

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.
4

5 Claire E. Tanner¹, Adolfo Marco^{2,3}, Samir Martins², Elena Abella-Perez², Lucy A. Hawkes^{4*}
6

7 ¹ University of Exeter, College of Life and Environmental Sciences, Penryn Campus, Cornwall,
8 TR10 9FE, UK

9 ² BIOS.CV, Rua Milagro, Sal Rei, Boa Vista, Cape Verde

10 ³ Estacion Biologica de Donana, Consejo Superior de Investigaciones Científicas (CSIC), C
11 Americo Vespuccio, 41092 Sevilla, Spain

12 ⁴ University of Exeter, College of Life and Environmental Sciences, Hatherley Laboratories,
13 Streatham Campus, Exeter, Devon, EX4 4PS, UK

14 *Corresponding author L Hawkes l.hawkes@exeter.ac.uk
15

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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.

47

48 **1. INTRODUCTION**

49 Climate change is considered one of the greatest modern threats to biodiversity (Urban
50 2015). By 2050 models predict that up to 54% of species' extinctions could be attributed,
51 both directly (e.g. via temperature related embryo death) and indirectly (e.g. competition,
52 declining food sources), to climate change (Urban 2015). Global temperatures (mean air and
53 surface temperatures) have risen by approximately 0.6 °C in the past 100 years (IPCC 2014)
54 and are expected to rise a total of 2 °C between the pre-industrial period and 2030 (IPCC
55 2014), which is a much faster rate than the previous years and may be too fast to enable
56 species to adapt (Quintero & Wiens 2013). Ectothermic taxa, such as sea turtles, may be
57 more likely to be negatively affected by climate change (Bohm et al. 2016), as
58 environmental conditions affect their performance (Refsnider 2013), reproduction
59 (Starostova et al. 2012) and survival (Miller et al. 2004). Understanding and modelling the
60 response of species to climate change is a key future challenge (Urban et al. 2015).

61

62 ***1.1 Temperature dependent sex determination***

63 Many reptile species (e.g. turtles, crocodylians and some lizards) exhibit temperature
64 dependent sex determination (Refsnider 2013), where the temperature experienced during
65 development controls hormone expression and therefore determines offspring sex
66 (Tedeschi et al. 2016). In marine turtles, lower temperatures produce males and higher
67 temperatures produce females, with a 'pivotal temperature' (the constant incubation
68 temperature that produces a 1:1 ratio of hatchling males:females) of approximately 29 °C
69 for most marine species (reviewed in Hawkes et al. 2009). In most marine turtle rookeries
70 that have been studied, primary sex ratios (the sex ratio at the point of sex determination)
71 are strongly female biased, and may be expected to become more biased with increased
72 future temperatures (Hawkes et al. 2007, Katselidis et al. 2012, Jensen et al. 2018). If marine
73 turtles fail to adapt in pace with the rate of climate change, mortality could increase (Witt et
74 al. 2010, Fuentes et al. 2011) and male hatchling production could diminish to a point that
75 could reduce nest fertilisation rate (Witt et al. 2010, Katselidis et al. 2012, Jensen et al.
76 2018). Currently there is a debate as to whether marine turtles could buffer such effects
77 (Wright et al. 2012), through polygamy (Wright et al. 2012), and/or breeding frequency
78 (Tedeschi et al. 2014). Polygyny (a mating system where one male mates with multiple
79 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

112 host the third largest nesting population of loggerhead turtles in the world, with
113 approximately 12 to 20,000 nests laid per year, or between 9 and 15% of global nesting by
114 the species (López Jurado 2007, Marco et al. 2012, Casale & Tucker 2015), and may be the
115 oldest population in the Atlantic (Shamblin et al. 2014). Most of the nesting is concentrated
116 on 40km of beaches on just a few islands: Boa Vista, Maio, Sal and Sao Nicolau (López
117 Jurado 2007, Lino et al. 2010), which makes it possible to study the entire population. Laloë
118 et al. (2014) published an initial estimate of the sex ratio across the Cape Verdean rookery,
119 but their study was based on 24 temperature recorders on only one of the Cape Verdean
120 islands. The present study, by contrast, uses empirical measurements of temperature across
121 nine of the major islands (and 40 beaches) of the archipelago. We used previously published
122 equations to convert sand temperature to calculate primary sex ratios and estimate
123 potential future primary sex ratios considering climate change using predicted global
124 surface temperature increases.

