



Citation for published version:

Tanner, C, Marco, A, Martins, S, Abella Perez, E & Hawkes, L 2019, 'Highly feminised sex ratio estimations for the world's third largest nesting aggregation of loggerhead sea turtles', *Marine Ecology Progress Series (MPES)*, vol. 621, 621, pp. 209-219. <https://doi.org/10.3354/meps12963>

DOI:

[10.3354/meps12963](https://doi.org/10.3354/meps12963)

Publication date:

2019

Document Version

Publisher's PDF, also known as Version of record

[Link to publication](#)

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Highly feminised sex-ratio estimations for the world's third-largest nesting aggregation of loggerhead sea turtles

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ABSTRACT: Despite being a fundamental life-history character, there is a paucity of population-wide, data-driven studies of primary sex ratios for any marine turtle species. The Republic of Cape Verde hosts the third-largest nesting population of loggerhead turtles *Caretta caretta* in the world (hosting up to 15 % of global nesting by the species). Weighting for the spatial distribution of nests, we estimate that 84 % of female hatchlings are currently likely produced across the population, with 85 % of nests laid on Boa Vista, where incubation temperatures are coolest. In future climate change scenarios (by 2100), irrespective of beach, island or sand colour, sex ratios reach over 99 % female, and 3 islands (Fogo, Sao Nicolau, Santiago) would cease to produce males, with >90 % of nests incubating at lethally high temperatures. Given that most of the population cannot move to nest on cooler islands, we highlight that temporal refugia are amongst the primary means available to this population to adapt. Under a low-emissions scenario, without phenological adaptation, there would only be an estimated 0.14 % males produced across the whole population, while under mid- and high-emissions scenarios, male production may cease on most islands.

KEY WORDS: Climate change · Sex ratio · *Caretta caretta* · Loggerhead turtle · Marine turtle · Cape Verde

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1. INTRODUCTION

Climate change is considered one of the greatest modern threats to biodiversity (Urban 2015). By 2050, models predict that up to 54 % of species' extinctions could be attributed, both directly (e.g. via temperature-related embryo death) and indirectly (e.g. competition, declining food sources), to climate change (Urban 2015). Global temperatures (mean air and surface temperatures) have risen by approximately 0.6°C in the past 100 yr (IPCC 2014) and are expected

to rise a total of 2°C between the pre-industrial period and 2030 (IPCC 2014), which is a much faster rate than in previous years and may be too fast to allow species to adapt (Quintero & Wiens 2013). Ectothermic taxa, such as sea turtles, may be more likely to be negatively affected by climate change (Böhm et al. 2016), as environmental conditions affect their performance (Refsnider 2013), reproduction (Starostova et al. 2012) and survival (Miller et al. 2004). Understanding and modelling the response of species to climate change is a key future challenge (Urban 2015).

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1.1. Temperature-dependent sex determination

Many reptile species (e.g. turtles, crocodylians and some lizards) exhibit temperature-dependent sex determination (Refsnider 2013), where the temperature experienced during development controls hormone expression and therefore determines offspring sex (Tedeschi et al. 2016). In marine turtles, lower temperatures produce males, and higher temperatures produce females, with a 'pivotal temperature' (the constant incubation temperature that produces a 1:1 ratio of hatchling males:females) of approximately 29°C for most marine species (reviewed by Hawkes et al. 2009). In most marine turtle rookeries that have been studied, the primary sex ratio (the sex ratio at the point of sex determination) is strongly female-biased and may be expected to become more biased with increased future temperatures (Hawkes et al. 2007, Katselidis et al. 2012, Jensen et al. 2018).

If marine turtles fail to adapt in pace with the rate of climate change, mortality could increase (Witt et al. 2010, Fuentes et al. 2011) and male hatchling production could diminish to a point that could reduce nest fertilisation rate (Witt et al. 2010, Katselidis et al. 2012, Jensen et al. 2018). Currently there is a debate as to whether marine turtles could buffer such effects (Wright et al. 2012) through polygamy (Wright et al. 2012) and/or breeding frequency (Tedeschi et al. 2014). Polygyny (a mating system where 1 male mates with multiple females) has been shown in other species which display biased sex ratios, thereby stabilising the population (Wright et al. 2012). In marine turtles, females have a breeding interval of 2 to 3 yr, whereas it is assumed that males mate every year. This would therefore mean that fewer males would be required in the population to maintain a stable breeding population (Hays et al. 2014). The operational sex ratio (the ratio of breeding males to females) is not yet comprehensively described across global rookeries (but see Lee et al. 2018), but may not be balanced in some areas; for example, in Ghana 'by-catch' (or incidental fishing capture) data showed that only female loggerhead turtles *Caretta caretta* were captured in coastal waters throughout the 4 mo study period during the nesting season (Tanner 2014), which suggested a very low male presence in the overall population, or early departure from the breeding area by males. In contrast, in foraging areas in Greece, the percentage of males can be much higher, ranging from 31 to 55% (Rees et al. 2013). Furthermore, multiple paternity has been recorded in all marine turtle species (Wright et al. 2012, Tedeschi et al. 2014, Lee et al. 2018), which means a

polygamous mating system is already present. This would assist adaptive capacity, as it is a more flexible mating system allowing for sex ratio bias in a population without causing a population decline.

