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**POTENTIAL REFUGES FOR MALE PRODUCTION IN LOGGERHEAD
TURTLES WITHIN THE NORTHEAST ATLANTIC SUBPOPULATION**

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Female loggerhead turtle entering the sea in Maio Island, Cabo Verde

Title: Potential Refuges for Male Production in Loggerhead Turtles within the Northeast Atlantic Subpopulation

Declaration of authorship of work:

I declare that I am the author of this work, which is original and unpublished. Authors and works consulted are duly cited in the text and appear in the list of references included.

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Potential Refuges for Male Production in Loggerhead Turtles within the Northeast Atlantic Subpopulation

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ABSTRACT. – The variation in sand temperature between beaches is an important factor in sex determination in sea turtles. Rising temperatures due to climate change can cause a female-biased sex ratio in hatchlings. The importance of identifying microhabitats, which have potential to produce hatchlings with balanced sex-ratio should be a global priority in sea turtle conservation programmes. We evaluated the variation in nesting sand temperature between beaches and years at the maximum nesting depth (55cm) in an important nesting colony of loggerhead turtles (*Caretta caretta*) on the Maio island, Cabo Verde. The air as well as sand temperatures were monitored on three beaches with different sand colours (light, dark and mixed) during the breeding season of 2020, 2021 and 2022. The light sandy beach was cooler and recorded temperatures that favoured the production of male hatchlings at the beginning and end of the nesting seasons. The temperatures of dark and mixed sands were highly biased towards female hatchlings, reaching lethal levels for embryos. However, in short periods of heavy rain and flooding, the temperatures tend towards males in these types of sand. The observations thus reveal that there are few thermal microhabitats in this colony that are favourable to production of male hatchlings, located at the extremes of nesting periods and during extreme climate fluctuations.

KEYWORDS. – Incubation substrate, air and sand temperature, sex ratio, conservation, sea turtles, loggerhead turtles (*Caretta caretta*), Maio Island, Cabo Verde.

INTRODUCTION

Rising global temperatures are likely to affect sea turtles at many stages of their life cycle (Patrício et al., 2021). The egg incubation stage is one of the most vulnerable, because eggs develop successfully within a narrow range of incubation temperatures, from 27 to 33 °C (Ackerman, 1997; Fisher et al., 2014). Hatchlings incubating at higher temperatures becoming female and those at lower temperatures becoming male (Yntema & Mrosovsky, 1982; Standora & Spotila, 1985). The hatchling sex ratio can be approximately equal (50% males and 50% females) when the embryos are incubated at a temperature of 29.3°C, classified as the pivotal temperature (Mrosovsky & Pieau, 1991). In addition to sex determination, the incubation temperature directly affects incubation duration (Booth & Astill, 2001; Matsuzawa et al., 2002; Martins et al., 2020), hatching success, the success and pattern of emergence (Sim et al., 2015; Rivas et al., 2019; Martins et al., 2020), hatchling phenotype (Booth & Astill, 2001; Sim et al., 2015; Booth, 2017; Rivas et al., 2019; Martins et al., 2020), hatchling dispersal performance (Ischer et al., 2009; Mueller et al., 2019; Martins et al., 2020). Therefore, global warming is expected to cause highly female-biased sex ratios of hatchlings in many sea turtle populations, colonies and species (Fuentes et al., 2009; Hays et al., 2014; Santidrián-Tomillo et al., 2014; Jensen et al., 2018; Patrício et al., 2019; Tanner et al., 2019). However, the effect of the random choice of adult females for different beaches of different sand types for nesting (Patino-Martínez et al., 2022b), contributes to the variation in incubation temperature (Hays et al., 2003; Tanner et al., 2019), where there may be possible thermal refuges biased for males hatchlings (LeBlanc et al., 2012).

This study examines possible male-biased thermal refugia among the three main nesting sand types of female loggerheads in Cabe Verde (Tanner et al., 2019), at maximum nesting depth. This study was carried out in the volcanic archipelago of Cabe Verde, located 500 kilometres from Senegal in the Atlantic Ocean. The country is home to what may be the largest nesting subpopulation of loggerhead turtles in the world (Patino-Martínez et al., 2022a). The loggerhead turtle is classified by the IUCN as globally "Vulnerable" and regionally "Endangered" due to the ongoing decline in the area, extent and/or quality of its habitat (Casale & Tucker, 2017). This subpopulation has been identified as a separate genetic stock (Monzon-Arguello et al., 2010; Wallace et al., 2010) with multiple nesting groups within the colony (Stiebens et al., 2013; Baltazar-Soares et al., 2020). The island of Maio hosts a significant proportion of this subpopulation's annual

nests, with 4,063-46,160 (average 15,440) annual nests between 2016 and 2022. This study compared sand from three different beaches and assessed: 1. the variation in average daily temperature at 55cm depth between three nesting seasons; 2. the relationship between the variation of the daily average air and sand temperatures.

