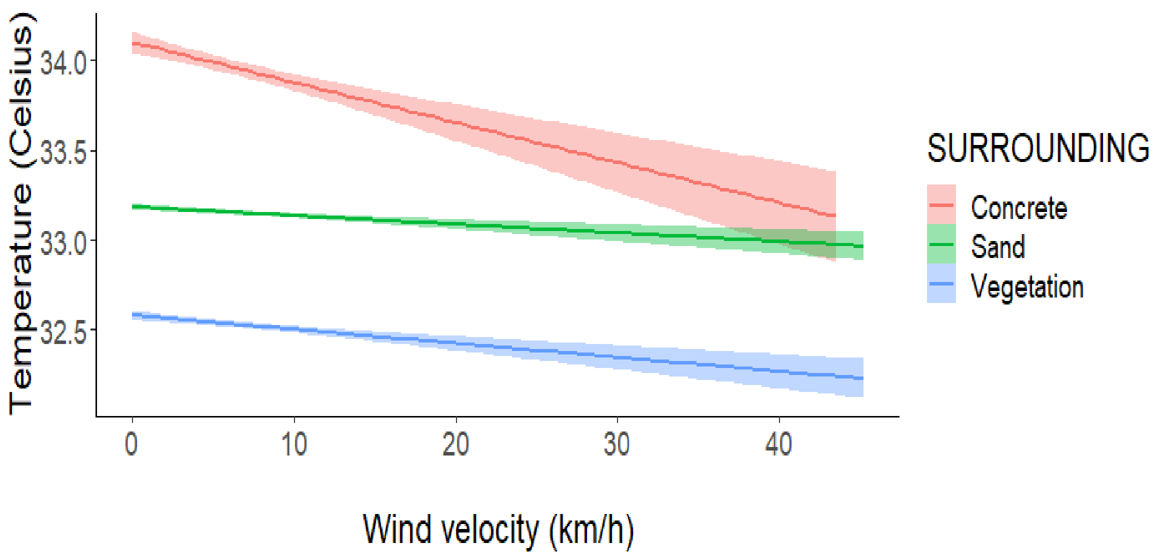


Figure 8. Relation between measured sand temperatures, surrounding environment (concrete/ sand/ vegetation) and wind velocity for El Banco and Hawaii.

With increased solar radiation, the sand temperature decreased (Table 2). This was true for temperature recorders surrounded by vegetation or exposed sand. Temperature recorders in sand close to concrete constructions measured temperature increase with increased solar radiation (Figure 9). The months with the highest measured solar radiation were March, July and December (Supplementary Figure 3).

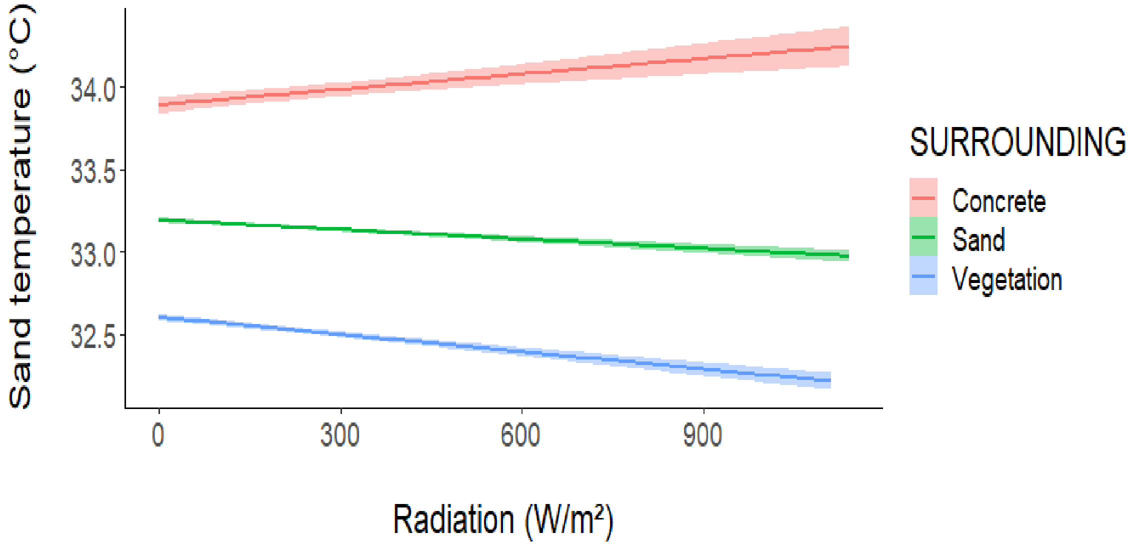


Figure 9. Relation between measured sand temperatures, surrounding environment (concrete/ sand/ vegetation) and solar radiation for El Banco and Hawaii.

The two years of measured temperatures 2018 and 2019 differed (Table 2), as the measured temperatures were higher in 2019 than in 2018. Mean temperature in 2018 were measured to be 32.27°C (±1.29°C) and in 2019 were measured to be 33.06°C (±1.29°C). In 2019 there was more variance in the measured temperatures than in 2018, with both lower and higher temperatures measured (Figure 6).

3.2. Impact of sand temperature on sea turtle hatching success

The mean temperature in 2018 was measured to be 32.27°C (±1.29°C) and in 2019 to be 33.06°C (±1.29°C), and so preceded the PT of 30.5°C. This is also true for the measured mean temperatures for all the months of the year (Figure 10). The mean temperature in 2018 and in 2019 did not precede the ULT for sea turtles at 35°C, but in March and April, the measured mean temperatures precede the ULT at 30 cm in both sand and vegetation transect. At 50 cm it was the measured temperatures in the vegetation transect that preceded ULT and not in the sand transect. In March the temperature was close to ULT with 34.9°C in both beaches (±0.4 Hawaii and ±0.5 El Banco). In April the temperature was above ULT in both beaches with 35.6°C (±0.5°C) in Hawaii and 35.7°C (±0.5°C) in El Banco. The months with the highest measured mean sand temperatures were April with 35.6°C (±0.5°C) at Hawaii and 35.7°C (±0.5°C) at El Banco. The months with the coolest measured mean sand temperatures were October with 30.2°C (±2.5°C) in Hawaii and 31.4°C (±1.9°C) in El Banco (Supplementary Figure 5). In the sand transect, the measured mean sand temperatures preceded the PT in all the months measured at both 30 cm and 50, including in the nesting season for all three nesting turtle species at El Banco and Hawaii. In the vegetation transect the measured mean sand temperatures preceded the PT in all the months measured at both 30 cm and 50, except from October in the vegetation transect.

