

Nesting preferences of the green sea turtle (*Chelonia mydas* L.) and the hawksbill sea turtle (*Eretmochelys imbricata* L.) in the SW of Mahe Island in the Seychelles

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Abstract

Nesting preferences of the green sea turtle (Chelonia mydas L.) and the hawksbill sea turtle (Eretmochelys imbricata L.) in the SW of Mahe Island in the Seychelles. Data concerning 212 turtles emerging on the southwest beaches of Mahe Island in the Seychelles were collected in 2017 and 2018. These data were used to model the probability of eggs being laid in relation to several variables. The probability of successful laying after emergence was highest on certain beaches and in areas of short vegetation, between open sand and trees. We found successful laying was related to the physical properties of the soil, indicating that survivability of embryos and hatchlings is higher in certain areas. The turtles appeared to choose zones where soil had low salinity, good drainage but ability to retain water, and absence of spring tides and extreme temperatures.

Key words: Nesting behaviour, Sea turtle, Seychelles, Soil properties

Resumen

Preferencias de la tortuga verde (Chelonia mydas L.) y la tortuga Carey (Eretmochelys imbricata L.) con respecto al anidamiento en el suroeste de la isla Mahé en las Seychelles. Los datos relativos a las 212 tortugas que llegan a las playas del suroeste de la isla Mahé de las Seychelles se recopilaron en 2017 y 2018 y se utilizaron para determinar la probabilidad de que se pongan huevos en función de distintas variables. Se encontró que la probabilidad de que la puesta sea exitosa después de la llegada es mayor en ciertas playas y en la zona de vegetación baja entre la arena y los árboles. Se estableció una relación con las propiedades físicas del suelo y se dedujo que las zonas elegidas favorecen la supervivencia de los embriones y las crías. Aparentemente, las tortugas eligieron zonas donde el suelo tenía poca salinidad y buen drenaje, aunque mantenía cierta capacidad para retener la humedad, y que quedaban resguardadas de las mareas vivas y las temperaturas extremas.

Palabras clave: Comportamiento de anidación, Tortuga marina, Seychelles, Propiedades del suelo

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Introduction

The Seychelles comprise around 150 granitic and coralline islands, believed to have been formed from the breakup of the supercontinent Gondwanaland in the Pre-cambrian (Salm, 1978). Mahe is the main island, located in the centre of a granitic group and characterised by a very narrow coastal plateau of calcareous reef materials building up as sand dunes and pocket beaches known as 'anse'. The two types of prevailing soil are the ferrolithic of granitic weathering origin with clay rich A and B horizons and a fine texture, and the calcareous coarse sands areas close to the sea (Government of Seychelles, 2006). Mahe has many small, steep watercourses, most of which have ephemeral flow that depends on monsoons, and subterranean water may contain traces of salt. (FAO, 2005).

Overexploitation of turtle and chelonian products in the Seychelle Islands contributed to the decline of sea turtles. Since the early 1970s, positive measures of protection have led to the recovery of the main species of sea turtles in the archipelago: the green turtle (*Chelonia mydas* L.) and the hawksbill turtle (*Eretmochelys imbricata* L.) (Frazier, 1974). Numbers remained low in the 1980s and 90s (Mortimer et al., 1996) but appear to have increased in the recent decades (e.g. Mortimer et al., 2003; Allen et al., 2010). Nevertheless, worldwide, green and hawksbill turtles are listed as endangered and critically endangered, respectively, by the International Union for Conservation of Nature Red List of Threatened Species since 1996 (IUCN, 2015).

Turtle reproduction has been affected by several environmental factors. Temperature, moisture and gaseous environment are of fundamental importance and are determinants of gender, embryo growth and hatchability (Júnior, 2009). The porosity of the turtle eggshell enables interaction between the embryo in the interior of the shell and the environment in the exterior. This porosity allows exchanges of fundamental importance for successful incubation (Ackerman, 1997). Ackerman (1997) reviewed the relationship between the embryonic development of the sea turtle and the nest environment in detail. He observed that possible survival of an egg clutch of sea turtles depended on the capacity of the female to select an optimal area and excavate a suitable nest chamber. The author considered climate, soil texture, drainage and salinity with water potential, gas exchange and temperature all played a role in hatchability and therefore in nest site selection. More recently, other authors, such as Miller et al. (2017), have revised the topic.

