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Nest site selection repeatability of green turtles, *Chelonia mydas*, and consequences for offspring

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Nest site selection is a critical behaviour, particularly in species with no parental care, as it can greatly impact offspring survival. Marine turtles depend on sandy beaches to nest, where they select from a range of microhabitats that may differently affect hatchling survival and phenotype. Here we describe the degree of nest site selection at one of the largest green turtle rookeries globally, in Guinea-Bissau, West Africa, and how this impacts offspring. In 2013 and 2014 we recorded the spatial distribution of 1559 nests, and monitored 657 females during oviposition, to assess population and individual preferences on nesting site. Overall, females tended to nest close to the vegetation, at a preferred elevation of 4.8–5.0 m, which was above the highest spring tide (4.7 m), enhancing clutch survival. Individuals displayed high repeatability in nesting microhabitat type (open sand, forest border and forest), distance along the beach, distance to the vegetation and elevation, which may result from this behaviour having a genetic basis or from fine-scale nest site philopatry. Hatchlings from cooler nests were larger, potentially dispersing faster and more able to evade predators, while smaller hatchlings, from warmer nests, retained more energetic reserves (residual yolk), which may also be advantageous for initial dispersal, particularly if food is scarce. Thus, individual preferences in nest site selection led to trade-offs in offspring phenotype, but overall, most nesting females selected sites that increased offspring survival, suggesting that nest site selection is an adaptive trait that has been under selection. As under future climate change scenarios females nesting in upper shaded areas should have higher fitness, individual consistency in nesting microhabitat provides opportunity for natural selection to occur.

Nest site selection is a key behaviour, because the surrounding environment can greatly impact offspring survival and phenotype (Spencer, 2002). This is particularly true in species without parental care, for which nest site selection is essentially the last step in parental investment. Marine turtles are an example of such species, as females lay multiple clutches each breeding season, typically every 2–4 years, and show no parental care (Ehrhart, 1982). Reproductive females usually exhibit natal philopatry, returning to their beach of origin to nest (Meylan, Bowen, & Avise, 1990). Upon emergence at the beach, however, nest site selection may be influenced by microhabitat conditions, most significantly beach morphology, dune vegetation and sediment attributes (e.g. sand temperature, moisture, grain size, Kelly, Leon, Gilby, Olds, & Schlacher, 2017). Preferences can differ between species and populations (Kelly et al., 2017), yet a range of microhabitats is often used, each differently affecting clutch success (Kamel & Mrosovsky, 2004; Pfaller, Limpus, & Bjorndal, 2009).

Clutches laid closer to the sea will be more vulnerable to tidal inundation and erosion, while those near the vegetation may have roots piercing through the eggs or entangling hatchlings (Kamel & Mrosovsky, 2004). Also, a higher risk of misorientation is predicted for hatchlings emerging in forested areas at the back of the beach (Godfrey, Barreto, & Mrosovsky, 1996; Kamel & Mrosovsky, 2004). On the other hand, shaded areas promote lower incubation temperatures leading to larger hatchlings with superior locomotion

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abilities (Booth & Evans, 2011; Kobayashi, Wada, Fujimoto, Kumazawa, & Arai, 2017; Wood, Booth, & Limpus, 2014). Additionally, as sea turtles have temperature-dependent sex determination (Mrosovsky & Yntema, 1980), the nesting site will further determine the sex of hatchlings. Thus, nest site selection may involve trade-offs in hatchling fitness, which can shift under changing environmental conditions. Overall, population level preferences for nesting site, observed in different species, seem to benefit offspring survival (Spencer & Thompson, 2003; Turkozan, Yamamoto, & Yilmaz, 2011; Zare, Vaghefi, & Kamel, 2012), suggesting that nest site selection is an adaptive trait.

Individual fidelity in nest site selection has also been observed in some turtle species, using repeatability analysis (Spencer & Thompson, 2003; Kamel & Mrosovsky, 2004, 2005, 2006). Such behaviour, under spatially variable threats, could accelerate natural selection if only a few females consistently select conditions that increase the fitness of their offspring. However, knowledge of individual nest site selection among sea turtles, its consequences for fitness and its evolutionary potential is still very limited (but see Hays & Speakman 1993; Kamel & Mrosovsky, 2004, 2005, 2006). The evolution of a behaviour, or of any trait, is a result of both selection on phenotypic variation and inheritance of the variants (Fisher, 1930). In the context of selection, repeatability is directly useful, as it measures the proportion of total variation that is due to differences between individuals (Falconer & Mackay, 1996), therefore revealing the within-individual consistency (Boake, 1989). Regarding inheritance, a high heritability in a behavioural trait should correspond to high repeatability in this trait, and a statistically significant repeatability suggests potential for a genetic basis (Dohm, 2002).