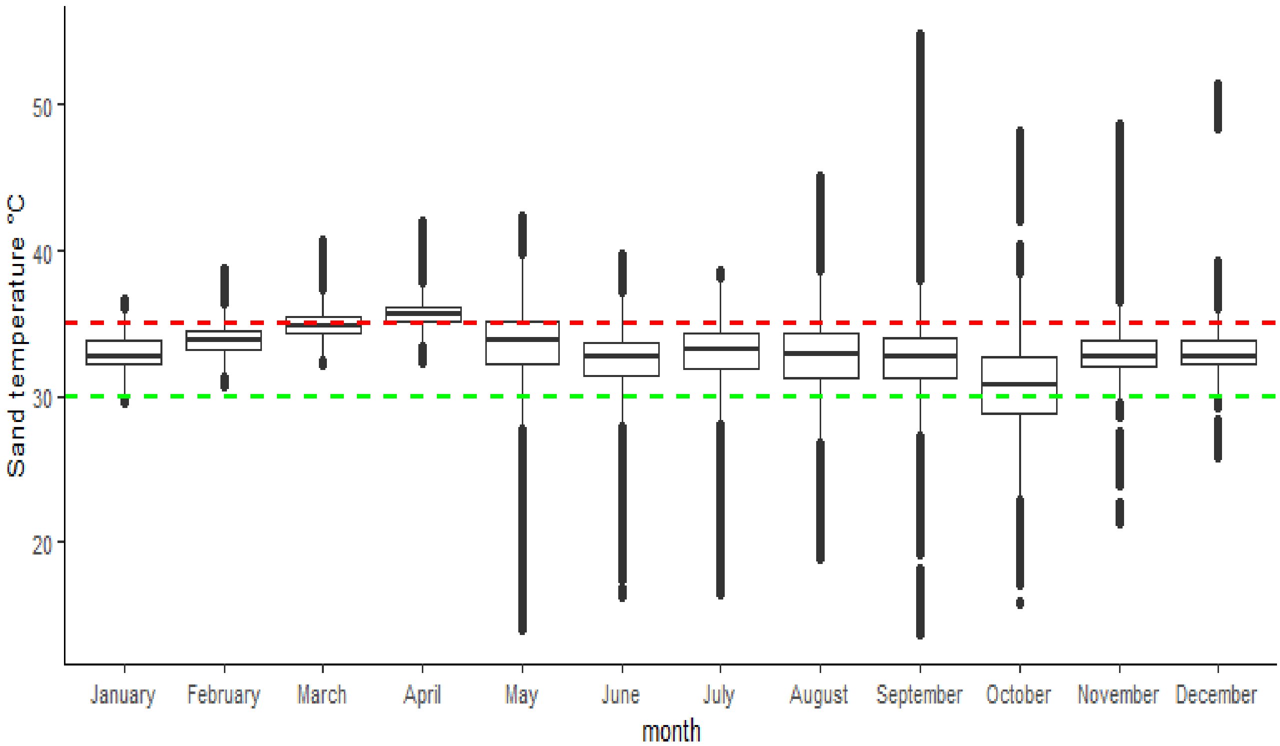


Figure 10. Box plot showing measured sand temperatures pr. month for 2018 and 2019 in El Banco and Hawaii. The box plot shows median values (black horizontal line), 25th and 75th percentile. Pivotal temperature (PT) marked by dashed green line. Upper lethal incubation temperature (ULT) marked with red dashed line.

4. Discussion

Species with temperature dependent sex determination rely on the surrounding environment for the development of their hatchlings (Bull and Vogt 1979, Janzen 1994, Lang and Andrews 1994). Sand temperatures at sea turtle nesting sites are warming along with a changing climate (Lang and Andrews 1994, Laloë et al. 2016, 2017). I set out to investigate if sand temperatures differed according to external factors and found that most of these predictions were supported in the results. I found that burial depth, type of surrounding environment at surface, precipitation, wind velocity, solar radiation and year (2018 and 2019) had an effect on the sand temperatures. I also investigated if the measured mean temperatures precede the PT for the three nesting sea turtle species at El Banco and Hawaii, and will result in a female-based sex ratio during their nesting seasons. This prediction was also supported. The prediction that the mean measured temperatures precede the ULT for the three nesting sea turtle species, and will result hatching failure during their nesting seasons, were however not supported by the findings in this study.

4.1. Impact of environmental factors on sand temperatures

Sand temperature was lower at 50 cm depth compared to 30 cm depth as expected. In other studies, differences in temperature at different depths in nests of loggerhead turtles (*Caretta caretta*) have been reported to vary from 0.3-1.4 °C (Lutz et al. 2002). Deeper nesting depth have been found to be correlated positively on clutch survival rates (Mortimer 1990, van de Merwe et al. 2006). Preferred nesting depths will differ between species, populations and even individuals of sea turtles. For example, in the Caribbean, leatherback mean nesting depth was measured at 63.3 cm and green turtle at mean 48.8 cm (Laloë et al. 2016). An implication of higher temperatures during incubation is that the sea turtle hatchlings develops smaller in size. This favours the survival of adult turtles with smaller body size (Horne et al. 2014). Further, incubation depth in the sand is depending on the size of the female sea turtles. Small female turtles tend to bury their clutches at a lesser depth than large females (Burgess et al. 2006, Horne et al. 2014), leading to eggs being more exposed to higher temperatures and potentially harmful thermal variance (Horne et al. 2014, Laloë et al. 2016).

With increased land use on the beaches and nesting sites for sea turtles, comes constructions and increased use of vegetation. El Banco and Hawaii are no exceptions, as both contains buildings and planted green gardens that faces the beach front and turtle nesting sites. A study of important nesting sites in the Caribbean showed that 20% of the historical sites had been lost, and 50% reduced to dangerously low populations (McClenachan et al. 2006). Such a study has, to my knowledge, not yet been conducted in Guatemala, but with an increasing population and tourism, the country could most likely be heading towards similar scenarios. The measured sand temperatures near concrete constructions were higher than the temperature measured in exposed sand and under vegetation, suggesting that human impact and constructions on the beach close to sea turtle nesting sites will affect the nesting temperature conditions for sea turtles. Also, vegetation has been shown to have an impact on nesting temperatures. Mean temperatures in exposed sands has been found to be ∼2 °C warmer than sand with shading vegetation. At 50 cm it is interestingly the measured temperatures in the vegetation transect that precedes ULT and not in the sand transect. The reason for this is not clear, but a theory could be that when temperatures rise to a certain level, the shading effect from vegetation stops, and it will instead trap heat in the sand as shown in a similar study, where temperature in exposed soils was found to be much lower than soil under cover, due to evaporation and the heat gets stored under the surface (Asaeda and Ca 1993). However, the structure or height of vegetation seems to be important to consider as vegetation directly on the sand has shown not to have an effect on the sand temperature (Staines et al. 2019). In a study in Tortuguero, Costa Rica, green turtle who nested on the open beach produced mainly females, while those under shade from vegetation produced 94% male hatchlings (Standora and Spotila 1985). Sand from Costa Rica is known to be of a dark color similar to the beaches of Guatemala (Hays et al. 2001). Studies have shown differences in nesting behaviour trends over time, and inter species differences and local adaptations have been observed between populations of sea turtles (Liles et al. 2015). The olive ridley in Colombian beaches have tended to nest on both the lowest, mid and the highest part of the beach, between the high tide line and vegetation line, or even higher, from driftwood to the vegetation (Barrientos-Muñoz et al. 2014). A study of nest site selection conducted on hawksbill turtles in Trois Ilets, Guadeloupe showed that the nests in the forest line compared with the nests in the open sands would have higher percentage of hatchlings emerge from the nests, and that the clutches laid in the forest zone were larger. It also indicated that the nests that had been laid further from the shoreline would have a greater hatching success, compared to nests close to the shoreline, that would be more at peril during storms and big waves inundating the nests (Kamel and Morovsky 2005). In the same study there were observations of turtles aborting nesting due to obstructions like roots and tree branches. This indicates that some of the vegetated locations of this study where the shrub is quite dense and hard to dig through, even with a shovel, it is not likely to be used as a nesting site for sea turtles. Studies with leatherbacks and green turtles done in Surinam with leatherbacks and green turtles has also shows that there are interspecies differences in sea turtles nesting site selections. The leatherbacks would prefer open sand areas, while green turtles would choose vegetated locations to bury their clutches, favouring the success of the clutches of the green turtles in a larger part than the leatherback as their clutches was more at risk of nests being inundated (Whitmore and Dutton 1985).