1.2. Maternal behaviour

Although there is no parental care in marine turtles, turtles usually select nest sites that should be beneficial for the development of offspring. It has been suggested that to maintain current nest temperatures in future warmer climates, turtles could nest closer to the water, where evaporative cooling may be increased, in cooler parts of the nesting range (e.g. at higher latitudes, or on a smaller scale, on lighter sand beaches or on beaches with more shade) or at earlier and later times of the year where and when temperatures may be cooler (Witt et al. 2010, Fuentes et al. 2011, Abella-Perez et al. 2016).

There have been few data-driven assessments to date of primary sex ratios across entire nesting rookeries for any marine turtle species and even fewer across an entire population of marine turtles (Fuentes et al. 2011, Jensen et al. 2018). Most studies measure sand or nest temperature at just a few key sites and extrapolate (Wyneken & Lolavar 2015), which fails to recognise intra-beach (spatial and geomorphological), intra-individual, intra-regional and intra-annual variation or differences in nesting seasonality between years. Such insights into likely change to primary sex ratios are therefore helpful but potentially misleading at a population level (Wyneken & Lolavar 2015).

The Republic of Cape Verde is considered to host the third-largest nesting population of loggerhead turtles in the world, with approximately 12 000 to 20 000 nests laid per year, or between 9 and 15% of global nesting by the species (López Jurado 2007, Marco et al. 2012, Casale & Tucker 2017), and may be the oldest population in the Atlantic (Shamblin et al. 2014). Most of the nesting is concentrated on 40 km of beaches on just a few islands: Boa Vista, Maio, Sal and Sao Nicolau (López Jurado 2007, Lino et al. 2010), which makes it possible to study the entire population. Laloë et al. (2014) published an initial estimate of the sex ratio across the Cape Verdean rookery, but their study was based on 24 temperature recorders on only 1 of the Cape Verdean islands. The present study, by contrast, uses empirical measurements of temperature across 9 of the major islands (and 40 beaches) of the archipelago. We used previously published equations to convert

sand temperature to calculate primary sex ratios and estimate potential future primary sex ratios considering climate change using predicted global surface temperature increases.

2. MATERIALS AND METHODS

2.1. Sand temperature

Between 18 July and 15 November (inclusively) of 2012, 2013 and 2014, sand temperature data were recorded using Tidbit HOBO temperature data loggers (TDLs; accuracy $\pm 0.25^\circ\text{C}$; <https://www.tempro.com>) buried at a depth of 40 cm (the mean depth of loggerhead nests in Cape Verde; Varo-Cruz et al. 2007) on 9 of the Cape Verde islands: Sao Vicente, Santa Lucia, Sao Nicolau, Sal, Boa Vista, Maio, Santiago, Fogo and Ilheu de Cima (Fig. 1). Islands and beaches were selected based on historical nesting data from The Cape Verdean Sea Turtle Network (TAOLA), from which the beaches with the highest nesting densities were chosen. All TDLs were inter-compared prior to use and were only accepted for the

study if they were accurate to within $\pm 0.1^\circ\text{C}$ of the National Measurement Accreditation Service standards. TDLs were programmed to record temperature every 30 min. In total, 31 TDLs were buried in 2012, 31 in 2013 and 32 in 2014 on 40 beaches on the 9 islands (mean: 4 beaches island⁻¹, range 2–8; Fig. 1). Due to logistical reasons (TDLs lost, damaged or broken), not all the beaches could be measured every year, and consequently only 18 beaches on 6 islands have temperature data for all 3 study years. Some islands (Sao Nicolau, Sao Vicente, Maio and Santiago) have nesting beaches with light and dark sand, and hence TDLs were buried in both light and dark sand beaches for this study (Fig. 1). TAOLA found that significant nesting occurs on the Cape Verde archipelago from 1 July to 10 October. The thermosensitive period was determined by assuming that the sex-determination period starts approximately 18 d after egg laying and finishes on Day 36 of incubation (Mrosovsky et al. 1999, Woolgar et al. 2013). Given that the thermosensitive period occurs in the middle third of incubation (Woolgar et al. 2013), we therefore only considered data from 18 July until 15 November.