Together with a panel of worldwide experts on sea turtles, Hamann et al. (2010) established key priority topics of research for their management and conservation, the first (Q1) of which was 'factors that underpin nest site selection and behaviour of nesting turtles'. In a review of the pertinent literature, these authors identified 'the factors (biotic and abiotic) driving where and when turtles lay their clutches', and 'management strategies that would help to protect or enhance the suitability of nesting habitat for sea turtles', as aspects

of particular interest to address this key priority area of research. In a study of nest site selection, Dittmer and Stapleton (2012) highlighted the need for future research to explore the roles of sand structure, nest moisture, and local weather conditions.

Rees et al. (2016) reviewed how these key priority areas were being addressed in relation to Q1. Several authors have published studies on this topic (e.g. Neeman et al., 2015; Santos et al., 2016). However, they state that there remains a lack of understanding regarding how turtles select the nesting sites at intra and inter beach level.

In our study, we attempted to establish a relationship between nest site selection, the microenvironment of the site, and the edaphoclimatic variables of the southwest beaches of Mahe Island. The aim of was to contribute to the previously cited key priority area of research. Mahe is the largest of the Seychelle Islands, and it has the highest population density, especially around beaches, as tourism is an important local industry. Knowledge generated from this study could contribute to the establishment of priority areas of protection and conservation, stimulating the sustainability and coexistence of humans and turtles.

Material and methods

Between 13 XI 17 and 11 I 18 we collected data regarding 212 turtles emerging on the southwest beaches of Mahe Island in order to evaluate the probability of eggs being laid.

The beaches considered were located (from north to south) in: Anse Intendance (INT) at 4°47'05" S, 55°30'00" E; Anse Cachee (CAC) at 4°47'44" S, 55°30'20" E; Anse Corail (COR) at 4°47'49" S, 55°30'30" E; Anse Bazarca (BZC) at 4°48'02" S, 55°30'50" E; Anse Petit Police (PPO) at 4°48'10" S, 55°31'03" E; Anse Grand Police (GPO) at 4°48'09" E, 55°31'19" E; and Anse Petit Boileau (APB) at 4°48'06" S, 55°31'42" E.

Beaches were monitored every morning between 8 a.m. and 2 p.m. and the following variables were recorded for every turtle emerging: the each, progression inland (measured as distance to high tide line), eggs laid (yes, no), and zone of the beach at maximum progression and eventual lay (open sand, shrub, or trees). The exact location of the nest was also recorded by GPS, as were variables regarding the vegetation covering the soil: percentage of ground or canopy cover and dominant species.

A generalised linear model from the binomial family was used to model egg laying probability. The dependent variable considered was the success or failure of laying after each emergence. The independent variables investigated were the beach (INT, CAC, COR, BZC, PPO, GPO, and APB), the zone of the beach (open sand, bushes and trees), distance to high tide and the variables related with vegetation. Several link functions were tested (logit, log, log complement, negative log-log and complementary log-log) with the best fit after evaluation of Deviation and the Akaike's Information Criterion being chosen as the model.

Table 1. Parameters of model 1. Probability of a turtle laying eggs after an emergence depending on the beach and the distance to high tide. Deviance was 116 and AIC 132: SE, standard error; CI, confidence interval; OR, odds ratio; DHT, distance to high tide. Studied beaches: CAC: Anse Cachee; INT: Anse Intendance; GPO: Anse Grand Police; PPO: Anse Petite Police; APB: Anse Petite Boileau; BZC: Anse Bazarca; COR: Anse Corail.