Precipitation decreases the measured sand temperatures as expected. This correlates with other studies on sea turtles that have shown similar results. Studies that has gone deeper into the effect of precipitation shows that rainfall and tides have been documented to cool down the nest temperatures until pivotal temperatures, and male-producing temperatures (Laloë et al. 2016). Evaporation of moist is also known to decrease the sand temperatures (Song et al. 2013). However, rainfall alone would not contribute much to long term predictions about the temperatures in the sand, but only for a shorter period of time (Staines et al. 2019) as rainfall is not consistent through the year (Laloë et al. 2016). Too much water can interfere negatively, with the gas exchange between air and sand in the nests, suffocating the nest (Laloë et al. 2016). This suggest that for a country such as Guatemala with a rainy season, sand temperatures and nesting conditions for sea turtles will benefit from the increased and prolonged periods of precipitation during these seasons. The nesting season of the olive ridley (July to October) and the green turtle (May to August) is within the rainy season (May until October) (Hastenrath 1967), while the nesting season for the leatherback (December to February) is not (CONAP 2015, Muccio 2019). In fact, the leatherback nests in the months with least measured precipitation in El Banco and Hawaii.

Increased wind velocity decreases the measured temperatures in sand as expected. However, the temperature drop is strongest in sand near concrete constructions than in exposed sand or in sand under vegetation cover. This finding is different from what was expected, as it would be expected a larger effect from wind where it can access freely, as e.g. over exposed sand. The effect could be correlated with solar radiation and evaporation as wind has been found to influence the soil evaporation process, with decreased evaporation rate with increased wind speed (Song et al. 2013). Another theory could be that wind has a cooling effect on the concrete and so affects the sand temperature as well. Wind velocity and sea turtle nesting conditions does not seem to have been studied to a great extent, but wind has been shown to influence current direction, sand movement and erosion, affecting the number of sea turtle nests deposited on beaches (Lamont and Carthy 2007). Studies on bird nesting and wind shows that the hatching success increase in sites less exposed to wind, as bird eggs in exposed nests is more prone to damages due to wind (Heenan and Seymour 2012, Millones and Frere 2018). Sea turtle eggs buried in sand would not be exposed to such damages, unless eggs would be buried at too shallow depths. There will be several factors that can influence these results, and the effects of wind velocity will most likely be correlated with air temperature, that is known to influence sand temperatures (Bentley et al. 2020). With the effect from wind being stronger close to concrete constructions than in exposed sand and sand under vegetation cover shows again that urban development affects the nesting conditions for sea turtles.

Solar radiation had the opposite effect on sand temperatures than expected, as the sand temperature decreases with increased solar radiation in exposed sand and sand under vegetation cover. In similar studies, temperature in exposed soils have been found to be much lower than soil under cover, due to evaporation and the heat is stored under the surface (Asaeda and Ca 1993). Sand temperatures near concrete constructions, however, is the only variable that follows what was predicted, that with increased solar radiation, the sand temperature also increases. The reason for this might be correlated with evaporation, as moist from sea breeze will accumulate in sand and vegetation during the night. When the sun rises, the moist would begin to evaporate and evaporation decreases the temperature of the sand (Asaeda and Ca 1993, Song et al. 2013). This does not happen with concrete, as concrete does not collect sea breeze. The color of the sand at nesting beaches has also been found to have a significant effect on sand temperature in relation to solar radiation. A study done in Cyprus, found that the lowest temperature measured on dark beaches almost never came below the highest temperature measured on light beaches (Hays et al. 2001). The darker color on the beaches of El Banco and Hawaii could have an affect correlated with solar radiation and heat exchange. Darker beaches have been found to have higher sand temperature than beaches of lighter color, as the sand of darker beaches absorb solar radiation during the day (Hays et al. 2001).

4.2. Impact of sand temperature on sea turtle hatching success

Being a species with presumed little capacity of adapting to impacts brought on by climate changes (Hays et al. 2014) sea turtles are especially vulnerable to warming temperatures. As predicted, the measured mean temperatures at both beaches all precede the highest PT for sea turtles (30.5°C) (Wibbels et al. 1998) in all the months measured except from October. This is also true regarding PT for the green turtle (28.5–30.3°C) (Lutz et al. 2002a). The PT of the leatherback (29.4°C) (Lutz et al. 2002a) was preceded by mean temperatures in all the months measured. The olive ridley, who nests from May until October could have slightly better chances of producing closer to PT, if the eggs are deposited in time so that October month is within the defining period of embryo sex development, i.e. the middle third of the incubation period (Spotila 2004, Wyneken et al. 2013). When working with temperature recordings, it is important to be aware of the importance of accuracy in the recordings. When the temperatures are close to the pivotal temperature, very small changes in temperature would be able to have large impact on the sex ratio, as differences as small as one tenth of a temperature could change the outcome of one clutch (Lutz et al. 2002). This suggests that a female skew in sea turtle populations at El Banco and Hawaii is likely to occur when sea turtles' nest in the wild. A female skew could, at worst case scenario, result in extinctions of sea turtles on a local level (Laloë et al. 2016). It could also mean that these beaches provide female hatchlings, while other beaches provide male turtle hatchlings into the gene pool for sea turtles. Sea turtle populations can and will reproduce, even with more females than males, as the males will mate more frequently and with several females (Spotila 2004, Wright et al. 2012).

