1 **Highly feminised sex ratio estimations for the world's third largest nesting**

2 **aggregation of the loggerhead sea turtle**

3 **Running page head:** Feminised loggerhead sex ratios.

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15

32   **Abstract**

33   Despite being a fundamental life history character, there is a paucity of population-wide,

34   data-driven studies of primary sex ratios for any marine turtle species. The Republic of Cape

35   Verde hosts the third largest nesting population of loggerhead turtles in the world (hosting

36   up to 15% of global nesting by the species). Weighting for the spatial distribution of nests,

37   we estimate that 84% female hatchlings are currently likely produced across the population,

38   with 85% of nests laid on Boa Vista, where incubation temperatures were coolest. In future

39   climate change scenarios (by 2100), irrespective of beach, island or sand colour, sex ratios

40   reach over 99% female, and three islands (Fogo, Sao Nicolau, Santiago) would cease to

41   produce males, with >90% of nests incubating at lethally high temperatures. Given that

42   most of the population cannot move to nest on cooler islands, we highlight that temporal

43   refugia are amongst primary means available to this population to adapt. Under Low

44   Emissions Scenario, without phenological adaptation, there would only be an estimated

45   0.14% males produced across the whole population but in Mid and High Emissions

46   Scenarios, male production may cease on most islands.

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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 years (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 the previous years and may be too fast to enable species to adapt (Quintero & Wiens 2013). Ectothermic taxa, such as sea turtles, may be more likely to be negatively affected by climate change (Bohm 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 et al. 2015).

1.1 Temperature dependent sex determination

Many reptile species (e.g. turtles, crocodilians 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 in Hawkes et al. 2009). In most marine turtle rookeries that have been studied, primary sex ratios (the sex ratio at the point of sex determination) are 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 one male mates with multiple females) has been shown in other species which display biased sex ratios, thereby stabilising

80   the population (Wright et al. 2012). In marine turtles, females have a breeding interval of

81   two to three years, whereas it is assumed that males mate every year. This would therefore

82   mean that less males would be required in the population to maintain a stable breeding

83   population (Hays et al. 2014). The Operational Sex Ratio (the ratio of breeding males to

84   females) is not yet comprehensively described across global rookeries (but see Lee et al.

85   2017), but may not be balanced in some areas, for example, in Ghana 'by-catch' (or

86   incidental fishing capture) data showed only female loggerhead (*Caretta caretta*) turtles

87   were captured in coastal waters throughout the four month study period during the nesting

88   season (Tanner 2014), which suggested a very low male presence in the overall population,

89   or early departure from the breeding area by males. In contrast, in foraging areas in Greece

90   the percentage of males can be much higher, ranging from 31 to 55% male (Rees et al.

91   2013). Furthermore, multiple paternity has been recorded in all marine turtle species

92   (Wright et al. 2012, Tedeschi et al. 2014, Lee et al. 2017), which means a polygamous mating

93   system is already present. This would assist adaptive capacity as it is a more flexible mating

94   system allowing for sex ratio bias in a population without causing a population decline.

95

96   ***1.2 Maternal behaviour***

97   Although there is no parental care in marine turtles, turtles usually select nest-sites that

98   should be beneficial for the development of offspring. It has been suggested that to

99   maintain current nest temperatures in future warmer climates, turtles could nest closer to

100   the water, where evaporative cooling may be increased, in cooler parts of the nesting range

101   (e.g. at higher latitudes, or on a smaller scale, on lighter sand beaches, or beaches with

102   more shade), or at earlier and later times of the year where and when temperatures may be

103   cooler (Witt et al. 2010, Fuentes et al. 2011, Abella-Perez et al. 2016).

104   There have been few data-driven assessments to date of primary sex ratios across entire

105   nesting rookeries for any marine turtle species and even fewer across an entire population

106   of marine turtles (Fuentes et al. 2011, Jensen et al. 2018). Most studies measure sand or

107   nest temperature at just a few key sites and extrapolate (Wyneken & Lolavar 2015), which

108   fails to recognise intra-beach (spatial and geomorphological), intra-individual, intra-regional,

109   intra-annual variation or differences in nesting seasonality between years. Such insights into

110   likely change to primary sex ratios are therefore helpful but potentially misleading at a