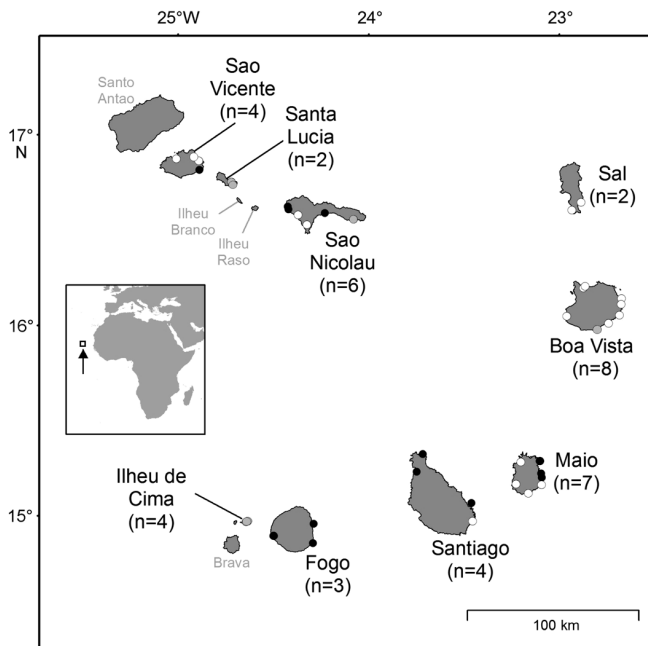


Fig. 1. Locations of 40 loggerhead turtle nesting beaches (dots, black labels) across 9 islands in the Republic of Cape Verde at which sand temperature and luminosity data were recorded. Black (white) dots show dark (light) sand beaches; grey dots show beaches from which luminosity data were not collected. Number of data loggers on each island is indicated. Major islands of the Cape Verdes that were not studied are labelled in grey

2.2. Sand reflectance

Sand samples ($n = 3$ from each beach), weighing 50 g each, were collected from 31 beaches where TDLs had been buried. Samples were collected from the sand column directly above the TDLs. The luminosity of each sand sample (measured in percentage reflectance to $\pm 0.01\%$ accuracy, where 0% = black and 100% = white) was recorded using a calibrated spectrophotometer (CM-2600d/2500d; Konica Minolta) in the Consejo Superior de Investigaciones Científicas laboratories in Seville, Spain (www.konicaminolta.eu/en/measuring-instruments/products/colour-measurement.html). Each sand sample was measured 3 times under lab conditions, and the mean of the 3 values was used per beach. Due to logistical reasons, sand samples were not collected at Ilheu de Cima and Santa Lucia.

2.3. Estimating sex ratio

The pivotal temperature (T_{PIV}) has not been determined for loggerhead turtles nesting in Cape Verde, but is relatively conserved across the populations in which it has been described (from $27.5\text{--}30.5^\circ\text{C}$; Hawkes et al. 2009; see Appendix). The actual tem-

peratures that turtle eggs experience during incubation also depends on the 3-dimensional location of nests and the time of year in which they were laid. In addition, Wyneken & Lolavar (2015) presented new data concerning nest moisture that suggested that male offspring can be produced above T_{PIV} if sufficient moisture is available. It is thus extremely challenging for any study to accurately estimate what the primary sex ratio may be, although a raft of previous studies have done so (Wyneken & Lolavar 2015). Taking this into account, we estimated the potential primary sex ratio using the following equation from Mrosovsky et al. (2002), with the median T_{PIV} for loggerhead turtles (see Appendix for minimum and maximum T_{PIV}):

$$Y = \frac{100}{1 + e^{((a-b) \times 2.767)}} \quad (1)$$

where Y = percent females, a = pivotal temperature for loggerhead turtles on the eastern beaches of the USA (29.25°C) (Marcovaldi et al. 1997), and b = mean thermosensitive period temperature. Mean thermosensitive period temperature was estimated as the product of sand temperature and metabolic heating, the heat produced by the eggs during incubation. Mean metabolic heating has been estimated at 0.5°C on Boa Vista and Sal (Laloë et al. 2014, Abella-Perez et al. 2016). It is important to note that the pivotal temperature varies between nesting sites (Mrosovsky et al. 2002, Woolgar et al. 2013, Wyneken & Lolavar 2015), and although this has never been empirically determined for the Cape Verde rookery, the pivotal temperature for the Mediterranean region, Brazil and the USA are all very similar, and hence we used the pivotal temperature of the US population for this study (Mrosovsky et al. 2002). Sex is determined during the middle third of embryogenesis, which may not be the same as the middle third of the total incubation period (Wyneken & Lolavar 2015). As we were unable to derive our own local pivotal temperature or monitor embryogenesis in the field, we cautiously used the middle third, generalised pivotal temperature approach but recognise that reality may differ.

Current hatchling production was estimated by weighting primary sex ratios (as calculated above) by spatial nest abundance, using previous estimates of annual nesting density in the Cape Verdean population from multi-year nest counts on all beaches using data provided by TAOLA and previously published data (López Jurado 2007, Lino et al. 2010). The sites selected include the islands with the majority of nesting (>100 nests laid each year) and

the beaches with the highest documented nesting densities (Marco et al. 2011), which represent approximately 99% of the current nesting activity in Cape Verde. These estimates do not include any locations with minimal (<100 nests yr⁻¹) or random nesting occurrences, as it would be difficult to include all nesting occurrences. However, we emphasise that they could be important for the population, as historical information has suggested that nesting was more uniform centuries ago, with loggerhead nesting abundant throughout the Cape Verde (López-Jurado 2007). Hence, we cautiously use the phrase 'entire archipelago' when referring to these results, because, although they are not exhaustive, they include the majority of nesting locations recorded for loggerheads in the Cape Verdean archipelago.