The measured mean temperatures for the year in total did not precede ULT (35°C) (Valverde et al. 2010), but when studying mean measured per months separately, April precede the ULT at 30 cm in both sand and vegetation transect, and March is close to the limit. The tolerance of temperatures close to ULT differs between species and populations, and several studies as reviewed by (Howard et al. 2014) indicate that some hatchlings are able to hatch close to the upper limit of lethal temperatures at 33-35°C. There is also some evidence that this limit is not necessarily lethal on a global level (Ackerman 1997, Miller 1997, Wyneken et al. 2013). A study done in the Mediterranean by (Horne et al. 2014) showed that the highest documented incubation temperature was at 35.9°C. However, warmer sands will have other effects for the sea turtle hatchlings. Decreased incubation time for the nests is another impact correlated with higher temperatures, and so decreased yolk mass of the hatchling for which they are fully dependent on during their first days after hatching. Higher incubation temperatures has also been correlated with reduced swimming speed in green turtles, making them more prone to predation as they emerge the open seas as hatchlings (Burgess et al. 2006). None of the three nesting sea turtle species at El Banco and Hawaii have their nesting seasons within the two months that measured preceding or close to the ULT, but it is important to take into consideration that the measured sand temperature has not been taken from actual sea turtle nests, but in sand without eggs, meaning that temperature conditions in natural nests could potentially even be higher. Metabolic heating from the clutch has been found to greatly influence mean nest heat, depending on nesting stage, with as much as 2.0–4.4 °C on daily mean temperatures (van de Merwe et al. 2006). It is therefore likely that sand temperatures as measured in this study will be even higher when containing sea turtle eggs.

5. Conclusion

Sand temperature measurements at sea turtle nesting sites is important to be able to find the proper form of conserve a species at population level. Long term measurements like provided in this study has not been done to a large extent in Central America yet, and little is yet known about the changes in extreme temperature in this region (Aguilar et al. 2005). In Guatemala there is yet no published studies of sand temperature at natural nesting locations for sea turtles neither. As found in this study, the impact of environmental factors on sand temperature such as urban development at nesting beaches, can potentially have a large effect on the sex ratio of sea turtles in this area. The relationship between urban development and sea turtle nesting sites in Guatemala should be investigated further for a knowledge-based regulation of future development. The measured mean sand temperatures in El Banco and Hawaii precede PT through the year and even comes close to preceding ULT in some months. The Guatemalan government has stated a law that a percentage (not defined) of sea turtle nests must be hatched and monitored in the wild, and not in artificial hatcheries (Figueroa Rodrigez 2017). The findings in this study provides no argumentation to defend that such a law is sustainable today. The global populations of sea turtles are currently aided by conservation practises at most of the worlds natural nesting sites, and it seems clear from this study that the beaches of Guatemala need to reconsider the regulation of their sea turtle nesting sites. This study shows the importance of incubating sea turtle eggs in controlled environments as in hatcheries. In these controlled forms, turtle eggs are also safe from predation and egg poachers that benefit from selling sea turtle eggs to the black marked.

References

Arnold, T. W. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. The Journal of Wildlife Management 74:1175–1178.

Asaeda, T., and V. Ca. 1993. The subsurface transport of heat and moisture and its effect on the environment: A numerical model. Boundary-Layer Meteorology 65:159–179.

Barrientos-Muñoz, K., C. Ramírez-Gallego, and V. Páez. 2014. Nesting ecology of the olive ridley sea turtle (Lepidochelys olivacea) (Cheloniidae) At El Valle Beach, Northern Pacific, Colombia. Acta Biológica Colombiana 19:437–445.

Bartoń, K. 2020. MuMIn: Multi-Model Inference.

Bentley, B. P., M. R. Kearney, S. D. Whiting, and N. J. Mitchell. 2020. Microclimate modelling of beach sand temperatures reveals high spatial and temporal variation at sea turtle rookeries. Journal of Thermal Biology 88:102522.

Bird, E. 2010. Encyclopedia of the World's Coastal Landforms. Springer Science & Business Media.

Bock, S. L., R. H. Lowers, T. R. Rainwater, E. Stolen, J. M. Drake, P. M. Wilkinson, S. Weiss, B. Back, L. Guillette, and B. B. Parrott. 2020. Spatial and temporal variation in nest temperatures forecasts sex ratio skews in a crocodilian with environmental sex determination. Proceedings of the Royal Society B: Biological Sciences 287:20200210.

Brittain, R., C. Muccio, and R. Nunny. 2007. Project parlama- sea turtle conservation on Guatemala's pacific coast:9.

Brothers, J. roger, and K. j Lohmann. 2015. Evidence for Geomagnetic Imprinting and Magnetic Navigation in the Natal Homing of Sea Turtles. Current Biology 25:392–396.

Bull, J. J., and R. C. Vogt. 1979. Temperature-dependent sex determination in turtles. Science 206:1186–1188.

Bull, J. J., R. C. Vogt, and M. G. Bulmer. 1982. Heritability of Sex Ratio in Turtles with Environmental Sex Determination. Evolution 36:333–341.

Burgess, E. A., D. T. Booth, and J. M. Lanyon. 2006. Swimming performance of hatchling green turtles is affected by incubation temperature. Coral Reefs 25:341–349.

Burnham, K., P., and D. Anderson R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Pages XXVI, 488. 2nd ed. Springer, New York.

Castheloge, V. D., M. Santos, J. C. Castilhos, P. R. J. Filho, L. Gomes, R. Clemente-Carvalho, and P. Ferreira. 2018. Pivotal temperature and hatchling sex ratio of olive ridley sea turtles lepidochelys olivaceafrom the south Atlantic Coast of Brazil. Herpetological Conservation and Biology 13:488–496.

CONAP 2015. Estrategia nacional de manejo y conservación de tortugas marinas de Guatemala. Documento técnico No. 02-2015. Documento técnico.

Fadini, L. S., A. G. Silva, and P. D. Ferreira-Júnior. 2011. Sedimentary characteristics and their effects on hatching success and incubation duration of Caretta caretta (Testudines: Cheloniidae) in Espirito Santo, Brazil. Zoologia (Curitiba) 28:312–320.

Figueroa Rodrigez, E. 2017. RESOLUCIÓN 03-17-2017 El Infrascrito Secretario Ejecutivo del Consejo Nacional de Áreas Protegidas. CONAP.

Fuentes, M. M. P. B., and J. E. Cinner. 2010. Using expert opinion to prioritize impacts of climate change on sea turtles’ nesting grounds. Journal of Environmental Management 91:2511–2518.

Fuentes, M. M. P. B., and W. P. Porter. 2013. Using a microclimate model to evaluate impacts of climate change on sea turtles. Ecological Modelling 251:150–157.

García-Fuentes, A., F. j. Castillo-Cabrera, C. v. Dávila-Pérez, A. s. Morales, C. Salazar-Mendías, M. l. Lendínez-Barriga, J. a. Torres-Cordero, and L. Ruiz-Valenzuela. 2014.

Study of the vegetation in the Multiple Use Natural Reserve of Monterrico (Guatemala). Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology 148:1064–1074.

Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, J. L. Greene, T. Mills, Y. Leiden, S. Poppy, and C. T. Winne. 2000. The Global Decline of Reptiles, Déjà Vu AmphibiansReptile species are declining on a global scale. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. BioScience 50:653–666.

González, E. J., M. Martínez-López, M. A. Morales-Garduza, R. García-Morales, P. Charruau, and J. A. Gallardo-Cruz. 2019. The sex-determination pattern in crocodilians: A systematic review of three decades of research. Journal of Animal Ecology 88:1417–1427.