METHODS

Study Area. — Fieldwork was carried in Maio Island, Cabo Verde (Fig. 1a; 15°13'24.2"N 23°9'28.9"W), during the nesting seasons (1 July to 17 November) of 2020, 2021 and 2022. The study beaches have a natural variation in the type of sand: light (Morro; Fig. 1c), black (Pajuana; Fig. 1d) and mixed (Ribeira Baía; Fig. 1e). The beaches studied have the following measurements: Morro measures 4050m in length and an average width of 90m, Pajuana measures 168m in length and an average width of 19m and Ribeira Baía measures 238m in length and an average width of 25m. The average width was measured from the low-water line to the dune vegetation (*Zygodphyllum waterlotii* and *Suaeda vermiculata*). These are undeveloped and undisturbed beaches, with no light pollution and minimal human activity.

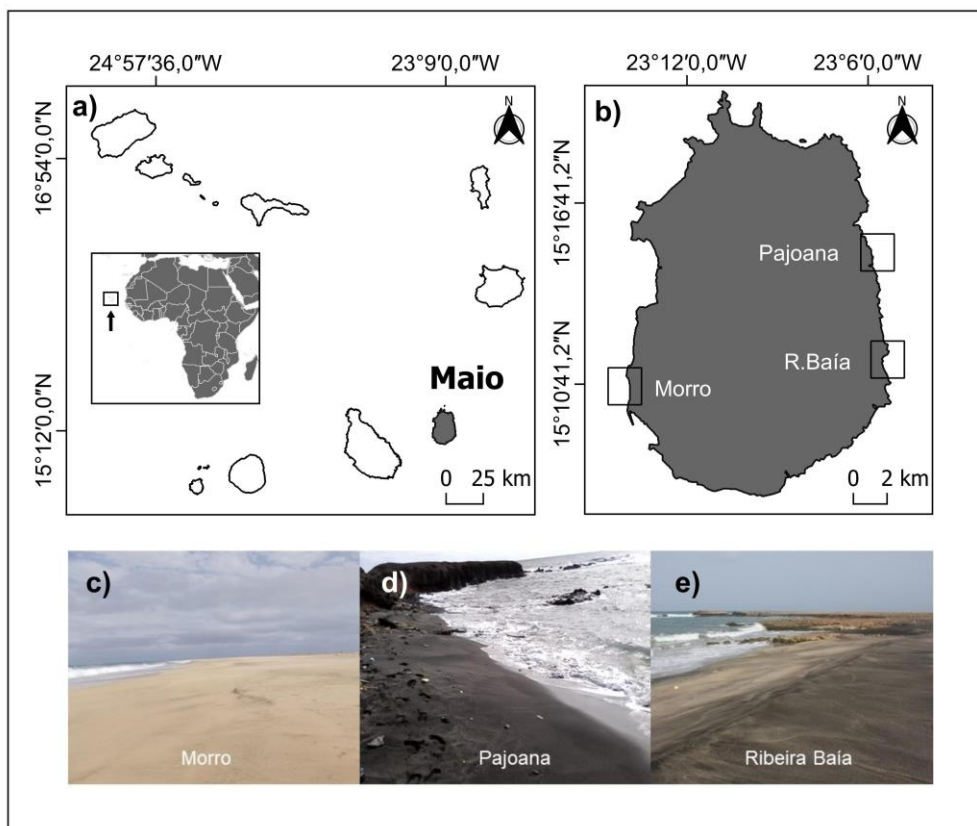


Figure 1. a) Map of Cabo Verde's location on the coast of West Africa and the Cabo Verde archipelago, b) The Maio island and study beaches in boxes, c) light sandy beach (Morro), d) dark sandy beach (Pajuana), e) mixed sand beach (Ribeira Baía).

Analysis of temporal and inter-beach variations in sand temperature. — The average daily sand temperature was recorded at a depth of 55 cm on three different sandy beaches (light, dark and mixed). A total of 48 daily data points (1 every 30 minutes) were recorded simultaneously from 1 July to 17 November during three nesting seasons (2020, 2021 and 2022). Hobo Stow Away TidbiT v2 Onset thermometers with an accuracy of $\pm 0.2^{\circ}\text{C}$ (1 per beach and per year) were used. The accuracy of the thermometers was checked by placing them in a box with a known temperature at least 48 hours before and after the experiment.

Analysing the relationship between air and sand temperature. — To check the relationship between the average daily temperature of the air and the sand, a recorder was installed in the air (hanging from the shadows of the roof) at 70m from the mean sea level during the same period as the recorders in the sand.

