

1

2 DR LEO CLARKE (Orcid ID : 0000-0002-1600-6197)

3

4

5 Article type : Research Article

6

7

8 Handling Editor - Hedley Grantham

9

10 **LOW-COST TOOLS MITIGATE CLIMATE CHANGE DURING**
11 **REPRODUCTION IN AN ENDANGERED MARINE ECTOTHERM**

12

13 **Clarke, L.J.¹, Elliot, R.L. ¹, Abella-Perez, E.^{2,3}, Jenkins, S.R.¹, Marco, A.², Martins, S.³ & Hawkes,**
14 **L.A.⁴**

15

16 ¹ School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, LL59 5AB, UK

17 ² Estacion Biologica de Donana (CSIC), C/ America Vespuccio, s/n, 41092 Sevilla, Spain

18 ³ BIOS.CV, Sal Rei, Boavista, Republic of Cape Verde

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

21

22 * Corresponding author: l.clarke@bangor.ac.uk

23 Tel: 01248 388141

24

25 **Key Words:** climate change, biodiversity, marine turtles, mitigation, management, conservation, *Caretta*
26 *caretta*, loggerhead

27

28 **Running Head:** Tools to mitigate climate change in an ectotherm

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/1365-2664.13874](https://doi.org/10.1111/1365-2664.13874)

This article is protected by copyright. All rights reserved

31 **Abstract**

32

- 33 1. The impacts of anthropogenic climate change will be most dramatic for species that live in narrow
34 thermal niches, such as reptiles. Given the imminent threat to biodiversity, and that actions to
35 reduce carbon emissions are not yet sufficient, it is important that a sound evidence base of
36 potential mitigation options is available for conservation managers.
- 37 2. Successful incubation and production of male sea turtle hatchlings is threatened by increased global
38 temperatures (sex is determined by the temperature at which eggs incubate). Here we test two
39 conservation tools to reduce incubation temperatures: clutch splitting and clutch shading, on a
40 nesting loggerhead turtle (*Caretta caretta*) population in the Eastern Atlantic Ocean.
- 41 3. During the thermosensitive period of incubation, split and shaded clutches were both 1.00 °C cooler
42 than control nests. Clutch splitting (mean: 45 eggs) reduced nest temperatures by reducing
43 metabolic heating during incubation compared to controls (mean: 92 eggs). Modelled primary sex
44 ratios differed between nest treatments, with 1.50 % (± 6 % S.E.) females produced in shaded
45 nests, 45.00 % (± 7 % S.E.) females in split nests and 69.00 % (± 6 % S.E.) females in controls.
46 Neither treatment affected hatchling size, success, mass or vigour. When clutch splitting was
47 repeated two years later, hatch success was higher in split clutches compared to controls.
- 48 4. *Synthesis and Applications*: Clutch splitting and clutch shading successfully altered the thermal
49 profile of incubating turtle nests. When there is sufficient knowledge to better understand the
50 effects of intervention on fundamental population demographics, they will be useful for reducing
51 incubation temperatures in sea turtle nests, potentially increasing nest survival and male hatchling
52 production. The effect of clutch splitting in reducing nest temperature was lower relative to clutch
53 shading, but requires significantly less funding, materials and specialist skill, key factors for
54 management of turtle rookeries that are often in remote, resource-limited areas.

55

56 **Introduction**

57 *1.1 Climate change and effects on biodiversity*

58 Conserving global biodiversity in a rapidly changing climate is one of the most significant challenges
59 currently faced by conservationists and practitioners. The International Panel on Climate Change (IPCC,
60 2018) predicts increases in global mean surface temperatures of 3.7 to 4.8 °C by 2100 unless significant
61 mitigation effort is expended, and biodiversity is on the brink of a sixth mass extinction event (Barnosky *et*
62 *al.*, 2011; Panetta *et al.*, 2018). The effects of this rapid and unprecedented shift in the Earth's climate will
63 be particularly dramatic for species that live and function within narrow temperature ranges and climatic
64 niches (Sodhi *et al.*, 2008; Rijnsdorp *et al.*, 2009; Bellard *et al.*, 2012), and there has been a recent increase

65 in efforts to adapt existing conservation management to incorporate climate change effects (Heller &
66 Zavaleta, 2009; Hagerman *et al.*, 2010; Shoo *et al.*, 2013). Such efforts include the mitigation and reduction
67 of non-climatic threats, increasing species connectivity, maintaining and increasing genetic diversity,
68 protection of climate resilient refugia and translocation of species (Chambers *et al.*, 2005; Heller &
69 Zavaleta, 2009). To date, these efforts have largely focused on terrestrial species (Feeley *et al.*, 2017),
70 although impacts on marine biodiversity are increasingly documented (Poloczanska *et al.*, 2016, Worm &
71 Lotze *et al.*, 2016; Tittensor *et al.*, 2019).