Hansen, J., M. Sato, R. Ruedy, K. Lo, D. W. Lea, and M. Medina-Elizade. 2006. Global temperature change. Proceedings of the National Academy of Sciences of the United States of America 103:14288–14293.

Hare, W. 2003. Assessment of Knowledge on Impacts of Climate Change - Contribution to the Specification of Art. 2 of the UNFCCC: Impacts on Ecosystems, Food Production, Water and Socio-economic Systems. Wissenschaftlicher Beirat der Bundesregierung Globale Umweltveränderungen.

Harris, R. B., S. M. Birks, and A. D. Leaché. 2014. Incubator birds: biogeographical origins and evolution of underground nesting in megapodes (Galliformes: Megapodiidae). Journal of Biogeography 41:2045–2056.

Harrison, X. A. 2015. A comparison of observation-level random effect and Beta-Binomial models for modelling overdispersion in Binomial data in ecology & evolution. PeerJ 3:e1114.

Hastenrath, S. L. 1967. Rainfall distribution and regime in Central America. Archiv für Meteorologie, Geophysik und Bioklimatologie Serie B 15:201–241.

Hays, G. C., J. S. Ashworth, M. J. Barnsley, A. C. Broderick, D. R. Emery, B. J. Godley, A. Henwood, and E. L. Jones. 2001. The importance of sand albedo for the thermal conditions on sea turtle nesting beaches. Oikos 93:87–94.

Hays, G. C., A. D. Mazaris, and G. Schofield. 2014. Different male vs. female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. Frontiers in Marine Science 1.

Heenan, C., and R. Seymour. 2012. The Effect of Wind on the Rate of Heat Loss from Avian Cup-Shaped Nests. PLoS One 7:e32252.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Marine and Freshwater Research 50:839–866.

Horne, C. R., W. J. Fuller, B. J. Godley, K. A. Rhodes, R. Snape, K. L. Stokes, and A. C. Broderick. 2014. The Effect of Thermal Variance on the Phenotype of Marine Turtle Offspring. Physiological and Biochemical Zoology 87:796–804.

Horst, O., H., W. Griffith J., C. Stanisfer L., and T. Anderson P. 2020. Guatemala | History, Map, Flag, Population, & Facts. https://www.britannica.com/place/Guatemala.

Howard, R., I. Bell, and D. Pike. 2014. Thermal tolerances of sea turtle embryos: Current understanding and future directions. Endangered Species Research 26:75–86.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? Trends in Ecology & Evolution 15:56–61.

ICC 2020. Instituto Privado de Cambio Climático (ICC).

Imbach, P., S. C. Chou, A. Lyra, D. Rodrigues, D. Rodriguez, D. Latinovic, G. Siqueira, A. Silva, L. Garofolo, and S. Georgiou. 2018. Future climate change scenarios in Central America at high spatial resolution.(Research Article)(Report). PLoS ONE 13:e0193570.

IPCC. 2018. IPCC, 2018: Global Warming of 1.5°C.An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty [Masson-Delmotte, V., P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield (eds.)]. In Press.

IUCN 2019, March. The IUCN Red List of Threatened Species. https://www.iucnredlist.org/en.

Janzen, F. J. 1994. Climate change and temperature-dependent sex determination in reptiles. Proceedings of the National Academy of Sciences of the United States of America 91:7487–7490.

Kamel, S., J., and N. Morovsky. 2005. Repeatability of nesting preferences in the hawksbill sea turtle, Eretmochelys imbricata, and their fitness consequences. Animal Behaviour 70:819–828.

Klein, C. J., J. Beher, M. Chaloupka, M. Hamann, C. Limpus, and H. P. Possingham. 2017. Prioritization of Marine Turtle Management Projects: A Protocol that Accounts for Threats to Different Life History Stages: Prioritizing projects for marine turtles. Conservation Letters 10:547–554.

Laloë, J.-O., J. Cozens, B. Renom, A. Taxonera, and G. C. Hays. 2017. Climate change and temperature-linked hatchling mortality at a globally important sea turtle nesting site. Global Change Biology 23:4922–4931.

Laloë, J.-O., N. Esteban, J. Berkel, and G. C. Hays. 2016. Sand temperatures for nesting sea turtles in the Caribbean: Implications for hatchling sex ratios in the face of climate change. Journal of Experimental Marine Biology and Ecology 474:92–99.

Lamont, M. M., and R. R. Carthy. 2007. Response of Nesting Sea Turtles to Barrier Island Dynamics. Chelonian Conservation and Biology 6:206–212.

Lang, J. W., and H. V. Andrews. 1994. Temperature-dependent sex determination in crocodilians. Journal of Experimental Zoology 270:28–44.

Leroux, S. J. 2019. On the prevalence of uninformative parameters in statistical models applying model selection in applied ecology. PLOS ONE 14:e0206711.

Liles, M. J., M. J. Peterson, J. A. Seminoff, E. Altamirano, A. V. Henríquez, A. R. Gaos, V. Gadea, J. Urteaga, P. Torres, B. P. Wallace, and T. R. Peterson. 2015. One size does not fit all: Importance of adjusting conservation practices for endangered hawksbill turtles to address local nesting habitat needs in the eastern Pacific Ocean. Biological Conservation 184:405–413.

Limpus, C., J. 2009. A Biological Reviw of Australian Marine Turtles. https://online.fliphtml5.com/pfyf/hfdd/.

Lutz, P. L., J. A. Musick, and J. Wyneken. 2002. The Biology of Sea Turtles, Volume 2. CRC Press.

McClenachan, L., J. B. Jackson, and M. J. Newman. 2006. Conservation implications of historic sea turtle nesting beach loss. Frontiers in Ecology and the Environment 4:290–296.

van de Merwe, J., K. Ibrahim, and J. Whittier. 2006. Effects of Nest Depth, Shading, and Metabolic Heating on Nest Temperatures in Sea Turtle Hatcheries. Chelonian Conservation and Biology 5:210–215.

Millones, A., and E. Frere. 2018. How Nest Site Characteristics Influence Breeding Success in Red-legged Cormorants Phalacrocorax gaimardi 52:239–244.

Mitchell, N. J., F. W. Allendorf, S. N. Keall, C. H. Daugherty, and N. J. Nelson. 2010. Demographic effects of temperature-dependent sex determination: will tuatara survive global warming? Global Change Biology 16:60–72.

Mortimer, J. A. 1990. The Influence of Beach Sand Characteristics on the Nesting Behavior and Clutch Survival of Green Turtles (Chelonia mydas). Copeia 1990:802–817.

Muccio, C. 2019, November. Análisis Situacional de la Conservación de la Tortuga Marina en Guatemala, versión 2019, 18pgs.

Nakaegawa, T., A. Kitoh, H. Murakami, and S. Kusunoki. 2014. Annual maximum 5-day rainfall total and maximum number of consecutive dry days over Central America and the Caribbean in the late twenty-first century projected by an atmospheric general circulation model with three different horizontal resolutions. Theoretical and Applied Climatology 116:155–168.

Pounds, J. A. 2001. Climate and amphibian declines. Nature 410:639–640.