111   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 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 2015), and may be the oldest population in the Atlantic (Shamblin et al. 2014). Most of the nesting is concentrated on 40km 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 one of the Cape Verdean islands. The present study, by contrast, uses empirical measurements of temperature across nine 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 18th July and 15th November (inclusively) of 2012, 2013 and 2014, sand temperature data were recorded using Tidbit HOBO temperature data loggers ('TDLs' from hereon; accuracy ± 0.25 °C; https://www.tempcon.co.uk) buried at a depth of 40cm (the mean depth of loggerhead nests in Cape Verde) (Varo-Cruz et al. 2007) on nine of the Cape Verde islands: Sao Vicente, Santa Lucia, Sao Nicolau, Sal, Boa Vista, Maio, Santiago, Fogo, and Illeu de Cima (Fig. 1). Islands and beaches were selected based on historical nesting data from TAOLA (The Cape Verdean Sea Turtle Network), from which the beaches with the highest nesting densities were chosen. All the TDLs were inter-compared prior to use and were only accepted for the study if they were accurate to within ± 0.1 °C of the National Measurement Accreditation Service (NAMAS) standards. TDLs were programmed to record temperature every 30 minutes. In total, 31 TDLs were buried in 2012, 31 in 2013, and 32 in 2014 on 40 beaches on the nine islands (mean four beaches per island, range two to eight, 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 six islands have temperature data for all three 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). The Cape Verdean Sea Turtle Network (TAOLA) have found that significant nesting occurs on the Cape Verde archipelago from 1st July to 10th October. The thermosensitive period was determined by assuming sex determination period starts approximately 18 days after egg laying and finishes at day 36 of incubation (Mrosovsky et al. 1999, Woolgar et al. 2013), and as the thermosensitive period occurs in the middle third of incubation (Woolgar et al. 2013), we have therefore only considered data from 18th July until 15th November.

2.2 Sand reflectance

Sand samples (n= three from each beach), weighing 50g each, were collected from 31 beaches where temperature data loggers had been buried. Samples were collected from the sand column directly above the temperature data loggers. The luminosity of each sand sample (measured in percentage reflectance to ± 0.01% accuracy, where 0% = black and 100% = white) was recorded using a calibrated Spectrophotometer CM-2600d/2500d

157 (Konica Minolta) in the Consejo Superior de Investigaciones Científicas (CSIC) laboratories, in

158 Seville, Spain, (http://www.konicaminolta.eu/en/measuring-instruments/products/colour-

159 measurement.html). Each sand sample was measured three times under lab conditions and

160 the mean of the three values used per beach. Due to logistical reasons, sand samples were

161 not collected at Illeu de Cima and Santa Lucia.

162

163 ### 2.3 Estimating sex ratio

164 The pivotal temperature (T_{PIV}) has not been determined for loggerhead turtles nesting in

165 Cape Verde, but is relatively conserved across the populations it has been described in (from

166 27.5 °C to 30.5 °C; Hawkes et al. 2009; Appendix Table 1.). The actual temperatures that

167 turtle eggs experience during incubation also depends on the three-dimensional location of

168 nests, and the time of year in which they were laid. In addition, Wyneken & Lolavar (2015)

169 presented new data concerning nest moisture that suggested that male offspring can be

170 produced above T_{PIV} if there is sufficient moisture. It is thus extremely challenging for any

171 study to accurately estimate what the primary sex ratio may be, although a raft of previous

172 studies have done so (Wyneken & Lolavar 2015). Taking this into account, we estimate the

173 potential primary sex ratios using the following equation from (Mrosovsky et al. 2002), with

174 the median T_{PIV} study for loggerhead turtles (please see Appendix Table 1 for minimum and

175 maximum T_{PIV}):

176
$$Y = \frac{100}{1 + e^{((a-b)\times 2.767)}}$$

177 Where Y = percent females, a = pivotal temperature for loggerhead turtles on the eastern

178 beaches of USA (29.25 °C) (Marcovaldi et al. 1997) and, b = mean thermosensitive period

179 temperature. Mean thermosensitive period temperature was estimated as the product of

180 sand temperature and metabolic heating, the heat produced by the eggs during incubation.

181 Mean metabolic heating has been estimated at 0.5 °C on Boa Vista and Sal (Laloë et al.

182 2014, Abella-Perez et al. 2016). It is important to note that the pivotal temperature varies

183 between nesting sites (Mrosovsky et al. 2002, Woolgar et al. 2013, Wyneken & Lolavar

184 2015) and although this has never been empirically determined for the Cape Verde rookery,

185 the pivotal temperature for the Mediteranean, Brazil and USA are all very similar, and hence

186 the USA population's pivotal temperature was used for this study (Mrosovsky et al. 2002).

187 Sex is determined during the middle third of embryogenesis, which may not be the same as

188 the middle third of the total incubation period (Wyneken & Lolavar 2015). Unable to derive

189 our own local pivotal temperature or monitor embryogenesis in the field, we therefore

190 cautiously use the middle third, generalised pivotal temperature approach but recognise

191 that reality may differ.