72 1.2 Marine Turtles and Climate Change

73 Global climate change will particularly affect reptiles, as multiple life history stages are strongly influenced
74 by environmental factors (Sinervo *et al.*, 2010; Ihlow *et al.*, 2012; Bohm *et al.*, 2016). In particular,
75 reptiles' reproductive biology is intrinsically linked to the thermal environment, with nesting phenology,
76 inter-nesting intervals, incubation duration, hatching success and hatchling sex and fitness all influenced by
77 environmental temperature (Braña & Ji, 2000; Clusella-Trullas *et al.*, 2011; Buckley *et al.*, 2012; Sim *et al.*,
78 2015).

79 Marine turtles are already of conservation concern and in addition to non-climatic stressors such as fishing
80 bycatch, plastic pollution and poaching (Wallace *et al.*, 2011), increased global temperatures will likely
81 carry significant population implications (Hamann *et al.*, 2007; Poloczanska *et al.*, 2009; Hawkes *et al.*,
82 2009; Abella-Pérez *et al.*, 2016; Fuentes & Saba, 2016). Forecasted warming will lead to extremely female-
83 biased offspring and reduced hatching success, which may compromise both viability and survivorship of
84 some populations (Fuentes *et al.*, 2009; Mitchell & Janzen, 2010; Witt *et al.*, 2010; Laloë *et al.*, 2014; Hays
85 *et al.*, 2017). Indeed, highly-feminised sex ratios (Hays *et al.*, 2014; Laloë *et al.*, 2014; Hays *et al.*, 2017;
86 Tanner *et al.*, 2019) and reduced hatching success (Tomillo *et al.*, 2012; Montero *et al.*, 2018) have been
87 documented in various populations in recent years.

88 With work demonstrating limited adaptive potential (Monsinjon *et al.*, 2019; Tilley *et al.*, 2019), it is
89 prudent to investigate potential mitigation strategies for biodiversity management (Hawkes *et al.*, 2009).
90 Past studies on marine turtles have investigated the use of artificial shading of nests, laboratory egg
91 incubation, watering of incubating clutches and even the addition of paler and thus less infra-red absorptive
92 sediments to beaches as management interventions (Hamann *et al.*, 2010; Fuentes *et al.*, 2012; Patino-
93 Martinez *et al.*, 2012; Wood *et al.*, 2014; Jourdan & Fuentes, 2015; Liles *et al.*, 2019). Many of these
94 strategies require substantial financial and/or labour investment and may be resource intensive. As the
95 majority of marine turtle nesting takes place in resource-scarce, developing countries, ideal strategies
96 ideally should be simple and cheap (Esteban *et al.*, 2018).

98 To inform potential strategies for the mitigation of climate change effects to marine turtles, we investigated
99 two potential nest intervention approaches to reduce nest incubation temperatures: (1) clutch splitting; and
100 (2) clutch shading. We also tested whether these approaches; (3) could significantly alter the primary sex
101 ratio produced and (4) whether they could be achieved without compromising hatching success and
102 hatchling size or vigour. Finally, we discuss the potential ramifications of intervening in such life history
103 metrics.

104 **Materials and Methods**

105 *2.1 Study Area*

106 The study took place on the island of Boa Vista, Cabo Verde, West Africa, the world's second largest
107 nesting aggregation of loggerhead sea turtles (*Caretta caretta*; (Marco *et al.*, 2012; Laloë *et al.*, 2019)).
108 Around 65% of nests in this population are laid on the island of Boa Vista (Laloë *et al.*, 2019) (Figure 1).

109 *2.2 Nest Collection*

110 Nesting females were encountered between 7th and 13th July 2012 and 24th July and 10th August 2014 and
111 clutches (n=136) were relocated to a 12 x 50 m beach front hatchery within six hours of laying. In 2012,
112 eggs were relocated to a hatchery at Ervatao beach, run by the Natura 2000 turtle conservation project, and
113 in 2014, to a hatchery at the nearby Joao Barrosa beach run by the BIOS.CV NGO conservation project.
114 Each hatchery was natural sand and ran alongshore, reaching the spring high tide line at its lowest point,
115 representing a realistic natural nesting environment. Clutches were reburied at 45cm depth (the bottom of
116 the nest); the average for loggerhead nests on Boa Vista Island (Abella-Pérez *et al.*, 2007; Marco *et al.*,
117 2018).