Song, W.-K., Y.-J. Cui, A. Tang, W.-Q. Ding, and T. Tran. 2013. Experimental study on water evaporation from sand using environmental chamber. Canadian Geotechnical Journal 51:115–128.

Spotila, J. R. 2004. Sea turtles: a complete guide to their biology, behavior, and conservation. Johns Hopkins University Press, Baltimore.

Staines, M. N., D. T. Booth, and C. J. Limpus. 2019. Microclimatic effects on the incubation success, hatchling morphology and locomotor performance of marine turtles. Acta Oecologica 97:49–56.

Standora, E. A., and J. R. Spotila. 1985. Temperature Dependent Sex Determination in Sea Turtles. Copeia 1985:711–722.

Tousignant, A., and D. Crews. 1995. Incubation temperature and gonadal sex affect growth and physiology in the leopard gecko (Eublepharis macularius), a lizard with temperature-dependent sex determination. Journal of Morphology 224:159–170.

Valverde, R., S. Wingard, F. Gómez, M. Tordoir, and C. Orrego. 2010. Field lethal incubation temperature of olive ridley sea turtle Lepidochelys olivacea embryos at a mass nesting rookery. Endangered Species Research 12:77–86.

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

Whitmore, C. P., and P. H. Dutton. 1985. Infertility, embryonic mortality and nest-site selection in leatherback and green sea turtles in Suriname. Biological Conservation 34:251–272.

Wright, L. I., K. L. Stokes, W. J. Fuller, B. J. Godley, A. McGowan, R. Snape, T. Tregenza, and A. C. Broderick. 2012. Turtle mating patterns buffer against disruptive effects of climate change. Proceedings of the Royal Society B: Biological Sciences 279:2122–2127.

Wyneken, J., K. J. Lohmann, and J. A. Musick. 2013. The Biology of Sea Turtles, Volume III (CRC Marine Biology Series): Jeanette Wyneken, Kenneth J. Lohmann, John A. Musick: 9781439873076: Amazon.com: Gateway. https://www.amazon.com/Biology-Sea-Turtles-III-Marine/dp/1439873070/ref=sr_1_1?crid=1N6Y4LT5WMYHL&keywords=biology+of+sea+turtles&qid=1559910382&s=gateway&sprefix=biology+sea+turtle%2Caps%2C227&sr=8-1.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.

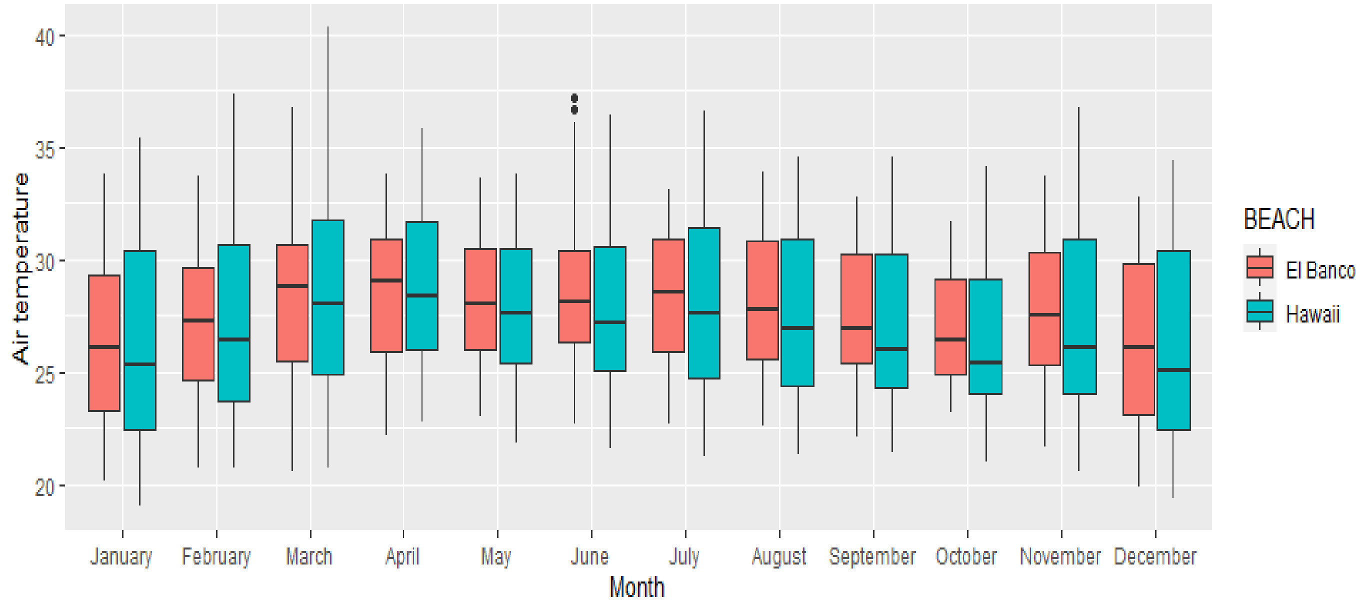
Supplementary tables and figures

Supplementary Table 1. Locations and coordinates (decimal degrees, DD) for the two study beaches in both 2018 and 2019. For the study in 2018, two recorders were placed in exposed sand at each location at 30 and 50 cm depth. In 2019 another transect line was added in the vegetation belt.