Tabla 1. Parámetros del modelo 1. Probabilidad de que una tortuga ponga huevos después de llegar a una playa, en función de la playa y de la distancia a la marea alta. La desviación fue 116 y AIC 132. (Para las abreviaturas, véase arriba).

Variables		β	SE (β)	<i>P</i> -value	95% CI (β)	OR (<i>e</i> β)	95% CI OR (<i>e</i> β)
Beach	CAC	1.165	0.764	< 0.05	0.401; 1.929	3.206	1.493; 6.883
	INT	0.849	0.765	0.084; 1.614		2.337	1.088; 5.023
	GPO	0.816	0.579	0.237; 1.395		2.261	1.267; 4.035
	PPO	0					
	APB	0.064	0.790	-0.726; 0.854		1.066	0.484; 2.349
	BZC	-0.211	0.547	-0.758; 0.336		0.810	0.469; 1.399
	COR	-0.377	0.581	-0.958; 0.204		0.686	0.384; 1.226
DHT (m)	0.738	0.041	< 0.05	0.697; 0.779		2.092	2.008; 2.179

Data were analysed using IBM® SPSS® Statistics for Windows, version 21.0. (IBM Corp., Armonk, NY, USA, 2012). Variables were selected for inclusion in the model through a forward stepwise procedure. The significance of the variables was evaluated using the Wald Chi-square test. The significance of the fitted model was evaluated by means of the likelihood ratio Chi-square test. All significance levels were set to $P < 0.05$.

Results

A first model was successfully fit ($P < 0.01$) with a negative log-log link, with the variables 'beaches' ($P < 0.05$) and 'distance to high tide' ($P < 0.05$) being found significant. A higher distance to the high tide (higher progression into the land) determines a higher probability of laying success. A second model was also successfully fit ($P < 0.01$), again with a negative log-being significant. We observed that the more distant the zone of the beach from the water, the higher the probability of laying. Therefore, both models were similar correlating successful laying behaviour with higher progression inland.

Tables 1 and 2 present the details of the model parameter estimates. Figure 1 is the graphic representation of model 1 with equation:

$$P(\text{laying}) = \text{Exp}(-\text{Exp}(-X_1 + X_2 \times D))$$

where X_1 is the parameter for 'beach', X_2 the parameter for distance from the high tide and D the 'distance to high tide'. Figure 2 is the graphic representation of model 2 with equation:

$$P(\text{laying}) = \text{Exp}(-\text{Exp}(-X_1 + X_2))$$

where X_1 is the parameter for 'beach' and X_2 the parameter for 'zone of the beach'.

Discussion

Incubation and hatchability of eggs is directly dependent on temperature, humidity, and the exchange of gases (Ackerman, 1997; Júnior, 2009). Refsnider and Janzen (2010) described oviposition site choice in several species as a major maternal effect factor affecting survival and phenotype of offspring. They considered that this maternal effect can be observed in fish, amphibians, reptiles and birds and described six hypotheses to explain the behaviour: maximization of embryo survival, maximization of maternal survival, modification of offspring phenotype, proximity to suitable habitat for the offspring, maintenance of natal philopatry, and factors related to mate choice. From these, only mate choice can be eliminated once turtles lack paternal care (Kamel and Mrosovsky, 2005).

In this discussion, we argue that the probability of successful laying after turtle emergence is positively correlated with the probability of the female turtle finding a place with a suitable microenvironment for laying, as hypothesised by Ackerman (1997) and suggested by Kamel and Mrosovsky (2005). In addition to the arguments made by these authors we relate site selection with the potential microenvironment of the clutch. The relation is established through the study of the physical properties of the soil with influence on the environmental variables, determining incubation and hatchability.

Table 2. Parameters of model 2. Probability of a turtle laying eggs after an emergence in relation to the beach and zone of the beach. Deviance was 111 and AIC was 129. SE: standard error; CI: confidence interval; OR: odds ratio; HT: high tide. Zones A, B, C are respectively open sand, shrub and tree zones. (For other abbreviations, see table 1).