For this study, although the sex ratios are weighted to account for spatial distribution, they are not weighted according to temporal distribution. We acknowledge that this assumes equal nesting across the nesting period, although this is likely not to be the case. However, as more nests are currently laid in warmer periods, our results may underestimate the percentage female sex ratios and should therefore be viewed cautiously when considering the effects of global climate change on the population.

2.4. Estimating future temperatures and sex ratios

The Intergovernmental Panel on Climate Change (IPCC) predicts that surface air temperature will likely increase by 1.8, 2.8 and 3.4°C for the B1, A1B and A2 scenarios by 2090 to 2099 (IPCC 2007), which will hereafter be referred to as the low-, mid- and high-missions scenarios (LES, MES and HES, respectively). These estimates are derived from a global climate model, so variation would be expected regionally and temporally (i.e. for seasonal differences). In previous studies in the USA and Greece (Hawkes et al. 2007, Katselidis et al. 2012), sand temperature increased by 0.72°C for every 1°C of air temperature increase, so we estimated future sex ratios by adding the corresponding sand temperature increase from predicted air temperature increases (IPCC 2007) to current sand temperatures (i.e. adjusting 'b' in Eq. 1 before calculating future sex ratios). This increase has been recorded for both Greece (Katselidis et al. 2012) and the USA (Hawkes et al. 2007), and we assume that the sand temperature increase is similar for Cape Verde as it is located between these 2 locations.

2.5. Statistical tests

All statistical analyses were completed in R (R Core Development Team; www.r-project.org). All data were tested for normality using Shapiro-Wilks tests; luminosity data were normal, while temperature data were non-normal. Non-parametric statistical analyses were completed on sex ratio estimates. As the data included multiple years (with data from different beaches collected in different years), the temperature was compared between years (for each beach) using a Kruskal-Wallis test. Reflectance was split into light and dark beaches based on *k*-means cluster analyses (visualised in a histogram; see Fig. 3), with luminosities above 40% of the perceived brightness classed as light beaches ($n = 19$), and those under 40% as dark beaches ($n = 11$). A Wilcoxon test was used to analyse the correlation between temperature and sand colour; an *F*-test was used to analyse any differences between sex ratios and sand colour; and Kruskal-Wallis tests were used to analyse any significant differences between sex ratios within and between islands. We used a significance level of $\alpha = 0.05$.

3. RESULTS

In total, 94 TDL deployments collected sand temperature data every half hour from 18 July to 15 November (inclusively) in 2012, 2013 and 2014 (mean

108 d TDL⁻¹, range 32–121 d). Sand temperature during the nesting season varied from a minimum half-hourly point count of 25.1°C (Porto Lapa, Sao Nicolau, 2013) to a maximum of 38.9°C (Sao Felipe, Fogo, 2013) (Fig. 2B). There was no significant difference in sand temperature between years (Kruskal-Wallis $\chi^2 = 1.485$, $p = 0.476$; Fig. 2A), hence average sand temperature for each beach irrespective of year was used in further analysis. Sand temperatures were significantly different between light and dark beaches (mean half-hourly point count for light sand beach: 30.0°C, range 26.1–37.0°C; for dark sand beach: 31.9°C, range 25.1–38.9°C; Wilcoxon $W = 1396$, $p < 0.001$; Fig. 3).

3.1. Estimated sex ratios by island

Mean estimated primary sex ratios ranged from a minimum of 67.5% females on Boa Vista to a maximum of 100% on Fogo, with 3 beaches on Boa Vista (Boa Esperanza, Lacacao and Varandinha) estimated to produce more than 75% male hatchlings, which accounts for 18.5% of nesting on Boa Vista (Fig. 4A,B). There was no significant difference between the estimated primary sex ratios produced on light ($n = 19$) and dark ($n = 11$) sand beaches across the archipelago ($F_{1,29} = 1.66$, $p = 0.208$), with 88.8% female (range 0.4–100%) produced on light sand beaches and 100% female on dark sand beaches. There was also no sig-