192

193 Current hatchling production was estimated by weighting primary sex ratios (as calculated

194 above) by spatial nest abundance, using previous estimates of annual nesting density in the

195 Cape Verdean population from multi-year nest counts in all beaches using Cape Verdean Sea

196 Turtle Network (TAOLA) and previously published data (López Jurado 2007, Lino et al. 2010).

197 The sites selected include the islands with the majority of nesting (over 100 nests laid per

198 year) and the beaches with the highest documented nesting densities (Marco et al. 2011),

199 which represent approximately 99% of the current nesting activity in Cape Verde. These

200 estimates do not include any locations with minimal (<100 nests per year) or random

201 nesting occurrences, as it would be difficult to include all nesting occurrences, but we

202 emphasise that they could be important for the population as historical information has

203 suggested that nesting was more uniform centuries ago, with loggerhead nesting abundant

204 throughout the Cape Verdes (López-Jurado 2007). Hence, we cautiously use the phrase

205 "entire archipelago" when referring to these results as although they are not exhaustive,

206 they include the majority of nesting locations recorded for loggerheads on the Cape

207 Verdean archipelago.

208 For this study, although the sex ratios are weighted to account for spatial distribution they

209 are not weighted according to temporal distribution. Due to this, we acknowledge that this

210 assumes equal nesting across the nesting period, whereas this is likely not to be the case.

211 However, as more nests are currently laid in warmer periods, our results may underestimate

212 the percentage female sex ratios and should therefore be viewed cautiously when

213 considering the effects of global climate change on the population.

214

215 ***2.4 Estimating future temperatures and sex ratios***

216 The Intergovernmental Panel on Climate Change (IPCC) predicts that surface air

217 temperature will likely increase to 1.8 °C, 2.8 °C and 3.4 °C for the B1, A1B and A2 scenarios

218 by 2090 to 2099 (IPCC 2007), which will be referred to as Low Emissions Scenario (LES), Mid

219 Emissions Scenario (MES), and High Emissions Scenario (HES) hereafter. As these estimates

220   are from a global climate model, there would be variation expected regionally and

221   temporally (i.e. for seasonal differences). In previous studies, in USA and Greece (Hawkes

222   et al. 2007, Katselidis et al. 2012), sand temperature increases by 0.72 °C for every 1 °C of

223   air temperature increase so we estimated future sex ratios by adding the corresponding

224   sand temperature increase from predicted air temperature increases (IPCC 2007) to current

225   sand temperatures (i.e. adjusting 'b' in the equation before calculating future sex ratios).

226   This has been recorded for both Greece (Katselidis et al. 2012) and USA (Hawkes et al.

227   2007), which assumes that this will be similar for Cape Verde as it is located between these

228   two locations.

229

230   *2.5 Statistical tests*

231   All statistical analyses were completed in R (R Core Development Team). All data were

232   tested for normality using Shapiro-Wilks tests; luminosity data were normal, temperature

233   data were non-normal. Non-parametric statistical analyses were completed on sex ratio

234   estimates. As the data included multiple years (with data from different beaches collected in

235   different years), the temperature was compared between years (for each beach) using a

236   Kruskal-Wallis test. Reflectance was split into light and dark beaches based on k-means

237   cluster analyses (visualised on a histogram; Fig. 3), with luminosities above 40% (of the

238   perceived brightness) classed as a light beach (n=19), and those under 40% as dark beaches

239   (n=11). A Wilcox-test was used to analyse the correlation between temperature and sand

240   colour; an F-test was used to analyse any differences between sex ratios and the sand

241   colour; and Kruskal-Wallis tests were used to analyse any significant differences between

242   sex ratios within and between islands. We considered that statistical significant was

243   denoted by an alpha <0.05.

3. RESULTS

In total 94 TDL deployments collected sand temperature data every half hour from 18th July to 15th November inclusively in 2012, 2013 and 2014 (mean 108 days per TDL, range 32 to 121 days per TDL). Sand temperature during the nesting season varied from a minimum half hourly point count of 25.1 °C (Porto Lapa, Sao Nicolau, 2013) to maximum 38.9 °C (Sao Felipe, Fogo, 2013) (Fig. 2a). There was no significant difference in sand temperature between years (Kruskal-Wallis x^2 = 1.485, p=0.476; Fig. 2b), 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 was 30.0°C, range 26.1 to 37.0 °C; mean dark sand beach 31.9 °C, range 25.1 to 38.9 °C; Wilcox W=1396, p<0.001; Fig. 3b).