Tabla 2. Parámetros del modelo 2. Probabilidad de que una tortuga ponga huevos después de llegar a una playa, en función de la playa y de la zona de la playa. La desviación fue 111 y AIC 129. (Para las abreviaturas, véase arriba y la tabla 1).

Variables		β	SE (β)	<i>P</i> -value	95% CI (β)	OR ($e\beta$)	95% CI OR ($e\beta$)
Beach	CAC	1.684	0.788	< 0.05	0.139; 3.229	5.387	3.188; 7.586
	INT	1.176	0.793		-0.379; 2.731	3.241	1.031; 5.451
	GPO	1.557	0.699		0.187; 2.928	4.745	2.733; 6.756
	PPO	0					
	APB	0.199	0.785		-1.340; 1.737	1.220	-0.972; 3.413
	BZC	0.075	0.581		-1.063; 1.213	1.078	-0.710; 2.866
	COR	-0.142	0.670		-1.255; 1.171	0.868	-1.087; 2.822
Zone	A	-1.208	0.656	< 0.05	-2.493; 0.078	0.299	-1.628; 2.226
	B	0.124	0.492		-0.841; 1.088	1.132	-0.504; 2.768
	C	0					

The relation between the variables in our models and clutch microenvironment

Relatively to distance to the high tide, the first model relates the increase in laying probability with turtle progression inland. In the second model, however, with distance entered in the analysis as 'zones of the beach', this probability decreases slightly, but without a significant difference ($P > 0.05$) if the area with trees (longer distance) is reached, increasing from open sand (shorter distance) to the shrub zone (intermediary distance). While studying the nesting behaviour of the green turtle on a beach of the Guanahacabibes Peninsula, southwest of Cuba, Sánchez et al. (2007) found that the majority of successful laying after emergence also took place in the zone of vegetation after the open sand (75.3% and 73% respectively in 2002 and 2003). This was also the case in the study of Neeman et al. (2015), with 88.3% in Tortuguero, Costa Rica. Neeman et al. (2015) also raised the hypothesis of choice due to optimal moisture and temperature. Santos et al. (2016) studied similar models and found some variation, however, but they refer to consistency as their main findings. They studied the behaviour over eight seasons and found the same turtle tended to prefer the same beach ecosystem. While researching on the Sunshine Coast of Eastern Australia, Kelly et al. (2017) also concluded nesting preference close to vegetation, as did Hatase and Omuta (2018) in their studies on Yakushima Island, Japan.

The physical properties of the soil in these three different zones vary. In open sand, the soil has a coarse texture and may be within reach of the seawater,

especially in spring tides. It is easy here for both turtle and hatchling to dig, respectively, in and out of the nest. The soil of the tree zone also has a sandy texture at the top, but is richer in organic matter and has some clay, as the typical ferrolitic soil, which is rich in clay, is closer to the surface. The tree zone has dense vegetation with strong rooting systems, making digging difficult. The shrub zone has intermediary characteristics, the transition between sand and sand richer in clay and organic matter, with clay in a deeper layer and sand with organic matter from the vegetation in the superficial layer. The different characteristics of the soils are responsible for different physical properties.

Moisture

Sands have a coarse texture with macro porosity, allowing excellent drainage, but capacity for water retention is low. In consequence, nests may become exposed to long dry periods with the moisture levels dropping below optimum levels. On the other hand, if the nest is placed too near seawater, it may be inundated by waves, leaving the clutch exposed or washing it away (Diamond, 1976; Kraemer and Bell, 1980).