125 **2. MATERIALS AND METHODS**

126 ***2.1 Sand temperature***

127 Between 18th July and 15th November (inclusively) of 2012, 2013 and 2014, sand
128 temperature data were recorded using Tidbit HOBO temperature data loggers ('TDLs' from
129 hereon; accuracy ± 0.25 °C; <https://www.temprocon.co.uk>) buried at a depth of 40cm (the
130 mean depth of loggerhead nests in Cape Verde) (Varo-Cruz et al. 2007) on nine of the Cape
131 Verde islands: Sao Vicente, Santa Lucia, Sao Nicolau, Sal, Boa Vista, Maio, Santiago, Fogo,
132 and Ilheu de Cima (Fig. 1). Islands and beaches were selected based on historical nesting data
133 from TAOLA (The Cape Verdean Sea Turtle Network), from which the beaches with the
134 highest nesting densities were chosen. All the TDLs were inter-compared prior to use and
135 were only accepted for the study if they were accurate to within ± 0.1 °C of the National
136 Measurement Accreditation Service (NAMAS) standards. TDLs were programmed to record
137 temperature every 30 minutes. In total, 31 TDLs were buried in 2012, 31 in 2013, and 32 in
138 2014 on 40 beaches on the nine islands (mean four beaches per island, range two to eight,
139 Fig. 1). Due to logistical reasons (TDLs lost, damaged or broken) not all the beaches could be
140 measured every year, and consequently only 18 beaches on six islands have temperature
141 data for all three years. Some islands (Sao Nicolau, Sao Vicente, Maio and Santiago) have
142 nesting beaches with light and dark sand, and hence TDLs were buried in both light and dark
143 sand beaches for this study (Fig. 1). The Cape Verdean Sea Turtle Network (TAOLA) have
144 found that significant nesting occurs on the Cape Verde archipelago from 1st July to 10th
145 October. The thermosensitive period was determined by assuming sex determination period
146 starts approximately 18 days after egg laying and finishes at day 36 of incubation
147 (Mrosovsky et al. 1999, Woolgar et al. 2013), and as the thermosensitive period occurs in
148 the middle third of incubation (Woolgar et al. 2013), we have therefore only considered
149 data from 18th July until 15th November.

150

151 ***2.2 Sand reflectance***

152 Sand samples (n= three from each beach), weighing 50g each, were collected from 31
153 beaches where temperature data loggers had been buried. Samples were collected from the
154 sand column directly above the temperature data loggers. The luminosity of each sand
155 sample (measured in percentage reflectance to $\pm 0.01\%$ accuracy, where 0% = black and
156 100% = 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-](http://www.konicaminolta.eu/en/measuring-instruments/products/colour-measurement.html)
159 [measurement.html](http://www.konicaminolta.eu/en/measuring-instruments/products/colour-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 Ilheu 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}):

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

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.

244 3. RESULTS

245 In total 94 TDL deployments collected sand temperature data every half hour from 18th July
246 to 15th November inclusively in 2012, 2013 and 2014 (mean 108 days per TDL, range 32 to
247 121 days per TDL). Sand temperature during the nesting season varied from a minimum half
248 hourly point count of 25.1 °C (Porto Lapa, Sao Nicolau, 2013) to maximum 38.9 °C (Sao
249 Felipe, Fogo, 2013) (Fig. 2a). There was no significant difference in sand temperature
250 between years (Kruskal-Wallis $\chi^2 = 1.485$, $p=0.476$; Fig. 2b), hence average sand
251 temperature for each beach irrespective of year was used in further analysis. Sand
252 temperatures were significantly different between light and dark beaches (mean half hourly
253 point count for light sand beach was 30.0°C, range 26.1 to 37.0 °C; mean dark sand beach
254 31.9 °C, range 25.1 to 38.9 °C; Wilcox $W=1396$, $p<0.001$; Fig. 3b).

255

256 **3.1 Estimated sex ratios by island**

257 Mean estimated primary sex ratios range from a minimum of 67.5% females on Boa Vista to
258 a maximum of 100% on Fogo, with three beaches on Boa Vista (Boa Esperanza, Lacacao and
259 Varandinha) estimated to produce more than 75% male hatchlings which accounts for
260 18.5% of nesting on Boa Vista (Fig. 4a,b). There was no significant difference between the
261 estimated primary sex ratios produced on light ($n=19$) and dark ($n=11$) sand beaches across
262 the archipelago ($F_{1,29}=1.66$, $p=0.208$) with 88.8% female (range 0.4 to 100%) produced on
263 light sand beaches and 100% female (range 100 to 100%) on dark sand beaches. There was
264 also no significant difference in estimated primary sex ratios between islands (Kruskal-Wallis
265 $\chi^2=8$, $p=0.434$; Fig. 4), or between beaches within each island ($\chi^2=39$, $p=0.47$).