Data Analysis. — All the data were tested for normality using the Shapiro-Wilk test and for homogeneity of variance using the Levene test. The difference in average daily temperature between the three types of sand was assessed using the non-parametric Kruskal-Wallis test to determine independence. The relationship between average daily air temperature and average daily temperature in the three types of sand was assessed using Spearman's non-parametric correlation test. All statistical analyses were carried out using R software version 4.2.2 (R Core Team, 2022) with a significance level of 5%.

RESULTS

Analysis of temporal and inter-beach variations in sand temperature. — In the 2020 season, the average daily temperature was significantly different between the three different sandy beaches at the maximum nesting depth (light = $30.84^{\circ}\text{C} \pm 0.57$ s. d, min = 28.97, max = 32.14, dark = $32.6^{\circ}\text{C} \pm 1.03$ s.d, min = 27.84, max = 34.52, mixed = $32.41^{\circ}\text{C} \pm 0.79$ s.d, min = 29.49, max = 33.95; Kruskal-Wallis test: $\chi^2 = 224.82$, df = 2, $p < 0.001$; Fig. 2a).

In 2021, the average daily temperature was also significantly different between the three beaches with different sand at maximum nesting depth (light = $30.49^{\circ}\text{C} \pm 0.89$ s.d, min = 28.8, max = 32.17, dark = $32.01^{\circ}\text{C} \pm 0.9$ s.d, min = 30.23, max = 33.65, mixed = $32.01^{\circ}\text{C} \pm 0.97$ s.d, min = 30.43, max = 33.8.; Kruskal-Wallis test: $\chi^2 = 148.99$, df = 2, $p < 0.001$; Fig. 2b).

In 2022, the average daily sand temperature remains significantly different between the three different sand beaches (light = $29.52\text{ }^{\circ}\text{C} \pm 0.99$ s.d, min = 25.3, max = 30.9, dark = $32.0\text{ }^{\circ}\text{C} \pm 0.83$ s.d, min = 29.93, max = 33.42, mixed = $31.66\text{ }^{\circ}\text{C} \pm 0.95$ s.d, min = 29.7, max = 33.16 ; Kruskal-Wallis test: $\chi^2 = 246.8$, df = 2, $p < 0.001$; Fig. 2c).

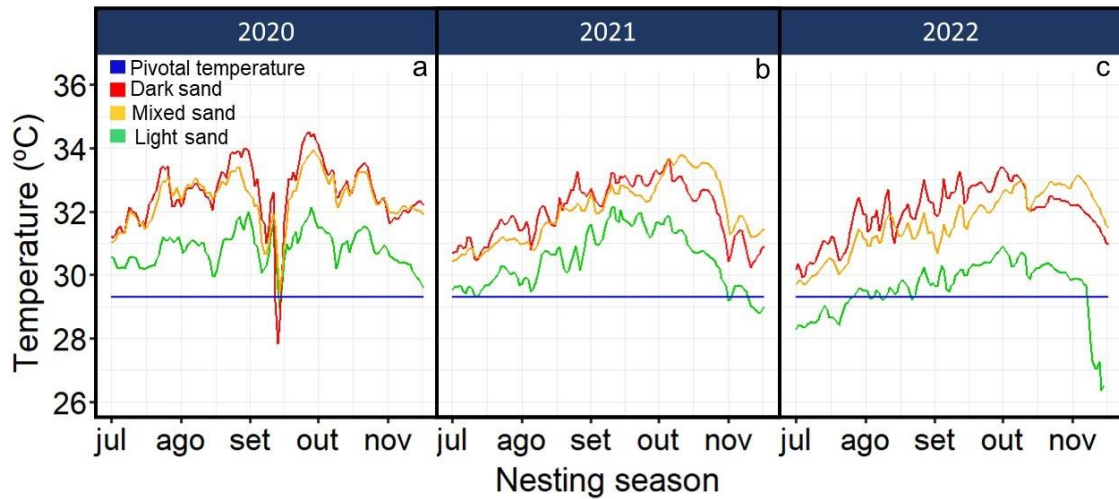


Figure 2. Comparison of the average daily temperature recorded (at 55 cm depth) from July to November between sand types (light - green line, dark - red line and mixed - orange line) during the 2020 (a), 2021 (b), 2022 (c) breeding seasons. The blue line corresponds to the pivotal temperature of $29.3\text{ }^{\circ}\text{C}$ (Mrosovsky & Pieau, 1991).

In the light sand, the year 2022 was statistically colder (light 2020 = $30.84\text{ }^{\circ}\text{C} \pm 0.57$ s.d, min = 28.97, max = 32.14, light 2021 = $30.49\text{ }^{\circ}\text{C} \pm 0.89$ s.d, min = 28.8, max = 32.17, light 2022 = $29.52\text{ }^{\circ}\text{C} \pm 0.99$ s.d, min = 25.3, max = 30.9; Kruskal-Wallis test: $\chi^2 = 137.39$, df = 2, $p < 0.001$; Fig. 3a).