3.1 Estimated sex ratios by island

Mean estimated primary sex ratios range from a minimum of 67.5% females on Boa Vista to a maximum of 100% on Fogo, with three 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 to 100%) produced on light sand beaches and 100% female (range 100 to 100%) on dark sand beaches. There was also no significant difference in estimated primary sex ratios between islands (Kruskal-Wallis x^2 =8, p=0.434; Fig. 4), or between beaches within each island (x^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 per year; Marco et al. 2012), a further 1,000 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,

275   99.9% in Low Emissions Scenario, 100% in Mid Emissions Scenario and 100% in High

276   Emissions Scenario (Fig. 4b, d, f, h).

277

278   ### 3.3 Estimated future sex ratios by island

279   In future Low Emissions Scenario (1.8 °C increase in mean air temperature) estimated

280   primary sex ratios would range from 98.7% females on the island of Boa Vista to 100% on

281   the islands of Fogo, Maio, Illeu de Cima, Sao Nicolau, and Santiago. Although only a few

282   beaches would cease to produce any male hatchlings in Low Emissions Scenario, only three

283   beaches on Boa Vista would produce more than 0.01% male hatchlings (Varandinha, 6.3%

284   male; Boa Esperanza, 0.9% male; Lacacao, 0.2% male). In future Mid Emissions Scenarios

285   only Boa Vista would be producing any male hatchlings (0.01% male hatchlings produced),

286   with no male hatchlings produced on any Cape Verdean island in High Emissions Scenarios.

287

288   ### 3.4 Incubation above critical upper temperatures

289   At current temperatures, nests on the island of Fogo already experience critically high

290   incubation temperatures above 35 °C for 25.2% (or 30.44 days) of the study period (Fig.

291   4a,b), with Sao Felipe (Fogo) exceeding the critical upper temperature for 75.5% (or 91.34

292   days) of the study period. In all (LES, MES and HES) future scenarios between 41.3 and

293   81.7% of nests on Fogo would be incubating above critical upper temperatures (LES: 41.3%,

294   MES: 72.5%, HES: 81.7% of the study period for the whole island). On Sao Felipe beach,

295   Fogo, the model suggests that over 93.2% of the study period would be over critical upper

296   temperatures by LES. By MES a total of 16 beaches (Sao Felipe (Fogo), Praia Cais (Fogo),

297   Praia Grande (Fogo), Djam Padja (Maio), Lomba Greija (Maio), Santa Clara (Maio), Soca

298   (Illeu de Cima), Bequinho (Illeu de Cima), Praia Canoa (Illeu de Cima), Porto Lapa (Sao

299   Nicolau), Praia Grande (Sao Nicolau), Achada Baleia (Santiago), Medronho (Santiago), Rib

300   das Pratas (Santiago), Sao Francisco (Santiago), Topim (Sao Vicente)) would have reached

301   critical upper temperatures for over 20% of the study period. Beaches on these six islands

302   constitute 13.3% of nesting in the Cape Verdean archipelago (López Jurado 2007, Lino et al.

303   2010, Marco et al. 2012, Cape Verdean Sea Turtle Network (TAOLA)). In HES Boa Vista would

304   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 populations and species may be negatively affected, and which 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. Bohm et al. (2016), for example, 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 by loggerhead turtles, and 22% of all loggerhead nesting in the Atlantic (Marco et al. 2012). Although the pivotal temperature 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 in the warmest part of the year, meaning that cooler conditions are available for them earlier or later in the year (Laloë et al. 2017, Abella-Perez et al. 2016). Earlier nesting has been shown, however, to reduce the length of nesting seasons (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 some >700km 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 sea towards the north

337 is much colder due to upwelling events, so loggerheads attempting to disperse to the North
338 Atlantic might have reduced fecundity due to longer nesting intervals (Hays et al. 2002).
339 Another point to note is that legal and illegal harvesting of marine turtles occurs on some
340 beaches of the west and central African continent (Tanner 2013, Humber et al. 2014), and
341 may be as high as the levels reported in Cape Verde (as much as 6% of nesting females,
342 hundreds of individuals per year; Marco et al. 2012) meaning successful colonisation of
343 nesting beaches there may be partially offset by hunting.