The fine texture of clay rich soils has a lower density and therefore greater porosity (micro pores are not normally perceived). This micro-porosity, where the capillarity force may overtake the gravity force, allows water to move vertically and horizontally, contributing to the maintenance of moisture levels. These soils have a higher capacity for water retention, but drainage tends to be relatively poor, and with intense

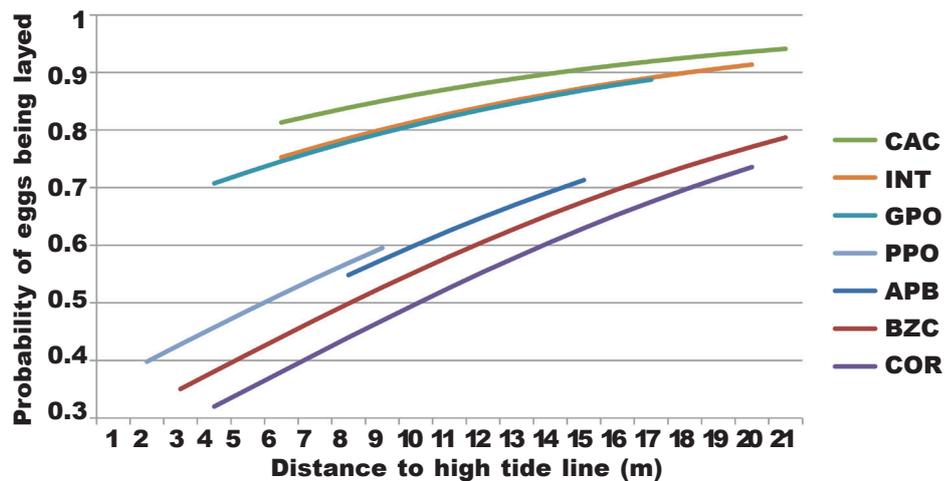


Fig. 1. Probability of a turtle laying eggs after an emergence depending on beach and distance to high tide (m). (For abbreviations of studied beaches see table 1).

Fig 1. Probabilidad de que una tortuga ponga huevos después de llegar a una playa, dependiendo de la playa y de la distancia a la marea alta (m). (Para las otras abreviaturas de las playas estudiadas, véase la tabla 1).

rain they may easily be flooded and cause hatching failure due to embryo death (Wood, 1986). A nest in clay is also very difficult for a turtle to create and very difficult for a hatchling to dig out of.

The transition soils have a lower layer with clay and an upper level with sand and organic matter. A clutch located in this type of soil is covered by the sandy

horizon and is relatively close to a clay layer. Moisture can reach the upper horizons from below and levels above the wilting point and below saturation can be expected. The top soil horizon, rich in sand, allows water to flow, and the level that is relatively higher relatively to the beach allows drainage to occur, if the clay horizon reaches saturation.

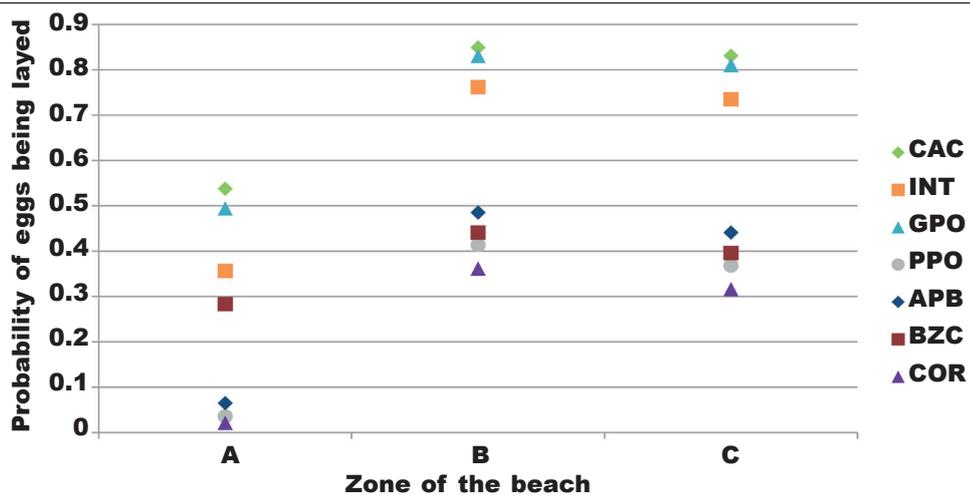


Fig. 2. Probability of a turtle laying eggs after an emergence depending on beach and zone of the beach. Zones A, B, C are respectively open sand, shrub and trees. (For abbreviations of studied beaches, see table 1).