266

267 **3.2 Estimated sex ratio of the population**

268 Loggerhead nesting is not spatially uniform across all islands of the Cape Verdean
269 archipelago, with highly variable annual densities, for example Boa Vista currently hosts
270 approximately 85% of all nests laid on Cape Verde (in excess of 10,000 nests per year; Marco
271 et al. 2012), a further 1,000 nests are laid per year in Sal (Lino et al. 2010) and minor nesting
272 occurs elsewhere. Accounting for spatial distribution of nests across the archipelago (i.e. the
273 proportion of all nests that are laid on each island, and assuming no future change), mean
274 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, Ilheu 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 Padjá (Maio), Lomba Greija (Maio), Santa Clara (Maio), Soca
298 (Ilheu de Cima), Bequinho (Ilheu de Cima), Praia Canoa (Ilheu 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.

305 **4. DISCUSSION**

306 In the face of climate change it is important to model the potential effects of temperature
307 increase on biodiversity to gain insight into which populations and species may be
308 negatively affected, and which may be able to adapt (Estrada et al. 2016). Patterns of
309 warming are expected to be heterogeneous across the planet (IPCC 2007), therefore it is
310 important to study biodiversity, where possible, at scales appropriate to detect such
311 adaptive capacity. Bohm et al. (2016), for example, suggested that one fifth of reptile
312 species may be 'highly vulnerable' to climate change, with hotspots for the wider Caribbean
313 and Australia. To date, few marine turtle rookeries have been studied at a population scale
314 regarding sex ratios (Jensen et al. 2018), yet this is key to ensure that climate change
315 interventions can be planned properly. The present study has collected empirical data for
316 the entire nesting range for the Cape Verde loggerhead turtle rookery, which hosts up to
317 15% of the global nesting by loggerhead turtles, and 22% of all loggerhead nesting in the
318 Atlantic (Marco et al. 2012). Although the pivotal temperature has not been determined for
319 the Cape Verde population, and thus our results are indicative, we suggest that the
320 population produces predominantly females and that it is likely to become extremely
321 skewed in the future with climate change.

322

323 ***4.1 Capacity to adapt***

324 In reality, it is likely that adaptation by loggerhead turtles to future climate conditions will
325 happen to some degree. In other rookeries, loggerhead turtle nesting appears to be shifting
326 to earlier (cooler) times of the year as sea surface temperatures increase (Weishampel et al.
327 2004), which could increase male hatchling production. In Cape Verde, turtles currently nest
328 in the warmest part of the year, meaning that cooler conditions are available for them
329 earlier or later in the year (Laloë et al. 2017, Abella-Perez et al. 2016). Earlier nesting has
330 been shown, however, to reduce the length of nesting seasons (Pike et al. 2006), which
331 could increase competition for nesting sites, or reduce total fecundity as females might nest
332 fewer times in a given nesting season (Pike et al. 2006). While some marine turtle
333 populations could also adapt by nesting at higher latitudes where incubation conditions
334 should be cooler, for turtles nesting on the Cape Verde archipelago, the next closest land at
335 higher latitude is some >700km away on the west African coast. As well as the long distance
336 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

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

409

410 **5. CONCLUSION**

411 We present the first ever population-wide assessment of both current and future estimated
412 primary sex ratios for the third largest loggerhead turtle rookery in the world (Marco et al.
413 2011, Marco et al. 2012). Previous work (Abella-Perez et al. 2016) has highlighted that Boa
414 Vista, where the majority of nesting occurs, should be relatively resilient to climate change,
415 but we showed that similar resilience does not exist on other islands. Worryingly, coastal
416 development of the Cape Verde islands is increasing at a huge rate (Marco et al. 2012), with
417 massive socio-economic implications for the Cape Verde economy. As marine turtles have
418 previously been exposed to climate change (between the Pleistocene and the Paleocene)
419 and survived (Nicholson et al. 2015), it is assumed that they may retain some capacity to
420 adapt to changing temperatures (Estrada et al. 2016). However, climate change is now
421 occurring at a faster pace than in the past (Refsnider 2013) which could potentially uncouple
422 adaptive capacity. This estimate could be improved by conducting experiments in Cape
423 Verde to determine the Cape Verdean pivotal temperature and the thermosensitive period
424 using a “switch-back” experiment (Stubbs et al. 2014).

425

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431 **REFERENCES**

432

433 Abella-Perez E, Marco A, Martins S, Hawkes LA (2016) Is this what a climate change-resilient
434 population of marine turtles looks like? *Biol Conserv* 193: 124–132

435 Bohm M, Cook D, Ma H, Davidson AD, Garcia A, Tapley B, Pearce-Kelly P, Carr J (2016) Hot
436 and bothered: using trait-based approaches to assess climate change vulnerability in
437 reptiles. *Biol Conserv* 204: 32–41

438 Casale P, Tucker AD (2015) *Caretta caretta*. The IUCN Red List of Threatened Species.

439 Estrada A, Morales-castilla I, Caplat P, Early R (2016) Usefulness of species traits in
440 predicting range shifts. *Trends Ecol Evol* 31: 190–203

441 Fuentes, M.M.P.B., Limpus, C.J., Hamann, M. (2011) Vulnerability of sea turtle nesting
442 grounds to climate change. *Glob Change Biol* 17: 140–153.