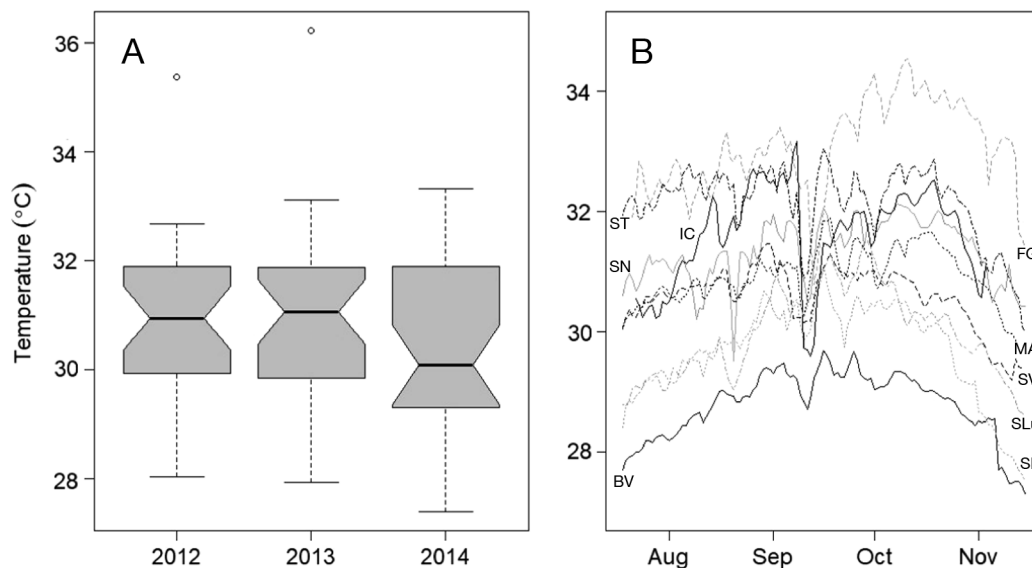


Fig. 2. (A) Sand temperatures recorded in the 3 study years (boxes show inter-quartile range, horizontal line shows median value, whiskers show range, notches indicate 95% confidence interval of the median). The 2 outliers in 2012 and 2013 are shown as white dots. (B) Mean sand temperature over the nesting season for 9 islands (SV: Sao Vicente; SLu: Santa Lucia; SN: Sao Nicolau; SL: Sal; BV: Boa Vista; MA: Maio; ST: Santiago; FG: Fogo; IC: Ilheu de Cima). A marked decrease in sand temperature can be seen in mid-September as this is the rainiest month of the year in Cape Verde

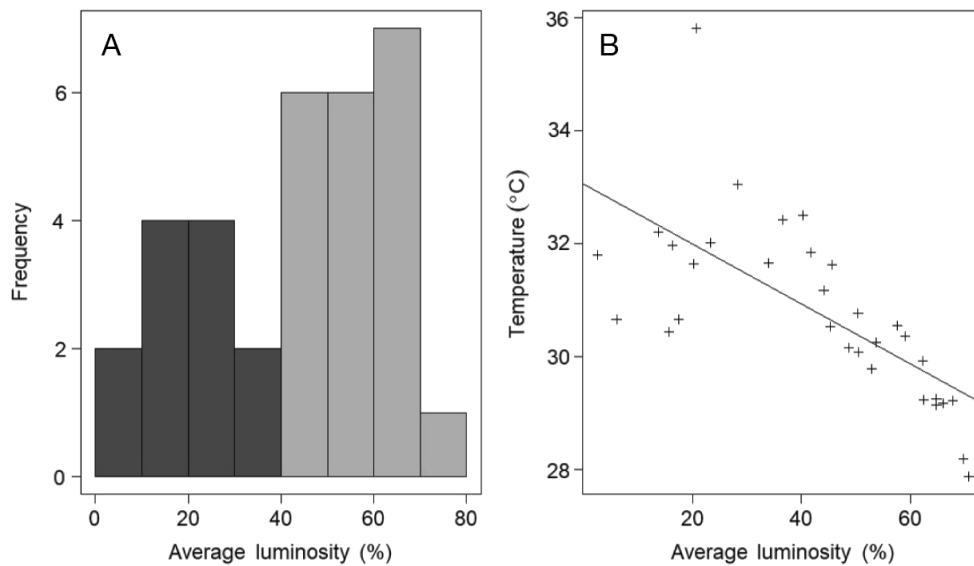


Fig. 3. (A) Luminosity data collected from each beach (where values <40% are classed as dark sand beaches and >40% classed as light sand beaches for the present study). (B) Average sand temperature (measured using buried temperature data loggers) plotted against average beach sand luminosity (measured as percent of light reflected, where 0 = black and 100 = white) for the 40 beaches studied across the Cape Verde archipelago

nificant difference in estimated primary sex ratios between islands (Kruskal-Wallis $\chi^2 = 8$, $p = 0.434$; Fig. 4), or between beaches within each island ($\chi^2 = 39$, $p = 0.47$).

3.2. Estimated sex ratio of the population

Loggerhead nesting is not spatially uniform across all islands of the Cape Verdean archipelago, with highly variable annual densities. For example, Boa Vista currently hosts approximately 85% of all nests laid on Cape Verde (in excess of 10 000 nests yr^{-1} ; Marco et al. 2012), a further 1000 nests are laid per year in Sal (Lino et al. 2010), and minor nesting occurs elsewhere. Accounting for spatial distribution of nests across the archipelago (i.e. the proportion of all nests that are laid on each island, and assuming no future change), mean estimated primary sex ratios for the whole archipelago were 84.3% female at present, 99.9% in the LES and 100% in both the MES and HES (Fig. 4B,D,F,H).