In dark sand, the year 2022 was also statistically colder (dark 2020 = $32.6\text{ }^{\circ}\text{C} \pm 1.03$ s.d, min = 27.84, max = 34.52, dark 2021 = $32.01\text{ }^{\circ}\text{C} \pm 0.9$ s.d, min = 30.23, max = 33.65, dark 2022 = $32\text{ }^{\circ}\text{C} \pm 0.83$ s.d, min = 29.93, max = 33.42; Kruskal-Wallis test: $\chi^2 = 37.25$, df = 2, $p < 0.001$; Fig. 3b).

In mixed sand, the year 2022 was also statistically colder (mixed 2020 = 32.41 ± 0.79 s.d, min = 29.49, max = 33.95, mixed 2021 = $32.01\text{ }^{\circ}\text{C} \pm 0.97$ s.d, min = 30.43, max = 33.8, mixed 2022 = $31.66\text{ }^{\circ}\text{C} \pm 0.95$ s.d, min = 29.7, max = 33.16; Kruskal-Wallis test: $\chi^2 = 40.15$, df = 2, $p < 0.001$; Fig. 3c).

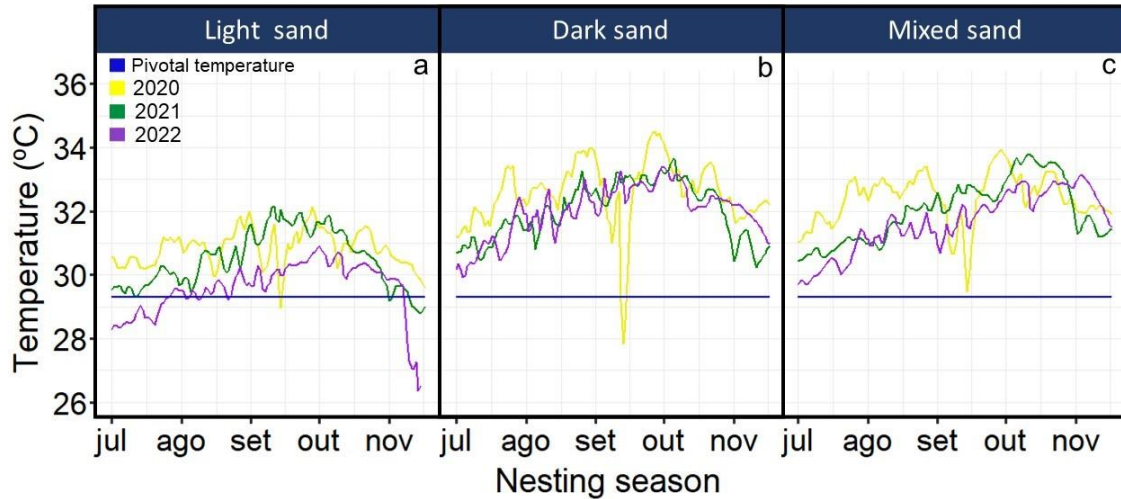


Figure 3. Average daily temperature recorded (at 55 cm depth) from July to November on light (a), dark (b) and mixed (c) sand beaches during 3 breeding seasons (2020 - yellow line, 2021 - green line, 2022 - violet line). The blue line corresponds to the pivotal temperature of 29.3 °C (Mrosovsky & Pieau, 1991).

Analysing the relationship between air and sand temperature. — There was a significant, positive and moderate correlation between the average daily air temperature and that of light sand ($r = 0.51$, $S = 221967$, $p < 0.001$; Fig. 4a), dark sand ($r = 0.55$, $S = 203540$, $p < 0.001$; Fig. 4b) and mixed sand ($r = 0.50$, $S = 226471$, $p < 0.001$; Fig. 4c).