443 Hawkes LA, Broderick AC, Godfrey MH, Godley BJ (2007) Investigating the potential impacts
444 of climate change on a marine turtle population. *Glob Change Biol* 13: 923–932

445 Hawkes LA, Broderick AC, Godfrey MH, Godley BJ (2009) Climate change and marine turtles.
446 *Endanger Species Res* 7: 137–154

447 Hays GC, Broderick AC, Glen F, Godley BJ, Houghton JDR, Metcalfe JD (2002) Water
448 temperature and internesting intervals for loggerhead (*Caretta caretta*) and green
449 (*Chelonia mydas*) sea turtles. *J Therm Biol* 27: 429–432

450 Hays GC, Mazaris AD, Schofield G (2014) Different male vs. female breeding periodicity helps
451 mitigate offspring sex ratio skews in sea turtles. *Frontiers Mar Sci* 1:1–9

452 Humber F, Godley BJ, Broderick AC (2014) So excellent a fish: A global overview of legal
453 marine turtle fisheries. *Divers Distrib* 20: 579–590

454 IPCC (2007) Contribution of Working Group I to the Fourth Assessment Report of the
455 Intergovernmental Panel on Climate Change, 2007. In: Solomon S, Qin D, Manning M,
456 Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) Cambridge University Press.

457 IPCC (2014) Climate Change 2014: Synthesis Report. In: Pachauri RK, Meyer LA (eds)
458 Contribution of Working Groups I, II and III to the Fifth Assessment Report of the
459 Intergovernmental Panel on Climate Change. Geneva, Switzerland.

460 IPCC (2018) Global warming of 1.5 °C an IPCC special report on the impacts of global
461 warming of 1.5 °C above pre-industrial levels and related global greenhouse gas
462 emissions pathways, in the context of strengthening the global response to the threat
463 of climate change, sustainable development, and efforts to eradicate poverty. In: Allen
464 M, Babiker M, Chen Y, et al. First Joint Session of Working Groups I, II and III,
465 Cambridge University Press.

466 Jensen MP, Allen CD, Eguchi T, Bell IP, Lacasella EL, Hilton WA, Hof CAM, Dutton PH (2018)
467 Environmental warming and feminization of one of the largest sea turtle populations in
468 the world. *Curr Biol* 28: 154–159

469 Kamel SJ, Mrosovsky N (2006) Deforestation: Risk of sex ratio distortion in hawksbill sea
470 turtles. *Ecol App* 16: 923–931

471 Katselidis KA, Schofield G, Stamou G, Dimopoulos P, Pantis JD (2012) Females first? Past,
472 present and future variability in offspring sex ratio at a temperate sea turtle breeding
473 area. *Anim Conserv* 15: 508–518

474 Laloë J-O, Cozens J, Renom B, Taxonera A, Hays GC (2014) Effects of rising temperature on
475 the viability of an important sea turtle rookery. *Nat Clim Change* 4: 513–518

476 Laloë J-O, Cozens J, Renom B, Taxonera A, Hays GC (2017) Climate change and temperature-
477 linked hatchling mortality at a globally important sea turtle nesting site. *Glob Change*

478 Biol. <https://doi.org/10.1111/gcb.13765>

479 Lee PLM, Schofield G, Haughey RI, Mazaris AD, Hays GC (2017) A review of multiple
480 paternity across sea turtle rookeries. *Adv Mar Biol* doi:10.1016/bs.amb.2017.09.004

481 Lino S, Goncalves E, Cozens J (2010) The loggerhead sea turtle (*Caretta caretta*) on Sal
482 island, Cape Verde: nesting activity and beach surveillance in 2009. *Arquipelago (Life*
483 *and Marine Sciences)* 27: 59–63

484 López Jurado L (2007) Historical review of the archipelagos of Macaronesia and the marine
485 turtles. In: López Jurado L, Liria A (eds) *Marine Turtles. Recovery of extinct populations*,
486 *Institute Canario de Ciencias Marinas No. 5*, p 53-76

487 Marco A, Abella Pérez E, Monzón Argüello C, Martins S, Araujo S, López Jurado LF (2011) The
488 international importance of the archipelago of Cape Verde for marine turtles, in
489 particular the loggerhead turtle *Caretta caretta*. *Zoologia Caboverdiana* 2: 1–11

490 Marco A, Abella E, Liria-Loza A, Martins S, López O, Jiménez-Bordón S, Medina M, Oujo C,
491 Gaona P, Godley BJ, López-Jurado LF (2012) Abundance and exploitation of loggerhead
492 turtles nesting in Boa Vista islands, Cape Verde: the only substantial rookery in the
493 Eastern Atlantic. *Anim Conserv* 15: 351–360