118 *2.3 Mitigation Strategies*

119 In 2012, 60 clutches were collected and allocated equally to three treatments. First, 20 clutches (range: 66
120 to 111 eggs (mean 88.35 ± 0.75 S.E.; Table 1)) were reburied in the hatchery under shading material
121 suspended 15cm above the nest. Second, 20 nests were "split" in two, whereby two equal clutches each
122 containing half the eggs that were collected were buried in two separate nests in the hatchery (range: 38 to
123 57 eggs (mean 45.44 ± 0.30 S.E.; Table 1)), with the second half buried separately as part of on-going
124 conservation work. This clutch splitting aimed to reduce metabolic heat produced due to embryonic growth
125 (Broderick *et al.*, 2001; Zbinden *et al.*, 2006), and thus the overall incubation temperature of the nest. Such
126 metabolic heating may contribute further to hatchling feminization above that of ambient incubation
127 temperatures (Önder & Candan, 2016). We chose to halve the number of eggs, rather than bury a constant,
128 smaller number of eggs, because this would more likely reflect a realistic management strategy. As
129 mentioned, all nests were reburied to a constant bottom depth of 45 cm. Eggs at the top of split clutches
130 would thus incubate at slightly deeper depths than those in natural clutches, although we did not consider
131 this to be a significant factor in influencing nest temperatures as this difference would be marginal and
132 previous work has shown clutch size to influence nest temperatures to a much larger extent than nest depth,
133 which has a negligible effect (Van De Merwe *et al.*, 2006). The final 20 clutches were reburied whole
134 without any manipulation and used as a control (range: 77 to 117 eggs (mean 92 ± 0.78 S.E.; Table 1)).
135 Nests in each treatment were buried in five plots (140 x 140 cm) of four nests, of a total of fifteen plots
136 across the hatchery (three rows of five), with each plot distributed randomly using a random number
137 generator. Nests were spaced at least 70 cm apart.

138 In 2014, the above methods were repeated, again burying split clutches (n = 53) and control clutches (n =
139 23) in the hatchery. No nests were shaded. Control (range: 36 to 126 eggs (mean 87.62 ± 4.46 S.E.)) and
140 split (range: 33 to 63 eggs (mean 48.83 ± 1.05 S.E.)) clutches were randomly distributed throughout the
141 hatchery in 2014 rather than in plots.

142 2.1 *Monitoring Incubation Temperatures and Metabolic Heating*

143 In 2012, individual temperature data loggers (TDL; TinyTag Plus2 TGP-4017, accuracy $\pm 0.4^\circ\text{C}$, n=50; and
144 TinyTag Aquatic 2, accuracy $\pm 0.5^\circ\text{C}$, n=10; Gemini Dataloggers, UK,
145 <http://www.gemindataloggers.com/>) were placed in the centre of each clutch after half the eggs had been
146 interred. Six control TDLs were also distributed equally throughout the hatchery at a sand depth of 45cm.
147 No sand-control logger was located further than 140cm away from any nest. The nearest sand-control
148 logger was used to calculate metabolic heat (MH) of each control and split clutch, relative to surrounding
149 sand temperatures. All loggers were calibrated before deployment. No temperature data loggers were
150 deployed in 2014.

151 2.2 *Hatchling Size and Vigour*

152 In 2012, hatchling size and vigour was recorded from 20 randomly selected hatchlings immediately
153 following hatching into pre-prepared corrals (see Supporting Information for methods for determining this
154 sample size). Hatchlings were weighed (Pesola MS500 microbalance, accuracy $\pm 0.01\text{g}$), and straight
155 carapace length and width measured (Vernier callipers, accuracy $\pm 0.1\text{mm}$). The remaining hatchlings were
156 released to the sea immediately. Hatchling vigour was assessed by recording: (1) time taken (seconds) for
157 each hatchling to right itself after being placed upside down on its carapace; and (2) time taken (seconds)
158 for each hatchling to travel a one-metre long section of plastic roof guttering filled with moist beach sand
159 (Van de Merwe *et al.*, 2013). Guttering was placed in a seaward orientation from the nest with a light at the
160 seaward end. No hatchling data were collected in 2014.

161 2.3 *Hatching Success*

162 In both 2012 and 2014, all study nests were excavated 48 hours after hatching to retrieve TDLs and to
163 measure hatching success, calculated as the proportion of empty eggshells from the initial number of eggs,
164 having subtracted any live or dead hatchlings observed.