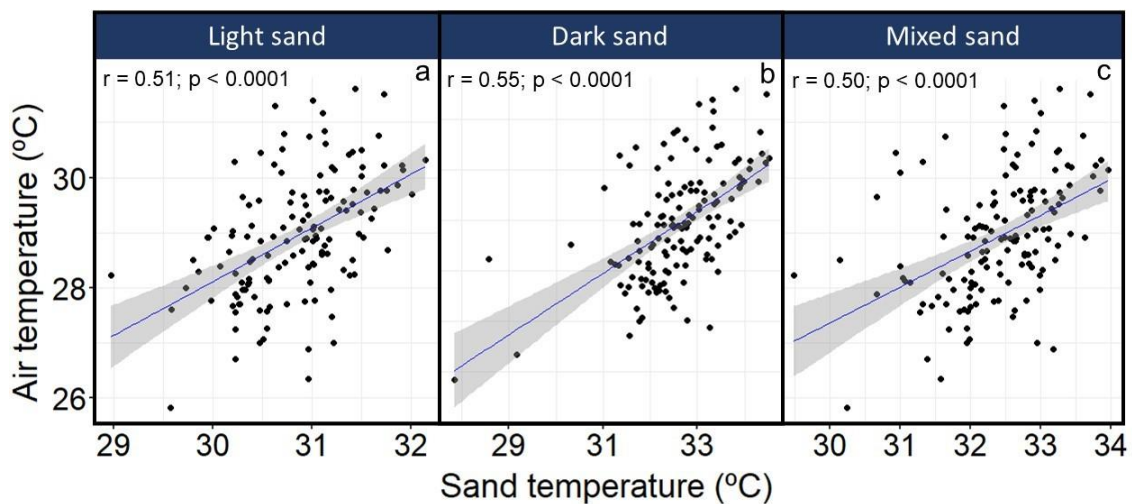


Figure 4. Relationship between average air temperature and average daily sand temperature at 55cm depth in white (a), dark (b), mixed (c) sand, used for nesting by female loggerhead turtles on the Maio island (Cabo Verde, North-east Atlantic). The blue line and gray areas correspond to the regression line and the 95% CI band, respectively.

DISCUSSION

There is growing interest in understanding how environmental temperature influences the survival and sex ratio of sea turtle hatchlings under future climate change scenarios (Abella et al., 2016; Hays et al., 2017; Laloë et al., 2017; Tanner et al., 2019; Martins et al., 2020). The results found here on the turtle nesting beaches of Maio Island are temperatures that may be highly biased towards female hatchlings in the three substrate types at maximum depth, and which may jeopardise the survival of hatchlings on dark sand beaches. If there is no adaptive response such as change in a geographical distribution (Abella et al., 2016; Patrício et al., 2019) or phenology (Weishampel et al., 2004; Pike et al., 2006) of the species in the future, the current temperatures are more than probable to cause extremely low production of males hatchlings. Moreover, the female hatchlings production will continue to increase (Standora & Spotila, 1985; Zbinden et al., 2007; Santidrián-Tomillo et al., 2014). Consequently, the natural viability of the subpopulation may be jeopardised.

The nest temperatures affecting the sex-ratio of sea turtle hatchlings varied with sand colour but also with time of the year (Pike et al., 2006; Tanner et al., 2019). In the coldest year (2022), the biased temperature for newborn males was recorded in the white sand only at the beginning and end of the nesting season (first weeks of July and the last weeks of November), reaching 4 °C below (25.3 °C) the pivotal temperature (29.3 °C). The pivotal temperature for this subpopulation is not yet known, and as in other studies in Cape Verde (Laloë et al., 2014; Abella et al., 2016), this study used the pivotal temperature known in other loggerhead turtle populations (Mrosovsky & Pieau, 1991). This result reinforces the hypothesis that temporal refuge are one of the main opportunities available for this subpopulation to adapt to global warming conditions (Tanner et al., 2019), where the group of females that arrives earlier or later in the nesting season and lays deeper nests may be more likely to produce male hatchlings (Hays et al., 2001; Weishampel et al., 2004; Pike et al., 2006; Lolavar & Wyneken, 2015). But the specific effects of choosing different nesting sites will also generally act to spread the likelihood of selective pressures on sex ratios (Patino-Martinez et al., 2022b). In mixed and dark sands, temperature was highly biased towards newborn females in all years, sometimes reaching temperatures (34.5°C) considered lethal for embryos (Ackerman, 1997; Segura & Cajade, 2010; Fisher et al., 2014; Martins et al., 2020). Dark sand is the warmest, due to the greater absorption of solar radiation than biogenic white sand (Hays

et al., 2001; Patino et al., 2022b). This result is in consonance with studies carried out on dark sand beaches in other parts of the Cabo Verde archipelago, where high incubation temperatures (average > 30 °C) have been recorded (Laloë et al., 2014; Tanner et al., 2019; Martins et al., 2020), as well as in other sea turtle populations (Hays et al., 2014). However, we observed that in a short period of great meteorological fluctuations caused by heavy rains and floods, the dark sand temperatures were 1.5 °C below the pivotal temperature thus male-biased sex-ratio may be present. Heavy rains and flash floods cool the sand on the beaches and thus favour male hatchlings production temperatures (Houghton et al., 2007; Lolavar & Wyneken, 2015). However, excessive rainfall and flooding may not be advantageous, as they can cause partial or total embryonic mortality (Kraemer & Bell, 1980; Milton et al., 1994). In the future, this might become more frequent, as studies show that global warming is not only increasing temperatures, but increases also the intensity of extreme precipitation events, from individual clouds and thunderstorms to cyclones and storms (Trenberth, 1999; Trenberth et al., 2003; Giorgi et al., 2019).

We found a correlation between mean daily air and sand temperatures, both in situ, this result is important for historical and future predictions of the primary sex ratios of this colony in the face of global warming and supports sex-ratio predictions made in other populations using the empirical relationship between air and sand temperatures (Hays et al., 2003; Katselidis et al., 2012; Laloë et al., 2014; Tanner et al., 2019).