344

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

358

359 ***4.2 Sex ratios and mortality***

360 Considering appropriate caveats (Wyneken & Lolavar 2015), the results of the present study
361 suggest that, overall primary sex ratios across the Cape Verde archipelago are presently
362 approximately 84% female. This study is the first to demonstrate this via empirical
363 measurements of sand temperatures across the whole nesting rookery, as previous studies
364 have focused on single islands, such as Boa Vista and Sal (Laloë et al. 2014, Abella-Perez et
365 al. 2016), and no previous studies have collected data on the islands of Fogo, Sao Nicolau,
366 Santiago or Maio, where approximately 12% of nesting (approximately 1,300 nests per year)
367 occurs (Marco et al. 2011). Our data suggests that hatchling production on these other
368 islands is strongly female biased.

369

370   The results also show that female production would increase in future Low, Medium and

371 High emissions scenarios without sufficient adaptation or selection (i.e. by temporal

372 selection, spatial selection, thermal physiological evolution). Under LES, there would only be

373 an estimated 0.14% males produced across the whole population but in MES and HES, male

374 production will completely cease on most islands. This has the potential to affect the

375 population, which hosts approximately 12 to 20,000 nests per year, or between 9 and 15%

376 of global nesting by the species (Marco et al. 2011, Marco et al. 2012, Casale & Tucker

377 2015). Boa Vista, however, would continue to produce a very small proportion of male

378 hatchlings until 3.4 °C of warming had occurred. At present mixed stock analysis suggests

379 that CC-A1 haplotypes appear to be shared across the Cape Verdean islands and between

380 Cape Verde and other Atlantic rookeries. This suggests that the few males from Boa Vista

381 could mate with females from other islands, although the shared haplotypes could be an

382 artefact of their relative evolutionary age, with the Cape Verdean loggerhead rookery being

383 the oldest in the Atlantic (Shamblin et al. 2014). The contrast in potential resilience between

384 Boa Vista and the other Cape Verdean islands is of note, and suggests that Boa Vista may

385 represent the best refuge from climate change for this globally important population. Minor

386 rookeries were not included in this study, and hence it is unknown as to the effect that

387 climate change will have on these minor islands and beaches. It could be that these minor

388 rookeries could also provide male hatchlings to support the population in the future

389 warming climate.

390 The results also suggest that a change in spatial nest distribution could have a significant

391 effect on the overall sex ratio for the Cape Verdean population. Currently, the majority of

392 nesting is occurring on Boa Vista, which is providing a refuge for the male production of

393 hatchlings. If the spatial nest distribution alters so that a lower proportion of nests are laid

394 on Boa Vista, this would decrease the proportion of male hatchlings being produced. On the

395 other hand, if the shift was to occur so that a larger proportion of nests occurred on Boa

396 Vista this would reduce the sex ratio skew to be less female biased. Continued long-term

397 nest monitoring on all the islands will be key to both further our understanding of the

398 spatial distribution of nesting on the national level and to follow the nation-wide trend in

399 nest numbers in the decades to come.

400

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. Current 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 a MES or HES scenario by 2100 rather than the LES scenario which has been included in this study.

5. 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, Marco et al. 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, but we showed that similar resilience does not exist on other islands. Worryingly, 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 (Refsnider 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).