165 2.4 *Data Analysis*

166 Metabolic heating and incubation temperatures were split into thirds based on known laying and hatching
167 dates. The middle third of incubation in 2012 was used as a proxy for the thermosensitive period of
168 incubation (Yntema *et al.*, 1982; Mrosovsky *et al.*, 2002) to calculate primary sex ratios using published
169 equations calculated for loggerhead turtles in the Mediterranean (Mrosovsky *et al.*, 2002), that have been
170 recently applied to the study population on Boa Vista (Tanner *et al.*, 2019). Statistical analyses were carried

171 out using R Studio (Version 1.3.959; R Studio Team, 2020). To expedite data processing, the raw
172 temperature data (~250,000 data points) was randomly subset to 10,000 data points when graphically
173 presenting trends in nest temperature and metabolic heating.

174 In order to avoid fitting overly complex models to temperature and metabolic heat data to deal with issues
175 surrounding temporal autocorrelation and non-independence of data points within each nest throughout
176 incubation, we averaged these data across the entire incubation period or a particular third of incubation,
177 where relevant. Given that the calculation and analysis of relevant responses (e.g. sex ratios, incubation
178 temperatures, middle third temperatures) are performed at these temporal scales, this allowed a more
179 biologically meaningful analysis of the data.

180 Treatment differences in 2012 were assessed using linear mixed-effects models including the fixed factor
181 'treatment' and the random factor 'plot', to account for spatial variation across the hatchery. Visual
182 assessment of model residuals determined that model assumptions were met. Post-hoc tests identified
183 differences between treatments. Given the random distribution of nests throughout the hatchery in 2014,
184 differences in hatching success in 2014 were identified using a one-way ANOVA between treatments.

185

186 **Results**

187 In 2012, four split clutches (at the seaward end of the hatchery) failed to hatch, probably due to heavy rain
188 and flooding around halfway through incubation. These nests were removed from our analyses. All other
189 nests hatched successfully, although hatchlings from one control clutch, two split clutches and one shaded
190 clutch escaped the plastic corrals. All nests hatched successfully in 2014.

191 *3.1 Nest Temperatures*

192 Temperature profiles (Figure 2a) show that throughout the first two thirds of incubation, nest temperatures
193 in shaded clutches (n = 20) were markedly lower than in split (n = 16, mean 0.70 °C lower) and control (n =
194 20, mean 0.86 °C lower) clutches, but during the final third, temperatures in shaded nests increased to
195 comparable temperatures to split clutches (mean 0.07 °C higher), whilst the difference relative to control
196 clutches increased (mean 1.06 °C lower). Split and control clutches showed a similar temperature profile
197 throughout the first third of incubation (mean < 0.01 °C difference), before diverging during the middle
198 third, when temperatures in control clutches increased relative to split clutches (mean 0.90 °C higher). The
199 difference in nest temperatures peaked at around 75% of incubation (Figure 2a).

200 Mean temperatures across the whole of incubation were significantly different between all three treatments
201 were evident in 2012 (Table 1), with post-hoc tests indicating higher mean incubation temperatures in
202 control clutches (mean 29.67 °C) than both split (mean 29.15 °C, t-statistic: 3.68; p = 0.008) and shaded
203 (mean 28.58 °C, t-statistic: 8.01; p < 0.001). Split clutches were also significantly warmer than shaded
204 clutches (t-statistic: 3.97; p = 0.005; Table 1).

205 Mean nest temperatures during the thermosensitive period (the middle third of incubation), were also
206 significantly different (Table 1) with control clutches significantly warmer (mean 29.40 °C) than both split
207 clutches (mean 28.51 °C, t-statistic: 4.04; p = 0.004) and shaded clutches (mean 28.32 °C, t-statistic: 5.45; p
208 = 0.001). There was no difference in middle third incubation temperatures between split and shaded
209 clutches (t-statistic: -1.30; p = 0.422).

210 *3.2 Incubation Periods*

211 In 2012, the incubation period of control clutches was significantly shorter than both split (mean 3.73 days
212 shorter, t-statistic: -3.38; p = 0.015) and shaded (mean 6.7 days shorter, t-statistic: -6.65; p < 0.001)
213 clutches. Split clutches incubated for significantly less time than shaded clutches (t-statistic: 2.69; p =
214 0.049), which took longest (66 days) to hatch (Table 1).