494 Marcovaldi M, Godfrey M, Mrosovsky N (1997) Estimating sex ratios of loggerhead turtles in
495 Brazil from pivotal incubation durations. *Can J Zool* 75: 755–770

496 McGaugh SE, Schwanz LE, Bowden RM, Gonzalez JE, Janzen FJ (2010) Inheritance of nesting
497 behaviour across natural environmental variation in a turtle with temperature-
498 dependent sex determination. *P R Soc B* 277: 1219–1226

499 Miller D, Summers J, Silber S (2004) Environmental versus genetic sex determination: A
500 possible factor in dinosaur extinction? *Fertil Steril* 81: 954–964

501 Mrosovsky N, Kamel SJ, Rees AF, Margaritoulis D (2002) Pivotal temperature for loggerhead
502 turtles (*Caretta caretta*) from Kyparissia Bay, Greece. *Can J Zool* 80: 2118–2124

503 Mrosovsky N, Baptistotte C, Godfrey M (1999) Validation of incubation duration as an index
504 of the sex ratio of hatchling sea turtles. *Can J Zool* 77: 831-835

505 Nicholson DB, Holroyd PA, Benson RBJ, Barrett PM (2015) Climate-mediated diversification
506 of turtles in the Cretaceous. *Nat Commun* 6: 1–8

507 Pike DA, Antworth RL, Stiner JC (2006) Earlier nesting contributes to shorter nesting seasons
508 for the loggerhead seaturtle, *Caretta caretta*. *J Herpetol* 40: 91–94

509 Quintero I, Wiens JJ (2013) Rates of projected climate change dramatically exceed past rates
510 of climatic niche evolution among vertebrate species. *Ecol Lett* 16: 1095-1103

511 Rees AF, Margaritoulis D, Newman R, Riggall TE, Tsaros P, Zbinden JA, Godley BJ (2013)
512 Ecology of loggerhead marine turtles *Caretta caretta* in a neritic foraging habitat:
513 Movements, sex ratios and growth rates. *Mar Biol* 160: 519–529

514 Refsnider JM (2013) High thermal variance in naturally incubated turtle nests produces
515 faster offspring. *J Ethol* 31: 85–93

516 Shamblin BM, Bolten AB, Abreu-Grobois FA, Bjorndal KA, Cardona L, Carreras C, Clusa M,
517 Monzón-Argüello C, Nairn CJ, Nielson JT, Nel R, Soares LS, Stewart KR, Vilaça ST,
518 Türkozan O, Yilmaz C, Dutton PH (2014) Geographic pattern of genetic variation in a
519 broadly distributed marine vertebrate: new insights into loggerhead turtle stock
520 structure from expanded mitochondrial DNA sequences. *PLoS One* 9: e85956

521 Starostova Z, Angilletta MJ, Kubicka L, Kratochvil L (2012) Thermal dependence of
522 reproductive allocation in a tropical lizard. *J Therm Biol* 37: 159–163

523 Stubbs JL, Kearney MR, Whiting SD, Mitchell NJ (2014) Models of primary sex ratios at a
524 major flatback turtle rookery show an anomalous masculinising trend. *Climate Change*

525 Resp 1: 3

526 Tanner C (2013) Sea Turtle Conservation in Ghana's Western Region: The Bigger Picture.
527 Marine Turtle Newsletter 136: 9–12

528 Tanner C (2014) Sea turtle bycatch off the Western Region of the Ghanaian coast. Marine
529 Turtle Newsletter 140: 8–11

530 Tedeschi JN, Kennington WJ, Tomkins JL, Berry O, Whiting S, Meekan MG, Mitchell NJ (2016)
531 Heritable variation in heat shock gene expression: a potential mechanism for
532 adaptation to thermal stress in embryos of sea turtles. P R Soc B 283:
533 doi:10.1098/rspb.2015.2320

534 Tedeschi JN, Mitchell NJ, Berry O, Whiting S, Meekan M, Kennington WJ (2014)
535 Reconstructed paternal genotypes reveal variable rates of multiple paternity at three
536 rookeries of loggerhead sea turtles (*Caretta caretta*) in Western Australia. Aus J Zool
537 62: 454–462

538 Urban MC (2015) Accelerating extinction risk from climate change. Science 348: 571–573

539 Varo-Cruz N, Cejudo D, López Jurado LF (2007) Reproductive biology of loggerhead turtle
540 (*Caretta caretta* L. 1758) on the island of Boa Vista (Cape Verde, West Africa). In: López
541 Jurado LF, Liria A (eds), Marine Turtles. Recovery of extinct populations. Institute
542 Canario de Ciencias Marinas No. 5, p 127-144

543 Weishampel, J.F., Bagley, D.A, Ehrhart, L.M. (2004) Earlier nesting by loggerhead sea turtles
544 following sea surface warming. Glob Change Biol 10: 1424–1427.