Fig. 2. Probabilidad de que una tortuga ponga huevos después de llegar a la playa, en función de la playa y de la zona de la playa. Las zonas A, B y C son, respectivamente, de arena, de arbustos y de árboles. (Para las abreviaturas de las playas estudiadas, véase la tabla 1).

Table 3. Typical values of thermal conductivity (TC) and thermal diffusivity (TD) (NERC, 2011).

Tabla 3. Valores típicos de conductividad térmica (TC) y difusividad térmica (TD) (NERC, 2011).

Soil	TC $\text{Wm}^{-1}\text{K}^{-1}$	TD $\text{m}^2\text{day}^{-1}$
Sand	0.77	0.04
Clay	1.11	0.05
Saturated sand	2.50	0.08
Saturated clay	1.67	0.06

Temperature

Water has a higher specific heat than soil, and therefore a higher capacity to store heat; this property also prevents rapid changes in water temperatures (Reysa, 2012). The thermal conductivity (the rate at which heat is transferred to the surroundings) of soil is dependent on bulk porosity and the degree of soil saturation; the same occurs for thermal diffusivity (the rate at which heat is transmitted through the medium) (NERC, 2011). Table 3 shows the typical values for these thermal properties of soil in relation to texture and moisture.

As observed, without moisture, clay has a high capacity to gain and lose heat more quickly. However, with moisture (the required conditions for optimum incubation), this is not the case. In humid sandy soils, temperature fluctuates between high levels during the day and low levels at night. In clay rich soils with a higher moisture percentage, temperature fluctuation is minimized and a stable temperature is achieved. Zones with vegetation can also protect the top soil with shade from extreme irradiation, therefore preventing scorching temperatures from reaching the clutch, as opposed to dry top layers of open sands. Incubation temperatures are profoundly influenced by the environment, such as air temperature, vegetation and sand albedo due to the colour (Esteban et al., 2016).

Clutch average depth was reported for the green turtle in the Lanyu Island of Taiwan, to be 66 cm (Cheng et al., 2009) or 85 cm in the bottom in Ascension Islands (Mortimer, 1990). For hawksbill turtles, Ditmer and Stapleton (2012) reported an average of 48 cm. From 50 cm depth, however, heat flow in the soil is minimal and soil temperature stabilizes around the daily average temperature at surface (Lavelle and Spain, 2003).

Exchange gases

The soil atmosphere is determined by the space left by porosity and eventual presence of moisture occupying that space. Sandy soils provide good circulation of air and water, while clay rich soils have

a higher probability of having some of the porosity occupied by water. The presence of vegetation is responsible for the existence of macro-porosity in clay rich soils, caused by root penetration. Richer soils with clay and organic matter also have a higher degree of particle aggregation, responsible for a good soil structure that creates macro pores, promoting good atmospheric circulation. Sandy soils very close to seawater run the risk of flooding in spring tides, removing all the air from the soil porosity and creating conditions for egg drowning (Diamond, 1976; Kraemer and Bell 1980). The same can happen in soils with poor drainage in heavy rain conditions (Kraemer and Bell, 1980; Wood, 1986)

Salinity

Soil salinity is expected to decrease the greater the distance from high tide. Seawater loses influence and freshwater from rain and freshwater courses washes out the salt from the soil. Salinity in soils causes chemical deflocculation of clays, with destruction of soil aggregation of particles and overall structure (Goldberg and Glaubig, 1987). The clay is dispersed, the structure becomes cloddy, the pores are plugged and the soil becomes very hard. As a result, the circulation of air and water decreases and a sub-superficial impermeable layer of deflocculated clay may drown the clutch. On the other hand, if drainage is not a problem, salinity may also be responsible for an opposite effect; an increased osmotic potential surrounding the clutch may create difficulties for egg water absorption, and may promote the loss of water from the egg interior, which may result in desiccation (Ackerman, 1997).