3.3. Estimated future sex ratios by island

In the future LES (1.8°C increase in mean air temperature), estimated primary sex ratios range from 98.7% females on Boa Vista to 100% on Fogo, Maio, Ilheu de Cima, Sao Nicolau and Santiago. Although only a few beaches would cease to produce any male

hatchlings in LES, only 3 beaches on Boa Vista would produce more than 0.01% male hatchlings (Varandinha: 6.3% male; Boa Esperanza: 0.9% male; Lacacao: 0.2% male). In the future MES, only Boa Vista would produce any male hatchlings (0.01%), and no male hatchlings would be produced on any Cape Verdean island in the HES.

3.4. Incubation above critical upper temperatures

At current temperatures, nests on the island of Fogo already experience critically high incubation temperatures above 35°C for 25.2% (or 30.44 d) of the study period (Fig. 2), with Sao Felipe (Fogo) exceeding the critical upper temperature for 75.5% (91.34 d) of the study period. In all future scenarios (LES, MES and HES), between 41.3 and 81.7% of nests on Fogo would be incubating above critical upper temperatures (LES: 41.3%, MES: 72.5%, HES: 81.7% of the study period for the whole island). On Sao Felipe beach, Fogo, the model suggests that over 93.2% of the study period would be above critical upper temperatures in the LES. In the MES, a total of 16 beaches (Fogo: Sao Felipe, Praia Cais and Praia Grande; Maio: Djam Padja, Lomba Greija and Santa Clara; Ilheu de Cima: Soca, Bequinho and Praia Canoa; Sao Nicolau: Porto Lapa and Praia Grande; Santiago: Achada Baleia, Medronho, Rib das Pratas and Sao Francisco; Sao Vicente: Topim) would have reached critical upper

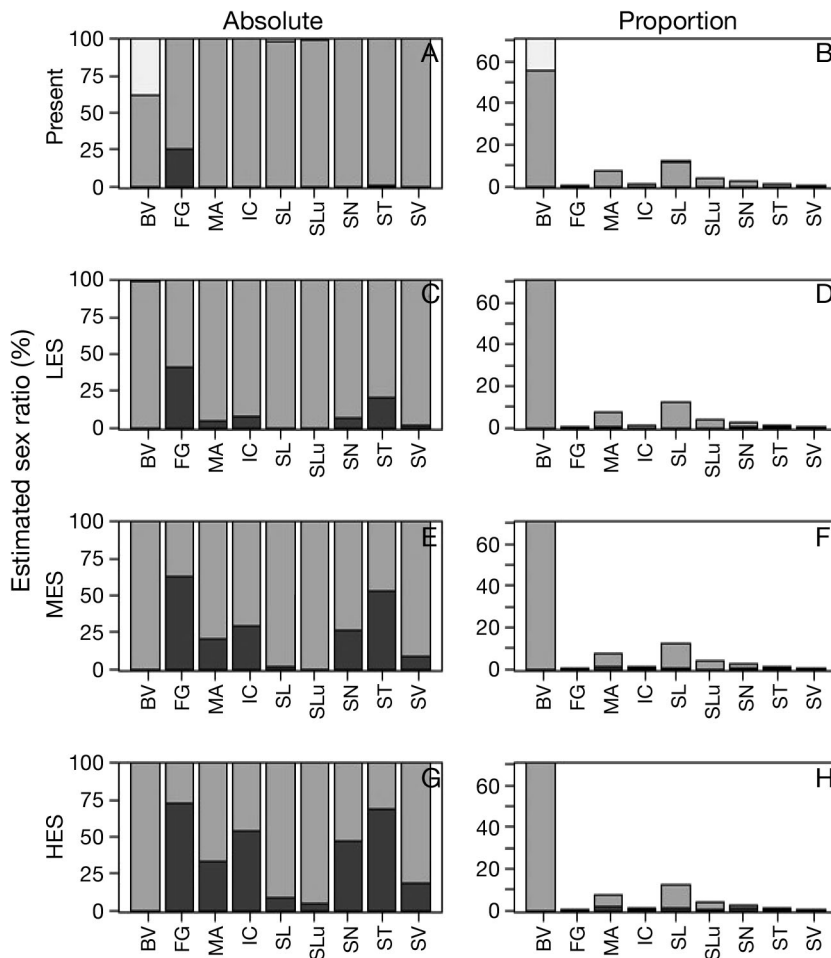


Fig. 4. (A,C,E,G) Absolute overall mean percent loggerhead turtle embryos incubating above the thermal maximum of 35°C (dark grey), estimated % female hatchlings (grey) and estimated % male hatchlings (light grey) for each of the 9 study islands (island abbreviations as in Fig. 2). (B,D,F,H) Spatially proportionally corrected production of female and male hatchlings and nests incubating over the thermal maximum across the Cape Verde rookery by Island (colours as in A,C,E,G). Rows show the present conditions, low-emissions scenario (LES), mid-emissions scenario (MES) and high-emissions scenario (HES)

temperatures for over 20% of the study period. Beaches on these 6 islands constitute 13.3% of nesting in the Cape Verdean archipelago (López Jurado 2007, Lino et al. 2010, Marco et al. 2012, TAOLA unpubl. data). In the HES, Boa Vista would be the only island to have no nesting beaches that would reach critical upper temperatures.