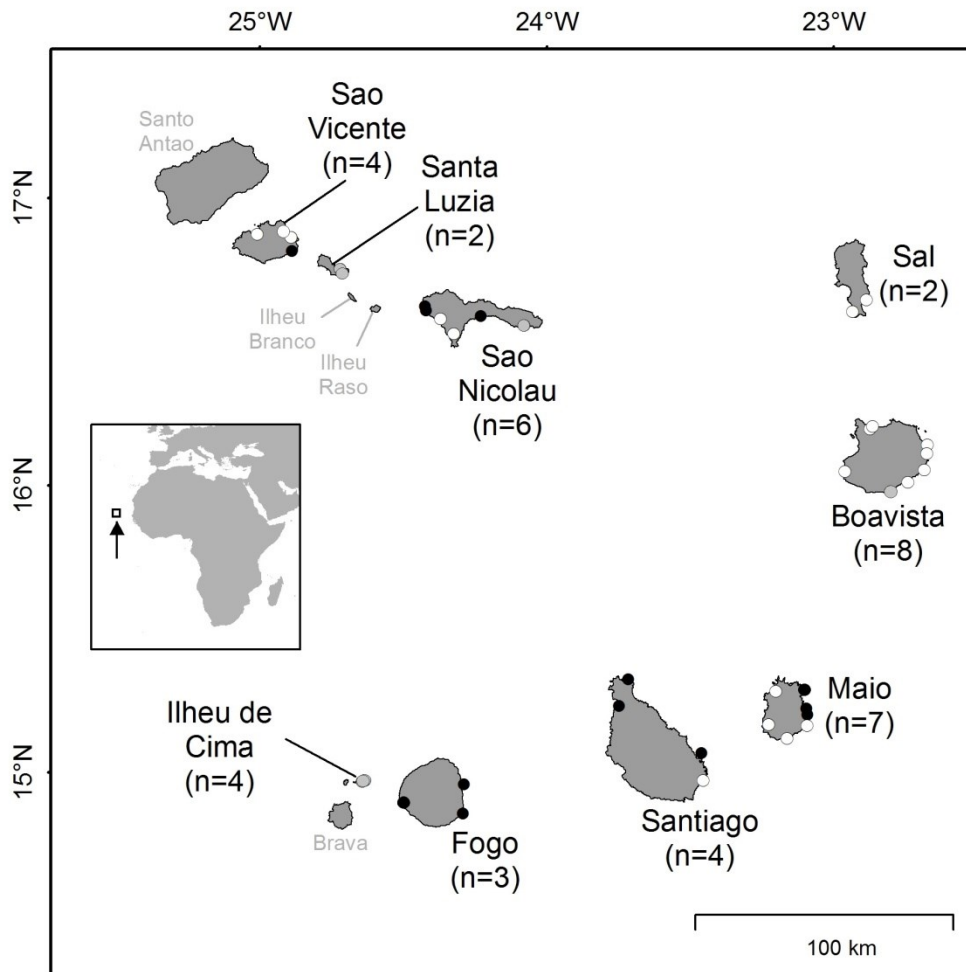
545 Witt MJ, Hawkes LA, Godfrey MH, Godley BJ, Broderick AC (2010) Predicting the impacts of
546 climate change on a globally distributed species: the case of the loggerhead turtle. J
547 Exp Biol 213: 901–911

548 Woolgar L, Trocini S, Mitchell N (2013) Key parameters describing temperature-dependent
549 sex determination in the southernmost population of loggerhead sea turtles. J Exper
550 Marine Biol Ecol 449: 77-84

551 Wright LI, Stokes KL, Fuller WJ, Godley BJ, McGowan A, Snape R, Broderick AC (2012) Turtle
552 mating patterns buffer against disruptive effects of climate change. P R Soc B 279:
553 2122–2127