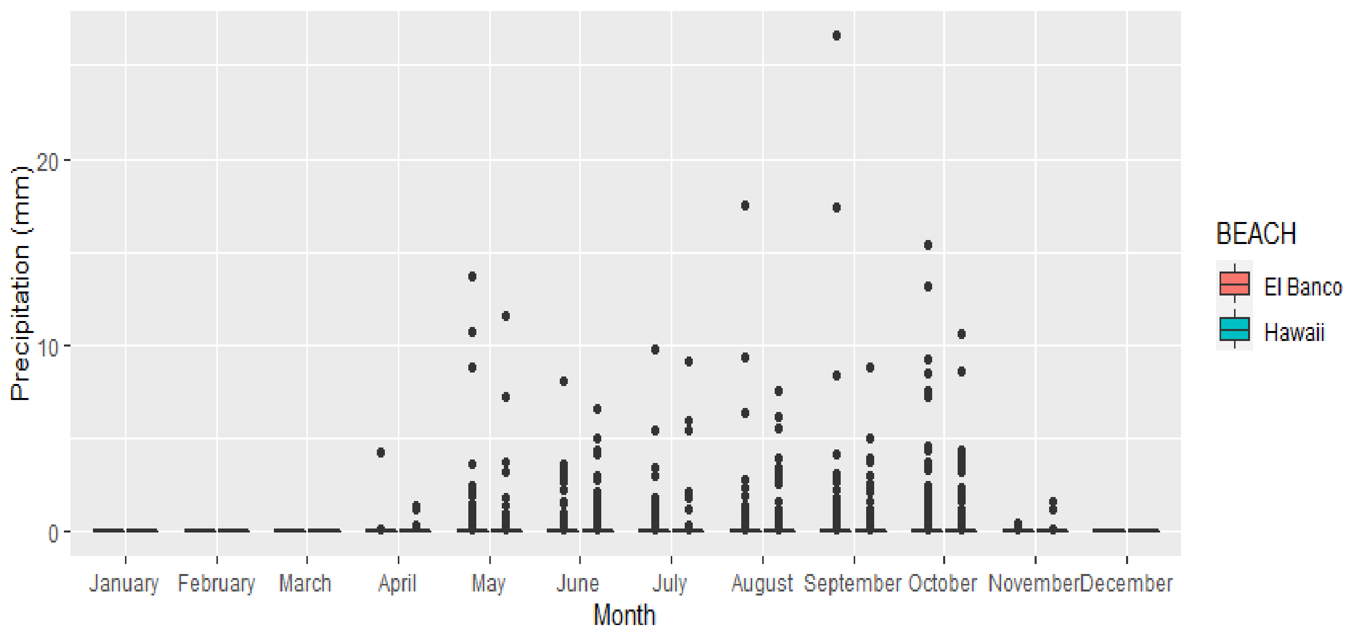
Location ID	Longitude (DD)	Latitude (DD)
El Banco 1	13.902501	-90.525234
El Banco 2	13.90281	-90.52627
El Banco 3	13.90313	-90.52733
El Banco 4	13.90334	-90.52834
El Banco 5	13.90361	-90.52928
El Banco 6	13.90225	-90.52409
El Banco 7	13.90196	-90.52305
El Banco 8	13.90166	-90.52206
El Banco 9	13.901342	-90.520897
El Banco 10	13.90112	-90.51999
Hawaii 1	13.8655	-90.41334
Hawaii 2	13.86591	-90.41433
Hawaii 3	13.86617	-90.41508
Hawaii 4	13.86664	-90.41618
Hawaii 5	13.86701	-90.41716
Hawaii 6	13.86742	-90.41837
Hawaii 7	13.86797	-90.41963
Hawaii 8	13.8684	-90.42056
Hawaii 9	13.86869	-90.42163
Hawaii 10	13.86905	-90.42259

Supplementary Table 2. Overview of temperature recorders with intact data used in this study for 2019, demonstrating position relative to shoreline (Sand (Middle)/ Vegetation (North)), burial depth, surrounding environment on surface (sand/ vegetation/ concrete), temperature recorder ID, Location ID (beach, Hawaii/El Banco) and number of recorders.

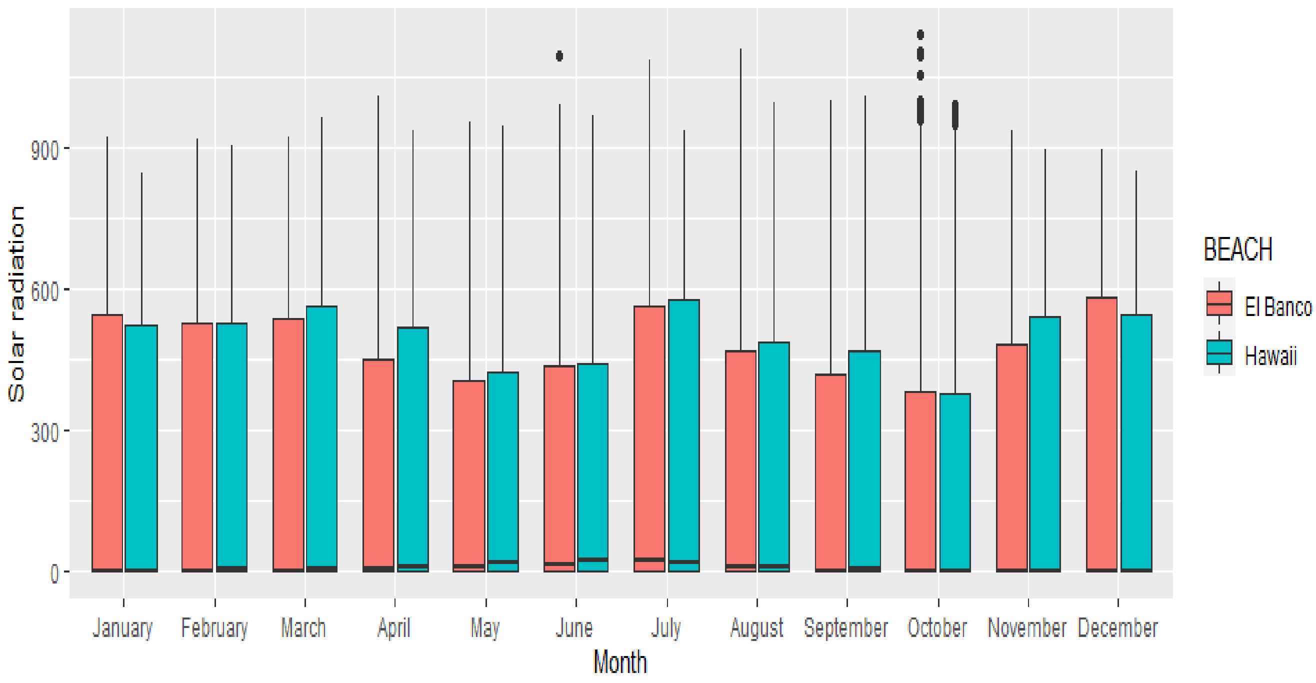
Beach	**Transect Position** *(relative to shoreline)*	**Burial depth**	**Surroundings**	**Temperature recorder ID**	**Location ID** *(Beach)*	**Number of recorders**
El Banco	Sand (Middle)	**30 cm**	**Sand**	B8_S_30	El Banco 8	6
			Sand	B10_S_30	El Banco 10	
			Concrete	B1_S_30	El Banco 1	
			Sand	B7_S_30	El Banco 7	
			Sand	B5_S_30	El Banco 5	
			Sand	B9_S_30	El Banco 9	
		50 cm	**Sand**	B5_S_50	El Banco 5	2
			Sand	B7_S_50	El Banco 7	
	Vegetation (North)	**30 cm**	**Sand**	B3_V_30	El Banco 3	5
			Vegetation	B6_V_30	El Banco 6	
			Vegetation	B9_V_30	El Banco 9	
			Vegetation	B5_V_30	El Banco 5	
			Vegetation	B4_V_30	El Banco 4	
		50 cm	**Concrete**	B1_V_50	El Banco 1	7
			Vegetation	B10_V_50	El Banco 10	
			Vegetation	B5_V_50	El Banco 5	
			Sand	B3_V_50	El Banco 3	
			Vegetation	B6_V_50	El Banco 6	
			Vegetation	B7_V_50	El Banco 7	
			Vegetation	B9_V_50	EL Banco 9	
Hawaii	Sand (Middle)	**30 cm**	**Sand**	H7_S_30	Hawaii 7	4
			Sand	H10_S_30	Hawaii 10	
			Sand	H8_S_30	Hawaii 8	
			Sand	H2_S_30	Hawaii 2	
	Vegetation (North)	**30 cm**	**Sand**	H1_V_30	Hawaii 1	2
			Vegetation	H7_V_30	Hawaii 7	
		50 cm	**Vegetation**	H7_V_50	Hawaii 7	3
			Vegetation	H6_V_50	Hawaii 6	
			Vegetation	H10_V_50	Hawaii 10	