Given the IPCC (2018) scenarios of predicted warming, that lead to development of progressively fewer males in loggerhead turtles, it becomes critical to identify male-biased thermal refuges, both spatial and temporal. This should be a priority among different colonies, subpopulations and populations threatened with extinction, where male-biased nesting temperatures become extremely important for persistence.

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REFERENCES

- Abella, E. P., Marco, A., Martins, S., & Hawkes, L. A. (2016). Is this what a climate change-resilient population of marine turtles looks like? *Biological Conservation*, 193, 124-132. <https://doi.org/10.1016/j.biocon.2015.11.023>
- Ackerman, R.A. (1997). The nest environment and the embryonic development of sea turtles. In: Lutz P, Musick J (eds) *The biology of sea turtles*, 1st edn. CRC Press, Boca Raton, Florida, pp 83–106.
- Baltazar-Soares, M., Klein, J. D., Correia, S. M., Reischig, T., Taxonera, A., Roque, S. M., ... & Eizaguirre, C. (2020). Distribution of genetic diversity reveals colonization patterns and philopatry of the loggerhead sea turtles across geographic scales. *Scientific reports*, 10(1), 18001. <https://doi.org/10.1038/s41598-020-74141-6>
- Booth, D. T., & Astill, K. (2001). Incubation temperature, energy expenditure and hatchling size in the green turtle (*Chelonia mydas*), a species with temperature-sensitive sex determination. *Australian Journal of Zoology*, 49(4), 389-396. <https://doi.org/10.1371/journal.pone.0114880>
- Booth, D.T. (2017). Influence of incubation temperature on sea turtle hatchling quality. *Integrative zoology* 12:352–360. <https://doi.org/10.1111/1749-4877.12255>
- Casale, P., & Tucker, A.D. (2017). *Caretta caretta* (amended version of 2015 assessment). The IUCN Red List of Threatened Species 2017: e.T3897A119333622. <http://dx.doi.org/10.2305/IUCN.UK.2017-2.RLTS.T3897A119333622.en>.
- Fisher, L.R., Godfrey, M.H., & Owens, D.W. (2014). Incubation temperature effects on hatchling performance in the loggerhead sea turtle (*Caretta caretta*). *PloS one* 9:1–22. <https://doi.org/10.1371/journal.pone.0114880>
- Fuentes, M. M. P. B., Maynard, J. A., Guinea, M., Bell, I. P., Werdell, P. J., & Hamann, M. (2009). Proxy indicators of sand temperature help project impacts of global warming on sea turtles in northern Australia. *Endangered Species Research*, 9(1), 33-40. <https://doi.org/10.3354/esr00224>
- Giorgi, F., Raffaele, F., & Coppola, E. (2019). The response of precipitation characteristics to global warming from climate projections. *Earth System Dynamics*, 10(1), 73-89.
- HAYS, G. C., ASHWORTH, J. S., BARNESLEY, M. J., BRODERICK, A. C., EMERY, D. R., GODLEY, B. J., ... & JONES, E. L. (2001). The importance of sand albedo for the thermal conditions on sea turtle nesting beaches. *Oikos*, 93(1), 87-94. <https://doi.org/10.1034/j.1600-0706.2001.930109.x>
- HAYS, G. C., BRODERICK, A. C., GLEN, F., & GODLEY, B. J. (2003). Climate change and sea turtles: a 150-year reconstruction of incubation temperatures at a major marine turtle rookery. *Global Change Biology*, 9(4), 642-646. <https://doi.org/10.1046/j.1365-2486.2003.00606.x>
- Hays, G. C., Mazaris, A. D., & Schofield, G. (2014). Different male vs. female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. *Frontiers in Marine Science*, 1:43. <https://doi.org/10.3389/fmars.2014.00043>
- Hays, G. C., Mazaris, A. D., Schofield, G., & Laloë, J. O. (2017). Population viability at extreme sex-ratio skews produced by temperature-dependent sex determination. *Proceedings of the Royal Society B: Biological Sciences*, 284(1848), 20162576. <https://doi.org/10.1098/rspb.2016.2576>
- Houghton, J. D. R., Myers, A. E., Lloyd, C., King, R. S., Isaacs, C., & Hays, G. C. (2007). Protracted rainfall decreases temperature within leatherback turtle (*Dermochelys coriacea*) clutches in Grenada, West Indies: ecological implications for a species