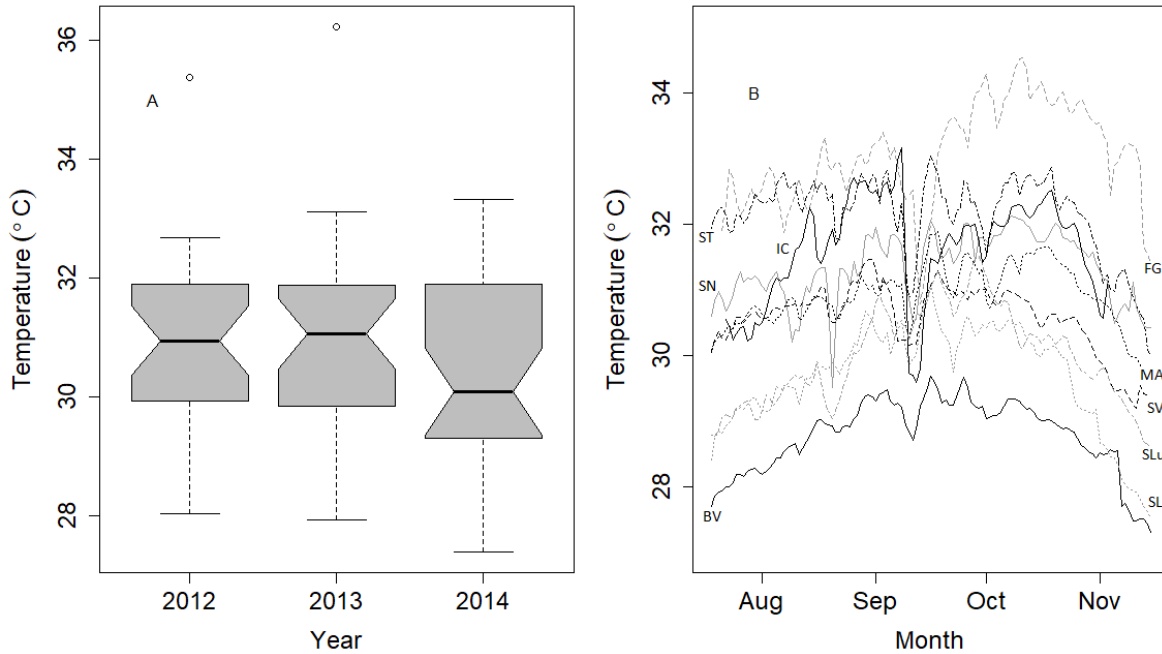
554 Wyneken J, Lolavar A (2015) Loggerhead sea turtle environmental sex determination :
555 Implications of moisture and temperature for climate change based predictions for
556 species survival. J Exp Zool 324: 295-314