Poilão Island, Guinea-Bissau, hosts one of the largest green turtle rookeries in the Atlantic, and worldwide, with an estimate of ca. 29 000 clutches laid annually (Catry, Barbosa, Paris, Indjai, & Almeida, 2009). The nesting microhabitat characteristics here vary across beach width and length (e.g. elevation, vegetation cover/shading and sand temperature), probably affecting offspring fitness differently. We investigated the nest distribution in this population and explored three questions. (1) Do females choose their nesting site randomly or based on specific microhabitat characteristics? (2) Are females repeatable in their nest site conditions? (3) How does nest site affect offspring survival and phenotype? The potential of this behaviour for selection and heritability is discussed.

METHODS

Study Site

Poilão Island (10.8°N, 15.7°W, Fig. 1), is part of the João Vieira and Poilão Marine National Park, in the Bijagós Archipelago, Guinea-Bissau, and it hosts one of the major green turtle nesting populations worldwide (Catry et al., 2002, 2009). Poilão has a total area of 43 ha, is covered by undisturbed tropical forest, and has sandy beaches extending for 2 km of the ca. 4 km of coastline. The island is surrounded by intertidal rocks (Fig. 1), which are exposed during low tide, blocking the access of nesting females to the beach and/or preventing them from returning to the sea, at the risk of getting stranded and dying of hyperthermia or desiccation. Thus, the temporal pattern of nesting activity at Poilão is centred on the peak of high tide, lasting approximately 2–3 h each night. The nesting season extends from mid-June to mid-December, peaking in August and September (Catry et al., 2002), largely coinciding with the rainy season (May to November, Catry et al., 2002). For this study we monitored green turtle nesting activity during the 2013 and 2014 nesting seasons.

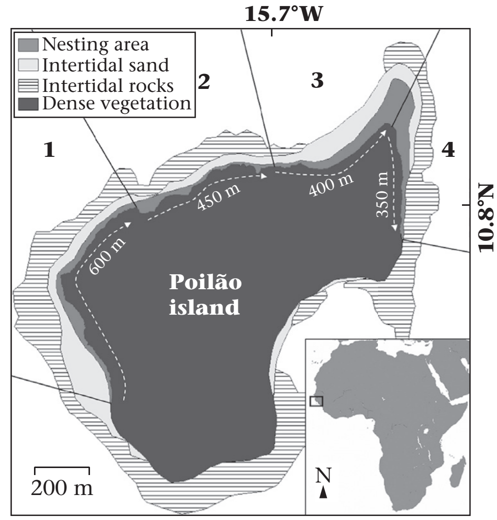

Figure 1. Map of study site: green turtle rookery at Poilão Island, Guinea-Bissau. The nesting beach is divided into four sections: 1: Farol; 2: Acampamento Oeste; 3: Acampamento Este; 4: Cabaceira. The island is surrounded by intertidal rocks, except at beach section 3.

Sampling Methods

Nesting distribution at the population level

The nesting area was divided into four beach sections, from west to east (1–4, Fig. 1). Within each section we classified the distribution of nests according to three microhabitats: ‘forest’, ‘forest border’ and ‘open sand’. The forest encompassed the nesting area under the vegetation and was shaded, the forest border comprised a band up to 1 m of the vegetation and experienced partial shade and the open sand characterized the area from >1 m of the vegetation to the high tide line (see Figure S1 in Patrício et al., 2017). Owing to the magnitude of nesting at Poilão, females mask one another's activities, precluding the identification of nests even in the following morning. Thus, to determine the nest distribution at the population level, we surveyed all females found laying on each of 3 nights in 2013 (407 nests) and 6 nights in 2014 (1152 nests), during the peak of the nesting season. During these focused assessments we surveyed all four beach sections, at high tide (see Catry et al., 2002), as fast as possible (typically < 1 h), to ensure that most females were detected. Only females that were laying, covering or camouflaging nests were counted, as otherwise turtles could still change their location or abandon nesting activity (Patrício et al., 2017). We recorded the GPS location of 1559 nests, using a hand-held GPS (Garmin GPSmap 62), assigning one of the three microhabitats to each of them. A chi-square test revealed that there was no significant difference in the nesting distribution across beach sections and microhabitats between years (Patrício et al., 2017). In Poilão, as in most sea turtle rookeries, the nesting females do not return to nest in subsequent years, (Hays, 2000); thus, as our sampling years represent independent samples, we pooled the data to describe the overall nesting distribution at Poilão.

Nesting microhabitat characteristics at the population level

Owing to the extent of nests monitored for the population level assessment, together with survey time constraints, we used remote sensing to measure nest distance to the vegetation line and nest surface elevation. From 11 to 12 November 2016 we flew a drone (35 m altitude), coupled with a digital compact camera, and took aerial photos of the nesting beach, with a minimum of 80% overlap,