- displaying temperature dependent sex determination. *Journal of experimental marine biology and ecology*, 345(1), 71-77. <https://doi.org/10.1016/j.jembe.2007.02.001>
- Ischer, T., Ireland, K., & Booth, D. T. (2009). Locomotion performance of green turtle hatchlings from the Heron Island Rookery, Great Barrier Reef. *Marine Biology*, 156, 1399-1409. 9. <https://doi.org/10.1007/s00227-009-1180-7>
- IPCC 2018. Summary for policymakers. In: Masson-Delmotte V, Zhai P, Pörtner HO et al (eds) 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. World Meteorological Organization, Geneva
- Jensen, M. P., Allen, C. D., Eguchi, T., Bell, I. P., LaCasella, E. L., Hilton, W. A., ... & Dutton, P. H. (2018). Environmental warming and feminization of one of the largest sea turtle populations in the world. *Current Biology*, 28(1), 154-159. <https://doi.org/10.1016/j.cub.2017.11.057>
- Katselidis, K. A., Schofield, G., Stamou, G., Dimopoulos, P., & Pantis, J. D. (2012). Females first? Past, present and future variability in offspring sex ratio at a temperate sea turtle breeding area. *Animal Conservation*, 15(5), 508-518. <https://doi.org/10.1111/j.1469-1795.2012.00543.x>
- Kraemer, J. E., & Bell, R. (1980). Rain-induced mortality of eggs and hatchlings of loggerhead sea turtles (*Caretta caretta*) on the Georgia coast. *Herpetologica*, 72-77.
- Laloë, J. O., Cozens, J., Renom, B., Taxonera, A., & Hays, G. C. (2014). Effects of rising temperature on the viability of an important sea turtle rookery. *Nature Climate Change*, 4(6), 513-518. <https://doi.org/10.1038/nclimate2236>
- Laloë, J. O., Cozens, J., Renom, B., Taxonera, A., & Hays, G. C. (2017). Climate change and temperature-linked hatchling mortality at a globally important sea turtle nesting site. *Global change biology*, 23(11), 4922-4931. <https://doi.org/10.1111/gcb.13765>
- LeBlanc, A. M., Drake, K. K., Williams, K. L., Frick, M. G., Wibbels, T., & Rostal, D. C. (2012). Nest temperatures and hatchling sex ratios from loggerhead turtle nests incubated under natural field conditions in Georgia, United States. *Chelonian Conservation and Biology*, 11(1), 108-116. <https://doi.org/10.2744/CCB-0915.1>
- Lolavar, A., & Wyneken, J. (2015). Effect of rainfall on loggerhead turtle nest temperatures, sand temperatures and hatchling sex. *Endangered Species Research*, 28(3), 235-247. <https://doi.org/10.3354/esr00684>
- Martins, S., Silva, E., Abella, E., de Santos Loureiro, N., & Marco, A. (2020). Warmer incubation temperature influences sea turtle survival and nullifies the benefit of a female-biased sex ratio. *Climatic Change* 163: 689–704. <https://doi.org/10.1007/s10584-020-02933-w>
- Matsuzawa, Y., Sato, K., Sakamoto, W., & Bjørndal, K. (2002). Seasonal fluctuations in sand temperature: effects on the incubation period and mortality of loggerhead sea turtle (*Caretta caretta*) pre-emergent hatchlings in Minabe, Japan. *Marine Biology* 140:639–646. <https://doi.org/10.1007/s00227-001-0724-2>
- Milton, S. L., Leone-Kabler, S., Schulman, A. A., & Lutz, P. L. (1994). Effects of Hurricane Andrew on the sea turtle nesting beaches of South Florida. *Bulletin of Marine Science*, 54(3), 974-981.
- Monzón-Argüello, C., Rico, C., Naro-Maciél, E., Varo-Cruz, N., López, P., Marco, A., & López-Jurado, L. F. (2010). Population structure and conservation implications