4. DISCUSSION

In the face of climate change, it is important to model the potential effects of temperature increase on biodiversity to gain insight into which popula-

tions and species may be negatively affected, and which populations may be able to adapt (Estrada et al. 2016). Patterns of warming are expected to be heterogeneous across the planet (IPCC 2007); therefore, it is important to study biodiversity, where possible, at scales appropriate to detect such adaptive capacity. For example, Böhm et al. (2016) suggested that one-fifth of reptile species may be ‘highly vulnerable’ to climate change, with hotspots for the wider Caribbean and Australia. To date, few marine turtle rookeries have been studied at a population scale regarding sex ratios (Jensen et al. 2018), yet this is key to ensure that climate change interventions can be planned properly. The present study has collected empirical data for the entire nesting range for the Cape Verde loggerhead turtle rookery, which hosts up to 15% of the global nesting population of loggerhead turtles and 22% of all loggerheads nesting in the Atlantic (Marco et al. 2012). Although T_{PIV} has not been determined for the Cape Verde population, and thus our results are indicative, we suggest that the population produces predominantly females and that it is likely to become extremely skewed in the future with climate change.

4.1. Capacity to adapt

In reality, it is likely that adaptation by loggerhead turtles to future climate conditions will happen to some degree. In other rookeries, loggerhead turtle nesting appears to be shifting to earlier (cooler) times of the year as sea surface temperatures increase (Weishampel et al. 2004), which could increase male hatchling production. In Cape Verde, turtles currently nest during the warmest part of the year, meaning that cooler conditions are available for them earlier or later in the year (Abella-Perez et al. 2016, Laloë et al. 2017). However, earlier nesting has been shown to reduce the length of the nesting season

(Pike et al. 2006), which could increase competition for nesting sites or reduce total fecundity, as females might nest fewer times in a given nesting season (Pike et al. 2006). While some marine turtle populations could also adapt by nesting at higher latitudes where incubation conditions should be cooler, for turtles nesting on the Cape Verde archipelago, the next closest land at higher latitude is ~700 km away on the west African coast. As well as the long distance to the continent, there is a strong barrier to dispersal, as the Atlantic Ocean towards the north is much colder due to upwelling events; thus, loggerheads attempting to disperse to the North Atlantic might have reduced fecundity due to longer nesting intervals (Hays et al. 2002). Another point to note is that legal and illegal harvesting of marine turtles occurs on some beaches of the west and central African continent (Tanner 2013, Humber et al. 2014) and may be as high as the levels reported in Cape Verde (as much as 6% of nesting females, hundreds of individuals per year; Marco et al. 2012), meaning that successful colonisation of nesting beaches in those locations may be partially offset by hunting.

Nesting turtles could also influence incubation temperature by changing the depth at which nests are laid (Kamel & Mrosovsky 2006) or by nesting in areas with vegetation cover (which could potentially increase shading and thus reduce incubation temperatures for the developing embryos; McGaugh et al. 2010). Whether these responses can be exhibited by loggerhead turtles nesting in Cape Verde remain to be investigated. Recent research has suggested that the role of sand moisture has been largely overlooked in its role in influencing primary sex ratios, with nests at female-producing temperatures still producing male offspring if sand moisture is sufficiently high (Wyneken & Lolavar 2015). If, as predicted, future climate conditions lead to increased frequency of storm events, some of the feminising effect of temperature could be offset by increased prevalence and intensity of rainfall. It is also possible that the population as a whole could evolve via thermal physiology, as there is significant variation in heat-shock gene expression both at clutch and population levels in sea turtles (Tedeschi et al. 2016).

4.2. Sex ratios and mortality

Considering appropriate caveats (Wyneken & Lolavar 2015), the results of the present study suggest that overall primary sex ratios across the Cape Verde archipelago are presently approximately 84%

female. This study is the first to demonstrate this via empirical measurements of sand temperatures across the whole nesting rookery, as previous studies have focussed on single islands, such as Boa Vista and Sal (Laloë et al. 2014, Abella-Perez et al. 2016), and no previous studies have collected data on the islands of Fogo, Sao Nicolau, Santiago or Maio, where approximately 12% of nesting (approximately 1300 nests yr^{-1}) occurs (Marco et al. 2011). Our data suggest that hatchling production on these other islands is strongly female-biased.