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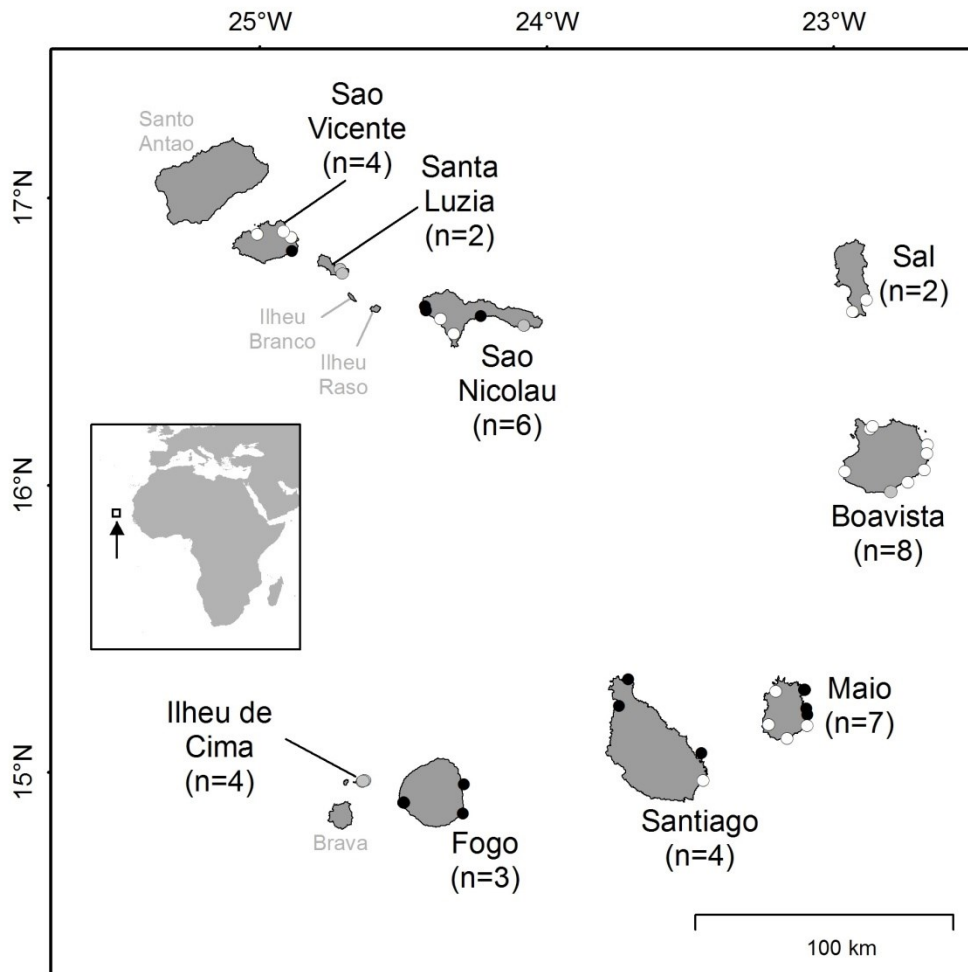
Figure 1: Map showing locations of the 40 nesting beaches (marked with dots; across the
nine islands, labelled in black) in the Republic of Cape Verde (inset showing location off the
West African coast) at which sand temperature and luminosity data was recorded in the
present study (black dots show dark sand beaches, white dots show light sand beaches, grey
dots show beaches from which luminosity data was not collected, number of loggers on
each island indicated). Also labelled in grey are major Islands of the Cape Verdes that were
not studied.
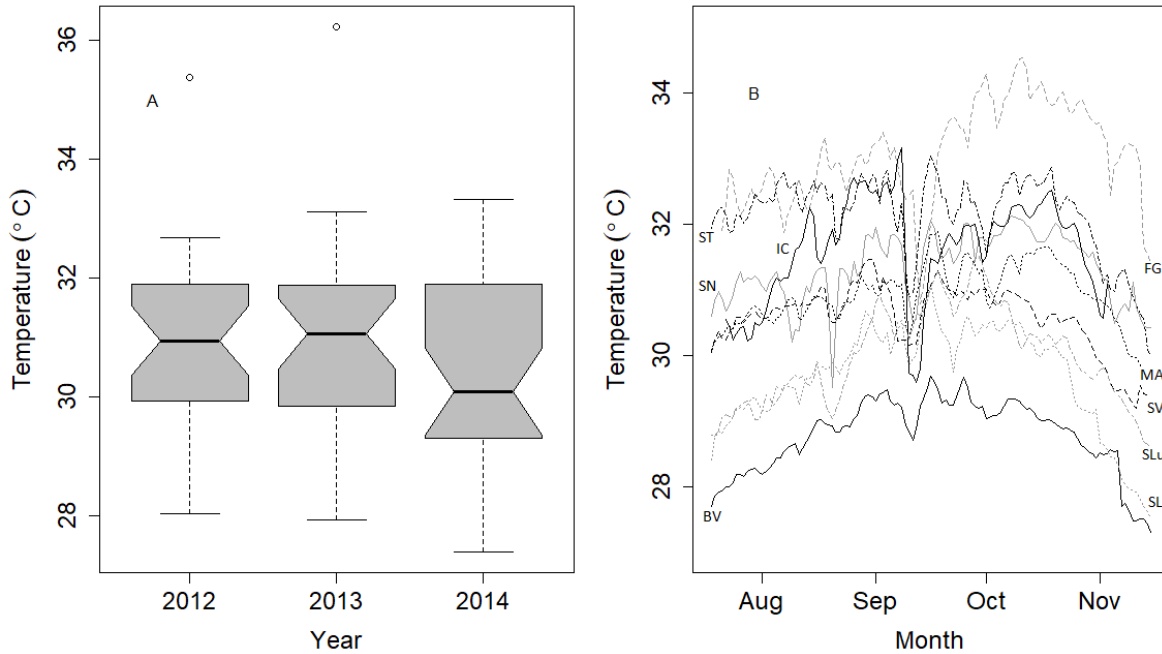
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569   Figure 2: (A) Boxplots showing sand temperatures recorded in the three study years (boxes

570   show inter-quartile range, horizontal line shows median value, whiskers show range,

571   notches indicate 95% confidence interval of the median). The two outliers in 2012 and 2013