- for the loggerhead sea turtle of the Cape Verde Islands. *Conservation Genetics*, 11, 1871-1884.
- Mrosovsky, N., & Pieau, C. (1991). Transitional range of temperature, pivotal temperatures and thermosensitive stages for sex determination in reptiles. *Amphibia-Reptilia*, 12(2), 169-179.
- Mueller, M. S., Ruiz-García, N. A., García-Gasca, A., & Abreu-Grobois, F. A. (2019). Best swimmers hatch from intermediate temperatures: Effect of incubation temperature on swimming performance of olive ridley sea turtle hatchlings. *Journal of Experimental Marine Biology and Ecology*, 519, 151186. <https://doi.org/10.1016/j.jembe.2019.151186>
- Patino-Martinez, J., Dos Passos, L., Afonso, I.O., Teixidor, A., Tiwari, M., Székely, T., & Moreno, R. (2022a). Globally important refuge for the loggerhead sea turtle: Maio Island, Cabo Verde. *Oryx* 56:54–62. <https://doi.org/10.1017/S0030605320001180>
- Patino-Martinez, J., Veiga, J., Afonso, I. O., Yeoman, K., Mangas-Viñuela, J., & Charles, G. (2022b). Light sandy beaches favour hatching success and best hatchling phenotype of loggerhead turtles. *Frontiers in Ecology and Evolution*, 10, 823118. <https://doi.org/10.3389/fevo.2022.823118>
- Patrício, A. R., Varela, M. R., Barbosa, C., Broderick, A. C., Catry, P., Hawkes, L. A., ... & Godley, B. J. (2019). Climate change resilience of a globally important sea turtle nesting population. *Global Change Biology*, 25(2), 522-535. <https://doi.org/10.1111/gcb.14520>
- Patrício, A. R., Hawkes, L. A., Monsinjon, J. R., Godley, B. J., & Fuentes, M. M. (2021). Climate change and marine turtles: Recent advances and future directions. *Endangered Species Research*, 44, 363-395. <https://doi.org/10.3354/esr01110>
- Pike, D. A., Antworth, R. L., & Stiner, J. C. (2006). Earlier nesting contributes to shorter nesting seasons for the loggerhead sea turtle, *Caretta caretta*. *Journal of Herpetology*, 40(1), 91-94. <https://doi.org/10.1670/100-05N.1>
- R Core Team (2022). R: A Language and Environment for Statistical Computing (Version 4.2.2). <https://www.r-project.org/>
- Rivas, M. L., Esteban, N., and Marco, A. (2019). Potential male leatherback hatchlings exhibit higher fitness which might balance sea turtle sex ratios in the face of climate change. *Climatic Change*, 156, 1-14. <https://doi.org/10.1007/s10584-019-02462-1>
- Santidrián-Tomillo, P., Oro, D., Paladino, F. V., Piedra, R., Sieg, A. E., & Spotila, J. R. (2014). High beach temperatures increased female-biased primary sex ratios but reduced output of female hatchlings in the leatherback turtle. *Biological Conservation*, 176, 71-79. <https://doi.org/10.1016/j.biocon.2014.05.011>
- Segura, L. N., & Cajade, R. (2010). The effects of sand temperature on pre-emergent green sea turtle hatchlings. *Herpetological Conservation and Biology* 5(2):196-206
- Sim, E. L., Booth, D. T., & Limpus, C. J. (2015). Incubation temperature, morphology and performance in loggerhead (*Caretta caretta*) turtle hatchlings from Mon Repos, Queensland, Australia. *Biology Open*, 4(6), 685-692. <https://doi.org/10.1242/bio.20148995>
- Standora, E. A., & Spotila, J. R. (1985). Temperature dependent sex determination in sea turtles. *Copeia*, 711-722. <https://doi.org/10.2307/1444765>
- Stiebens, V.A., Merino, S.E., Roder, C., Chain, F.J., Lee, P.L., & Eizaguirre, C. (2013). Living on the edge: how philopatry maintains adaptive potential. *Proceedings of*

- the Royal Society B: Biological Sciences* 280:1–9.
<https://doi.org/10.1098/rspb.2013.0305>
- Tanner, C. E., Marco, A., Martins, S., Abella-Perez, E., & Hawkes, L. A. (2019). Highly feminised sex-ratio estimations for the world's third-largest nesting aggregation of loggerhead sea turtles. *Marine Ecology Progress Series*, 621, 209-219.
<https://doi.org/10.3354/meps12963>
- Trenberth, K. E. (1999). Conceptual framework for changes of extremes of the hydrological cycle with climate change. *Climatic change*, 42(1), 327-339.
<https://doi.org/10.1023/A:1005488920935>
- Trenberth, K. E., Dai, A., Rasmussen, R. M., & Parsons, D. B. (2003). The changing character of precipitation. *Bulletin of the American Meteorological Society*, 84(9), 1205-1218. <https://doi.org/10.1175/BAMS-84-9-1205>
- Wallace, B. P., DiMatteo, A. D., Hurley, B. J., Finkbeiner, E. M., Bolten, A. B., Chaloupka, M. Y., ... & Mast, R. B. (2010). Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. *Plos one*, 5(12), e15465.
- Weishampel, J. F., Bagley, D. A., & Ehrhart, L. M. (2004). Earlier nesting by loggerhead sea turtles following sea surface warming. *Global Change Biology*, 10(8), 1424-1427. <https://doi.org/10.1111/j.1529-8817.2003.00817.x>
- Yntema, C. L., & Mrosovsky, N. (1982). Critical periods and pivotal temperatures for sexual differentiation in loggerhead sea turtles. *Canadian Journal of Zoology*, 60(5), 1012-1016. <https://doi.org/10.1139/z82-141>
- Zbinden, J. A., Davy, C., Margaritoulis, D., & Arlettaz, R. (2007). Large spatial variation and female bias in the estimated sex ratio of loggerhead sea turtle hatchlings of a Mediterranean rookery. *Endangered Species Research*, 3(3), 305-312. <https://doi.org/10.3354/esr00058>