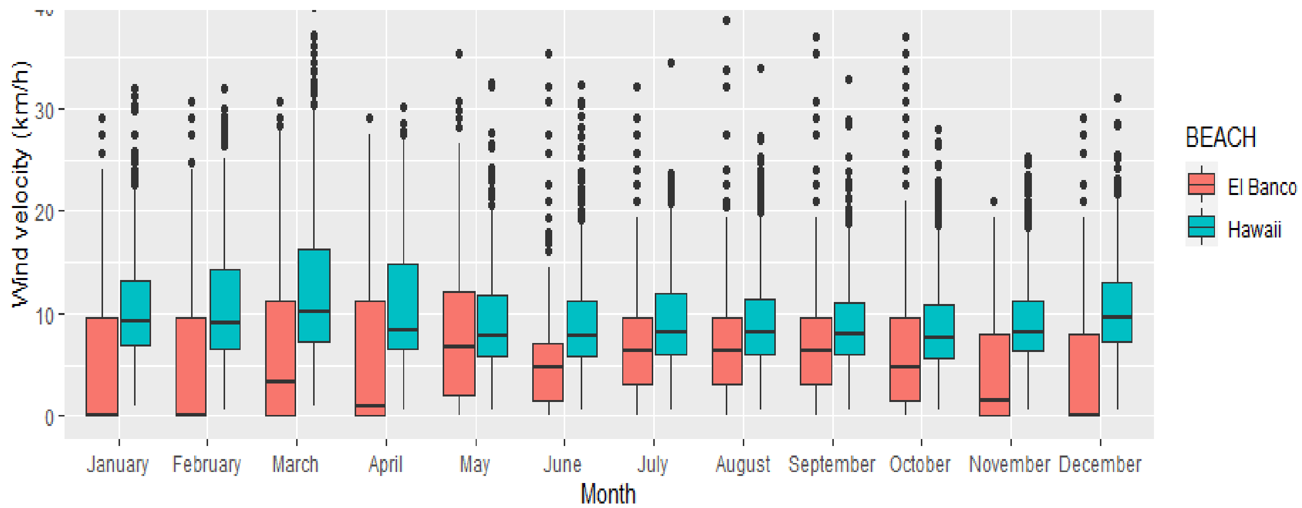
Supplementary Figure 1. Box plot showing measured air temperatures for the beaches El Banco and Hawaii from historical weather data at nearby weather stations through 2019. La Candeleria for the El Banco transect, and La Maquina for the Hawaii transect. The box plot shows median values (black horizontal line), 25 th and 75th percentile.



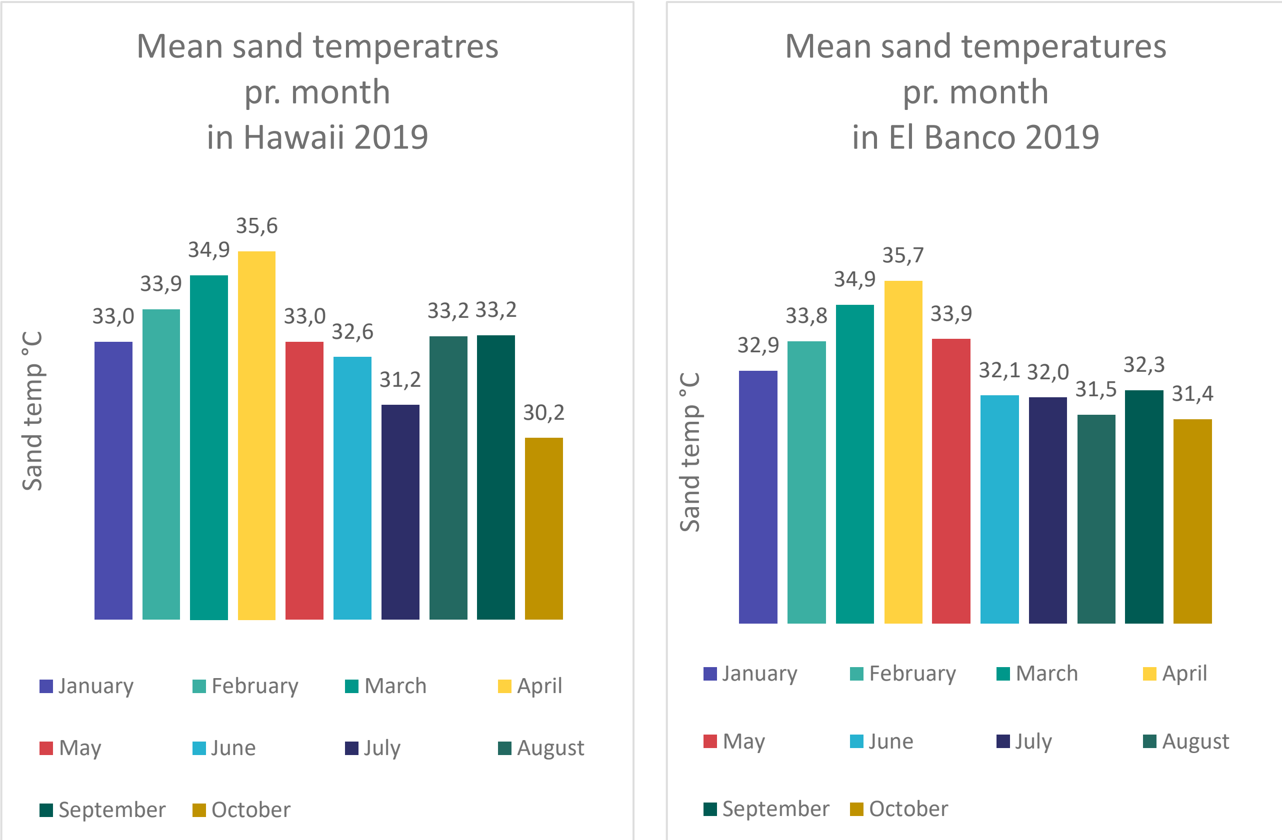
Supplementary Figure 2. Scatter plot showing measured precipitation for El Banco and Hawaii from historical weather data at nearby weather stations through 2019. La Candeleria for the El Banco transect, and La Maquina for the Hawaii transect.



Supplementary Figure 3. Box plot showing measured solar radiation (w/m2) for El Banco and Hawaii from historical weather data at nearby weather stations stations through 2019. La Candeleria for the El Banco transect, and La Maquina for the Hawaii transect.



Supplementary Figure 4. Box plot showing measured wind velocity (km/h) for El Banco and Hawaii from historical weather data at nearby weather stations stations through 2019. La Candeleria for the El Banco transect, and La Maquina for the Hawaii transect.



Supplementary Figure 5. Calculated mean sand temperatures pr. month in El Banco and Hawaii in 2019