572   are shown as white dots. (B) Line plot showing mean sand temperature over the nesting

573   season for the nine islands (differing line styles for each island; Sao Vicente as a black large-

574   dashed line, Santa Lucia a grey small dot-dashed line, Sao Nicolau as a grey solid line, Sal as

575   a grey dotted line, Boa Vista as a black solid line, Maio as a black dotted line, Santiago as a

576   black small dot-dashed line, Fogo as a black solid line, and Illeu de Cima as a small dashed

577   grey line). A marked decrease in sand temperature can be seen in mid September as this is

578   the rainiest month of the year in the Cape Verde, which reduces sand temperature.
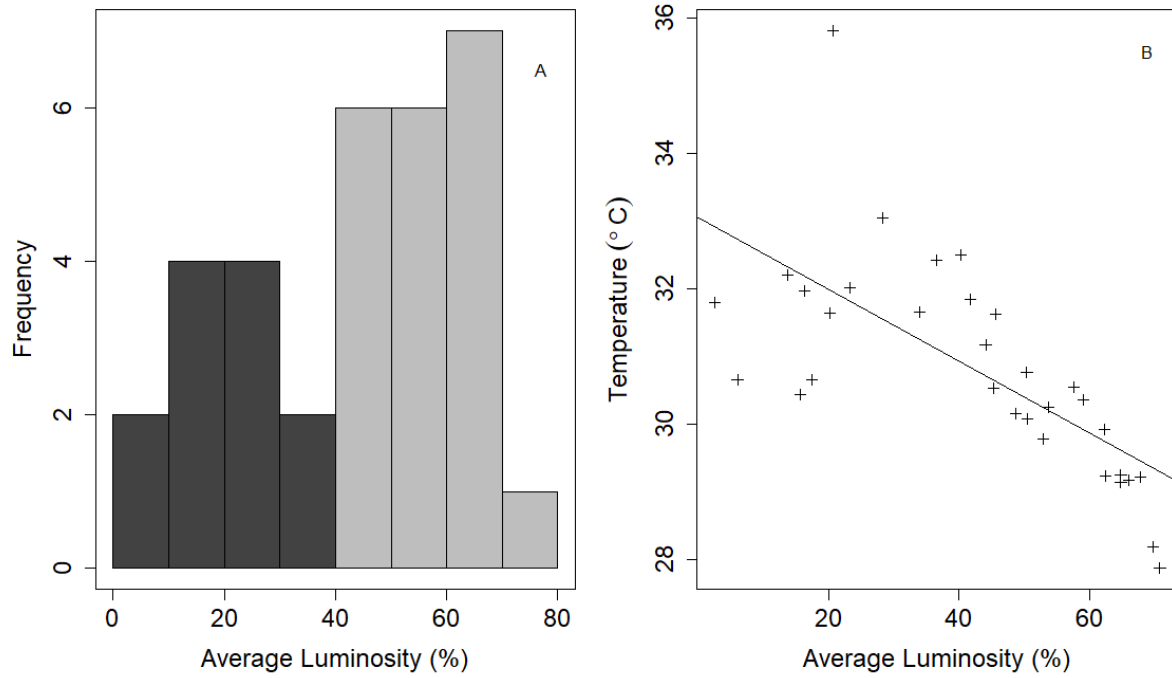
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580 Figure 3: (A) Frequency histogram of luminosity data collected from each beach (where

581 <40% are classed as dark sand beaches, and >40% classed as light sand beaches for the

582 present study), and (B) scatterplot showing average sand temperature (measured using

583 buried TDLs) plotted against average beach sand luminosity (measured as percent of light

584 reflected, where 0 = black and 100 = white) for the 40 beaches studied across the Cape