The results also show that female production would increase in future LES, MES and HES without sufficient adaptation or selection (i.e. by temporal selection, spatial selection or thermal physiological evolution). Under the LES, there would only be an estimated 0.14% males produced across the whole population, and under the MES and HES, male production will completely cease on most islands. This has the potential to affect the population, which hosts approximately 12 000 to 20 000 nests yr^{-1} , or between 9 and 15% of global nesting by the species (Marco et al. 2011, 2012, Casale & Tucker 2017). Boa Vista, however, would continue to produce a very small proportion of male hatchlings until 3.4°C of warming had occurred. At present, mixed-stock analysis suggests that CC-A1 haplotypes appear to be shared across the Cape Verdean islands and between Cape Verde and other Atlantic rookeries. This suggests that the few males from Boa Vista could mate with females from other islands, although the shared haplotypes could be an artefact of their relative evolutionary age, with the Cape Verdean loggerhead rookery being the oldest in the Atlantic (Shamblin et al. 2014). The contrast in potential resilience between Boa Vista and the other Cape Verdean islands is of note, and suggests that Boa Vista may represent the best refuge from climate change for this globally important population. Minor rookeries were not included in this study, and hence it is unknown what the effect of climate change will be on these minor islands and beaches. It is possible that these minor rookeries could also provide male hatchlings to support the population in the future warming climate.

Our results also suggest that a change in spatial nest distribution could have a significant effect on the overall sex ratio for the Cape Verdean population. Currently, the majority of nesting is occurring on Boa Vista, which provides a refuge for the production of male hatchlings. If the spatial nest distribution changes such that a lower proportion of nests are laid on Boa Vista, this would decrease the proportion of

male hatchlings being produced. On the other hand, if the shift was to occur such that a larger proportion of nests occurred on Boa Vista, this would reduce the sex ratio skew to be less female biased. Continued long-term nest monitoring on all of the islands will be key to both further our understanding of the spatial distribution of nesting on the national level and to follow the nation-wide trend in nest numbers in the decades to come.

Our study highlights the conservation concerns for the future of this major loggerhead population, including the need for a better understanding of management strategies and research into the potential for behavioural adaptation. Estimates suggest that if the current rate of temperature increase is sustained, climate change is likely to increase global mean temperatures by 1.5°C between 2030 and 2052 (IPCC 2018). As the rates of greenhouse gas emission are not currently slowing, the climate could be 'committed' to an MES or HES scenario by 2100 rather than the LES scenario which has been included in this study.

4.3. Conclusion

We present the first-ever population-wide assessment of both current and future estimated primary sex ratios for the third-largest loggerhead turtle rookery in the world (Marco et al. 2011, 2012). Previous work (Abella-Perez et al. 2016) has highlighted that Boa Vista, where the majority of nesting occurs, should be relatively resilient to climate change; here we showed that similar resilience does not exist on other islands. Coastal development of the Cape Verde islands is increasing at a huge rate (Marco et al. 2012), with massive socio-economic implications for the Cape Verde economy. As marine turtles have previously been exposed to climate change (between the Pleistocene and the Paleocene) and survived (Nicholson et al. 2015), it is assumed that they may retain some capacity to adapt to changing temperatures (Estrada et al. 2016). However, climate change is now occurring at a faster pace than in the past (Rafsnider 2013), which could potentially uncouple adaptive capacity. This estimate could be improved by conducting experiments in Cape Verde to determine the Cape Verdean pivotal temperature and the thermosensitive period using a 'switch-back' experiment (Stubbs et al. 2014).

Data archive. Data supporting the results are available at <https://zenodo.org/record/3262215>.

Acknowledgements. We thank the following people for their help during data collection in the field: Albert Taxonera, Berta Renom, Jessemine da Graça, Ravidson Monteiro, Tommy Melo, Jorge Melo, José Cabral, Sidney Abreu, Herculano Dinis, Adalzira Marques, Ilse Drescher, Mara Abu-Raya, Corrine Almeida, Franziska Koenen, Sonia Araujo and Ana Veiga.

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Appendix. Overall primary sex ratios (% female) of the Cape Verdean population of loggerhead turtles weighted by spatial nesting. Three different pivotal temperatures (T_{PIV}) are shown, including the minimum, median and maximum T_{PIV} for loggerhead populations globally (Hawkes et al. 2009). These were used to calculate the sex ratios for current temperatures, as well as for future low-, mid- and high-emissions scenarios

T_{PIV} (°C)	Emissions scenario	% female
30.5 (maximum)	Current	19.1
	Low	89.2
	Mid	97.9
	High	99.7
29.25 (median)	Current	87.8
	Low	99.8
	Mid	100
	High	100
27.5 (minimum)	Current	100
	Low	100
	Mid	100
	High	100

*Editorial responsibility: Graeme Hays,
Burwood, Victoria, Australia*

*Submitted: July 5, 2018; Accepted: April 8, 2019
Proofs received from author(s): June 29, 2019*