The clutch microenvironment during incubation

The nesting season of sea turtles in the Seychelles starts in August or September and continues until February or March (Diamond, 1976) or until April (Wood, 1986). During this time the climate in the Islands is temperate, between the cold season (mid-June to mid-May) and the warm season (mid-March to mid-May). Temperatures fluctuate between minimums of 25 to 26 °C, and maximums of 29 to 30 °C; precipitation has a high probability (88%) of being moderate to light; relative humidity varies in the season below daily average minimums of 65 to 73% and maximums of 90 to 95% (WeatherSpark, 2014).

Beach temperatures vary depending on seasonal effects and the diurnal cycle. However, at 50 cm depth, nocturnal/diurnal effects are mitigated and the temperature tends to have lower variability and approach the average environmental temperature (Lavelle and Spain, 2003). This is especially true if moisture levels are maintained high (Ackerman, 1997).

Incubation temperatures of sea turtles range between a minimum of 25–27 °C and a maximum of 33–35 °C (Ackerman, 1997); below 25 °C and above 33 °C embryos may die (Miller, 1982).

Like other reptiles, sea turtles are affected by environmental sex determination (Mrosovsky et

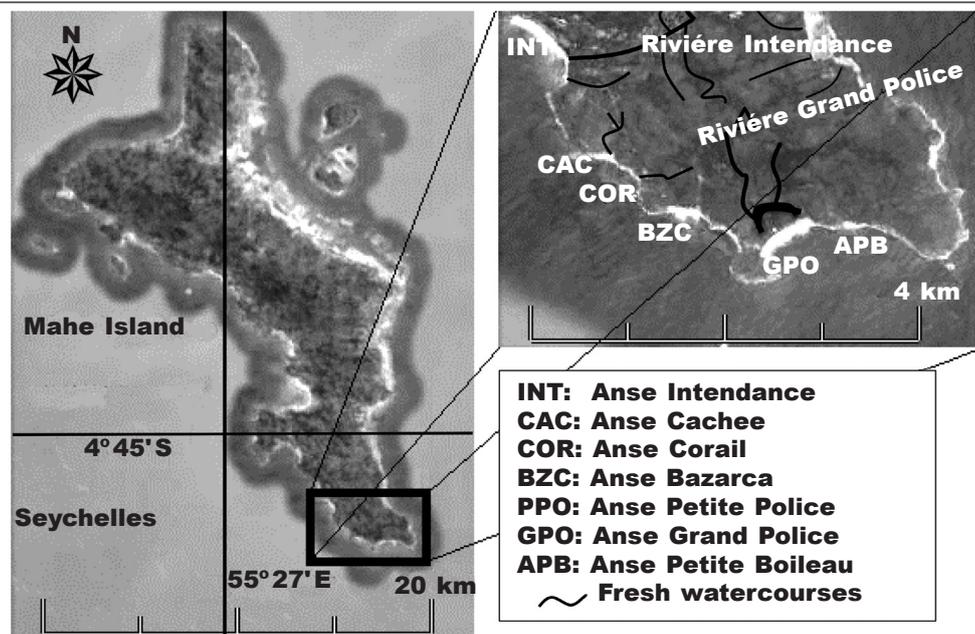


Fig. 3. Mahe Island, Seychelles. Expanded SW corner with beaches and local watercourses considered in the study.

Fig. 3. Isla Mahé, en las Seychelles. Esquina sudoccidental ampliada donde se pueden observar las playas consideradas en el estudio y los cursos de agua locales.

al., 1992). Pivotal temperatures (males above and females below) for hawksbill and green turtles were reported respectively as 29.32°C and 28.26°C (Ackerman, 1997).