585 Verde archipelago.
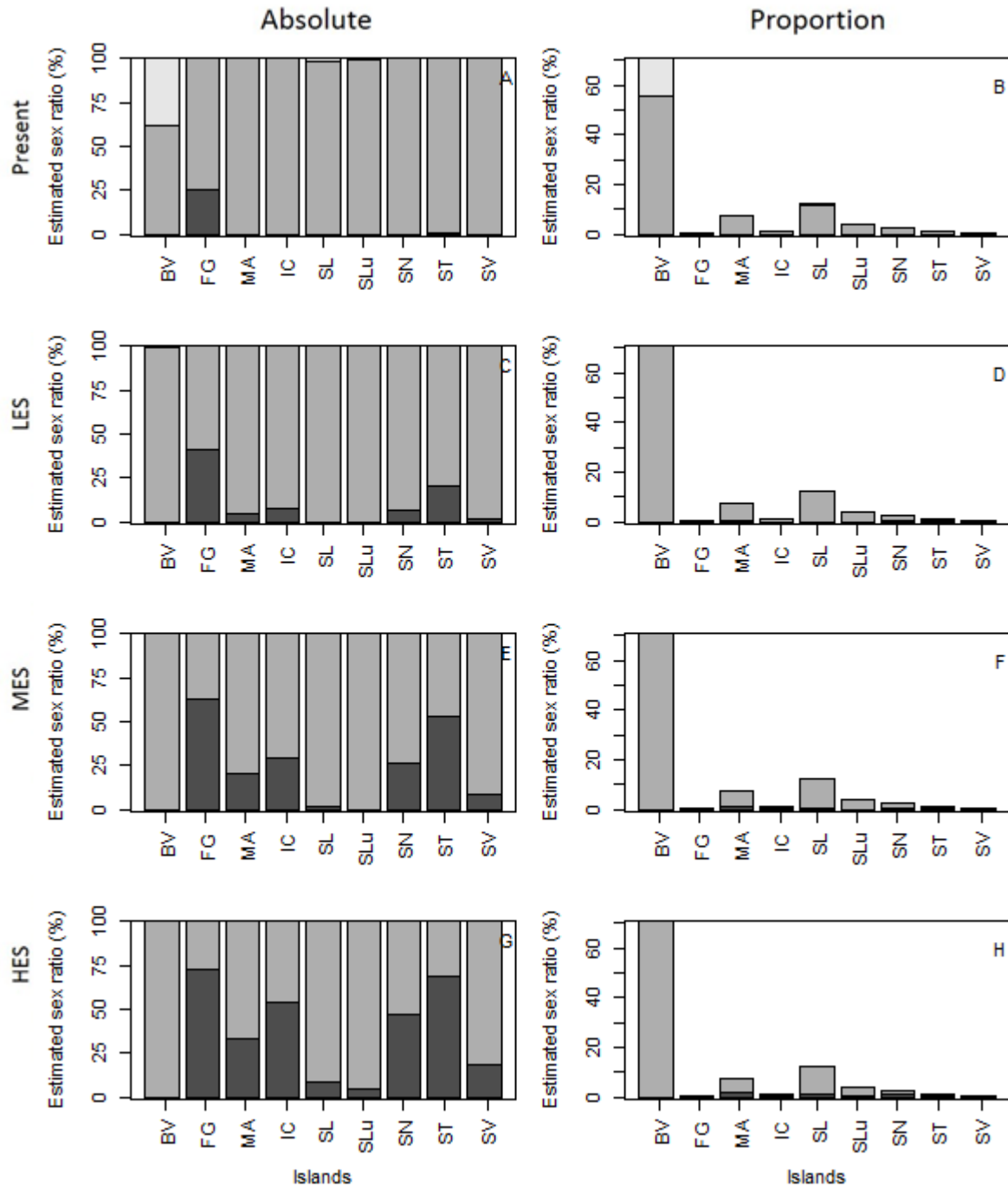
Figure 4: (A, C, E, G) Stacked histograms for each of the nine study islands showing absolute overall mean percent embryos incubating above the thermal maximum of 35 °C (dark grey shading), estimated % female hatchlings (mid grey shading), and estimated % male hatchlings (light grey shading). (B, D, F, H) Weighted histograms displaying the spatially proportionally corrected production of female and male hatchlings and nests incubating over the thermal maximum across the Cape Verde rookery by Island (symbology as in parts A, C, E, G). Top row (A, B) shows present conditions, second row (C,D) shows Low Emissions

594   Scenario, third row (E, F) shows Middle Emissions Scenario, and bottom row (G, H) shows

595   High Emissions Scenario (G, H).

596

597   **Appendix**

598   Table 1. Overall primary sex ratios (% female) of the Cape Verdean population of

599   loggerhead turtles weighted by spatial nesting. Three different T_{PIV} temperatures have been

600   used (°C), including the minimum, median and maximum T_{PIV} temperatures for loggerhead

601   populations globally (Hawkes et al. 2009). These have been used to calculate the sex ratios

602   for current temperatures, as well as future low, mid and high emissions scenarios.

T_{PIV} temperature (°C)	Emissions scenario	Primary sex ratio of Cape Verde (% female)
30.5 (Maximum)	Current	19.1
	Low	89.2
	Mid	97.9
	High	99.7
29.25 (Median T_{PIV})	Current	87.8
	Low	99.8
	Mid	100
	High	100
27.5 (Minimum)	Current	100
	Low	100
	Mid	100
	High	100

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