557

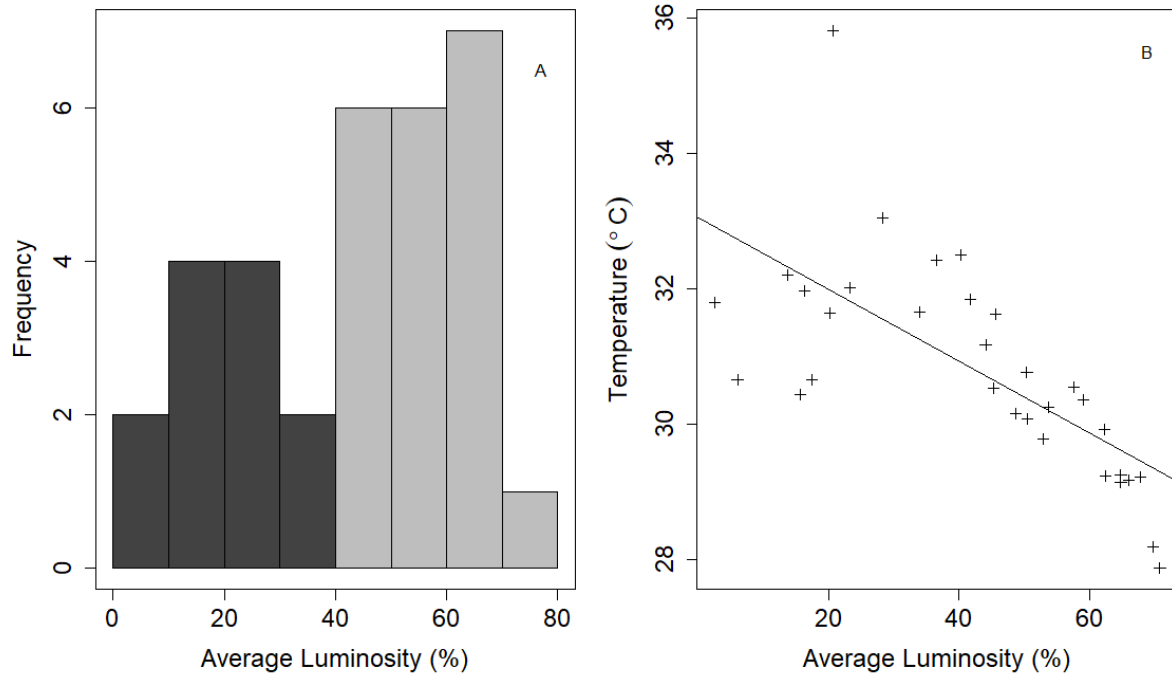


559
560

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

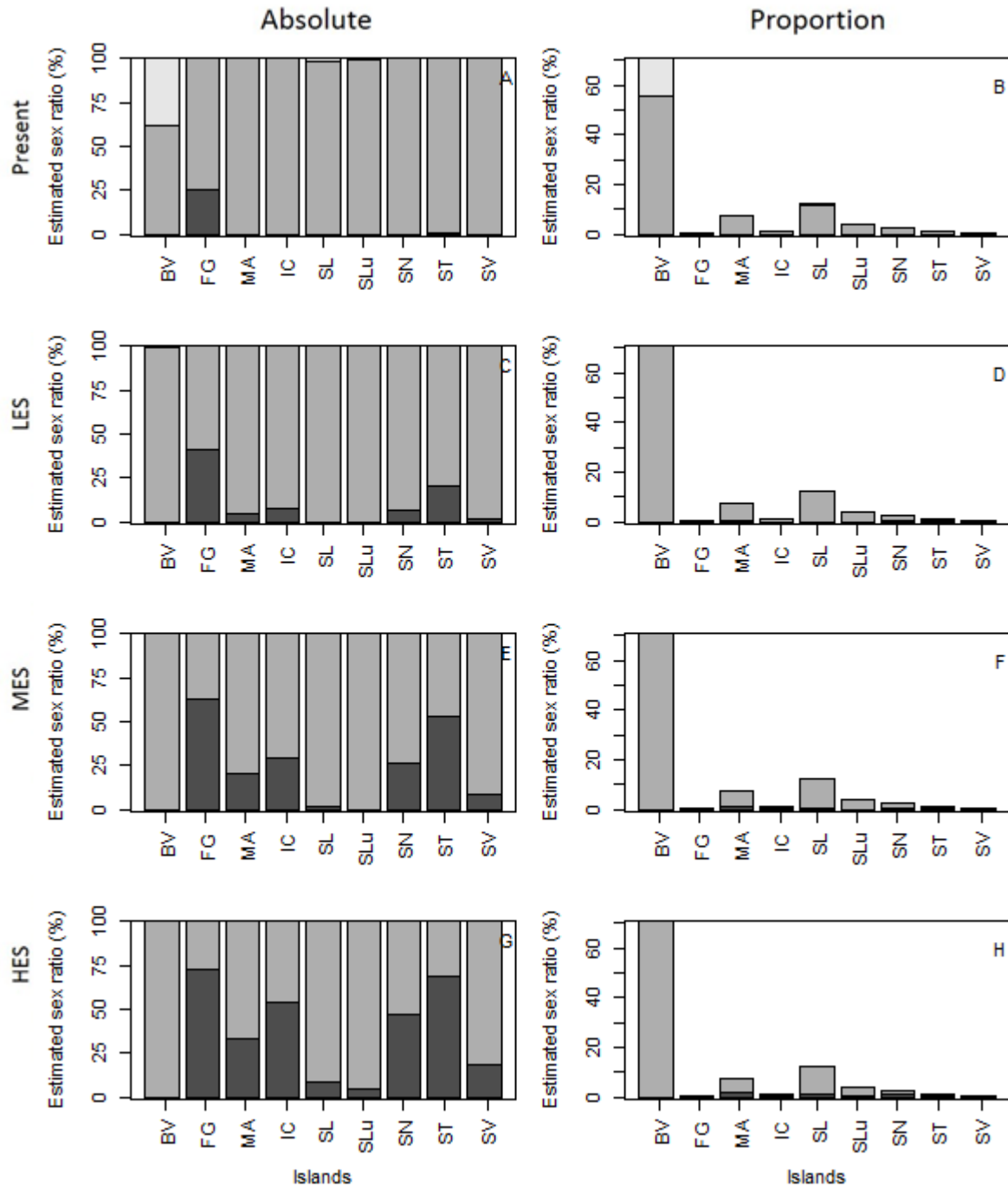


568
 569 Figure 2: (A) Boxplots showing sand temperatures recorded in the three study years (boxes
 570 show inter-quartile range, horizontal line shows median value, whiskers show range,
 571 notches indicate 95% confidence interval of the median). The two outliers in 2012 and 2013
 572 are shown as 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 Ilheu 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.



579

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.



586

587 Figure 4: (A, C, E, G) Stacked histograms for each of the nine study islands showing absolute
 588 overall mean percent embryos incubating above the thermal maximum of 35 °C (dark grey
 589 shading), estimated % female hatchlings (mid grey shading), and estimated % male
 590 hatchlings (light grey shading). (B, D, F, H) Weighted histograms displaying the spatially
 591 proportionally corrected production of female and male hatchlings and nests incubating
 592 over the thermal maximum across the Cape Verde rookery by Island (symbology as in parts
 593 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 ($^{\circ}C$), 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 ($^{\circ}C$)	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

603