Water exchange in turtle eggs is dependent on factors such as the structure of the eggshell, the water potential and temperature in the nest (Packard, 1999). An embryo with access to a good reserve grows to a larger size at hatching and has better survival conditions (Tracy et al., 1978; Packard, 1999). Also, if the absorption of water is higher than water loss, shrinking of the original egg shape is avoided, thereby ensuring enough space for normal embryo development (Tracy et al., 1978). A higher level of nest humidity is therefore advantageous (Packard, 1999).

Sea turtle eggs depend on humidity uptake from the surrounding environment (Miller et al. 2017), and according to McGehee (1990), it is convenient for the turtle to lay at a minimum soil humidity of 25%. High levels of humidity may drown the embryo (Wood and Bjorndal, 2000) and low levels cause desiccation (McGehee, 1990). In the breeding season, it is therefore expected to find ideal conditions for incubation at nesting depth with a good moisture level and the temperature levels reported.

What is the turtle best place to lay?

It is important for the turtle to find a place that guarantees the right levels of humidity, temperature and gas exchange. According to the soil properties

discussed, a clutch laid close to the tree zone is ideal as the texture is thinner, sand is not so coarse, and organic matter and clay are present. This type of soil allows the nest to be dug deep enough for the walls to be firm and not collapse. This soil has also a fair water retention capacity without compromising drainage and allows air circulation. While studying nesting behaviour of green turtles at Ascension Island Mortimer (1990) found that a lower mean particle diameter of the soil with higher water potential was associated with higher laying and hatching success and lower mortalities.

Another important aspect is salinity. Water exchanges are especially sensitive to the substrate water potential (Tracy et al., 1978). Turtles would be looking for a place with low levels of salinity to facilitate a positive water exchange between eggs and soil. This may explain the differences in the probabilities of successful laying after emergence in the different beaches. As can be observed in figure 3, Anse Intendance, Anse Grand Police and Anse Cachee are the only beaches that are fed by fresh watercourses, possibly accounting for the lower levels of salinity in the nesting areas of these beaches. While studying the green turtle, Johannes and Rimmer (1984) found that the mean salinity of the sand moisture in nesting beaches was half that of the non-nesting beaches in NW Cape Peninsula, Australia.

In favour of the theory that turtles actively evaluate a nesting place is the study by Hitchins et al. (2006) on hawksbill turtles in the Cousine Island of the

Seychelles. They found that when emerging, turtles not attempting to nest cover a shorter mean distance on land than those successfully or unsuccessfully attempting nesting. Also when crawling from the sea to the nest site, distances were longer and covered more slowly than those when crawling back to the sea. Studying the effect of experience on nest-site selection in loggerhead turtles in Queensland Australia, Pfaller et al. (2008) found that nesting-experienced females selected nest sites more successfully than those with little or no experience. The authors justify the behaviour with habituation to innocuous beach stimuli that encourage turtles to crawl farther from the sea in search of a nesting site. Sánchez et al. (2007) reported that the majority of the returns to the same beach happened with turtles laying in the vegetation area, which is the prime choice zone for laying in the beaches studied, and therefore turtles that previously identified a good laying place tended to return.

In conclusion, these findings to date allow an approach to the response to a key research question in sea turtles, as identified by Hamann et al. (2010) 'Why do turtles breed successfully at specific beaches and specific zones of the beach?'. They follow by saying this knowledge 'could lead to management strategies that maximise hatchling production in particular areas'.

The present study has the main limitation that environmental variables were not directly measured but deduced. Further research is needed to follow up on the results herein. Specifically, the environmental variables in nesting and non-nesting sites should be studied in greater depth. It is also evident that although the laying probability is higher at certain sites it is not null at others. Conservation efforts should centre attention on areas of higher laying probability but should not dismiss other areas, and eventual relocation of nests should be considered to improve hatchability. Relocation to more convenient sites would also have the advantage of concentrating hatching, allowing the establishment of zones of protection against predation, and thereby improving survivability.

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