215 *3.3 Metabolic Heat – Split vs. Control clutches*

216 In 2012 the mean clutch size was 92 eggs (\pm 3.48 S.E.) in control clutches and 45 eggs in split clutches (\pm
217 1.33 S.E.) (Table 1), hence split clutches contained approximately half the number of eggs of controls. We
218 found a significant relationship between the mean amount of MH generated across the entire incubation
219 period and the number of eggs within a clutch, with each additional egg contributing around 0.01°C to
220 mean incubation temperatures (Figure 3).

221 The amount of MH generated in the early stages of incubation was similar in control and split clutches, but
222 diverged later in incubation. The difference peaked in the final third (Figure 2a). When averaged across the
223 entire incubation period, mean MH was similar in control and split clutches (Table 1). The same was true
224 for both the first and second third of incubation separately (Table 1; Figure 4), although in the final third of
225 incubation, MH in controls was significantly higher than in split clutches (mean 1.36 °C warmer, Table 1;
226 Figure 4).

227 *3.4 Sex Ratios*

228 The proportion of female hatchlings was significantly lower in shaded clutches compared to both control
229 (mean 67.56 % lower, t-statistic: 8.01; $p < 0.001$) and split clutches (mean 43.92 % lower, t-statistic: -4.93;
230 $p = 0.001$) (Table 1; Figure 5a). The proportion of females in split clutches was 22.18 % lower than in
231 controls, although the difference was marginally non-significant (t-statistic: 2.65; $p = 0.051$; Table 1;
232 Figure 5a).

233 *3.5 Hatchling Measurements*

234 It was not possible to measure hatchling biometrics in eight clutches (n=6 split, n=1 shaded and n=1
235 control), due to adverse weather. For the remaining 52 clutches hatchling size (carapace width or length),
236 mass and vigour were similar across treatments (Table 1; Figure 5b – 5f).

237 *3.6 Hatch Success*

238 Mean hatch success was similar across all three nest treatments in 2012 (Table 1; Figure 6). When clutch-
239 splitting was repeated in 2014, however, hatch success was significantly higher (mean 21.53 % higher) in
240 split clutches than in control clutches (Table 1; Figure 6).

241

242 **Discussion**

243 Biodiversity conservation is increasingly considering the impacts of climate change (Hampe & Petit, 2005;
244 Willis & Bhagwat, 2009; Haward *et al.*, 2013; Dickinson, 2015; Urban *et al.*, 2016). Whilst marine turtles
245 have existed for hundreds of millions of years and survived numerous global climatic shifts (Hirayama,
246 1998), contemporary climate change is occurring at an unprecedented rate. Coupled with multiple other
247 anthropogenic stressors (Donlan *et al.*, 2010), their resilience and adaptive potential may be limited. Whilst
248 there is currently no evidence base that intervention is required for any population specifically, adaptive
249 responses may be limited (Monsinjon *et al.*, 2019; Tilley *et al.*, 2019) (albeit not for all existing populations
250 (Abella-Perez *et al.*, 2016)), and researchers must consider what mitigation might look like and analyse
251 costs, benefits, and potential impacts of such action (Dawson *et al.*, 2011).

252 The mitigation strategies trialled in the present study successfully altered the thermal profile of incubating
253 turtle nests, effectively reducing nest temperatures relative to controls. Furthermore, they did so without
254 any decrease in hatching success or emergence success and no change to hatchling size or vigour. Indeed,
255 when clutch splitting was repeated in 2014, hatch success was actually significantly higher in split clutches
256 than in control clutches. This perhaps indicates that in 2014 clutch splitting effectively reduced incubation
257 temperatures from those closer to the upper thermal limit of successful embryonic development, although
258 without nest temperature data from this year no further investigation into this observed trend was possible.
259 Nonetheless, the lack of a negative impact of clutch splitting on hatch success or hatchling biometrics in
260 our study is encouraging for researchers and managers who may wish to implement the tested strategies.

261 Clutch shading reduced incubation temperatures by 1.08 °C in the middle third of incubation (relative to
262 control nests), eliciting an enormous reduction in the modelled sex ratio to just 1.46% female. Clutch
263 splitting reduced nest temperature by a more modest amount (0.89 °C relative to control nests), and while
264 this reduced the mean proportion of female hatchlings by >20%, this change was not statistically
265 significant, possibly due to reduced power from the loss of four split clutches. The amount of metabolic
266 heating produced by incubating clutches can vary between individuals, nesting beaches, populations and
267 species, however (Miller, 1997) (e.g. 4.4 °C for green turtles (*Chelonia mydas*) in Antigua, Caribbean (van
268 de Merwe *et al.*, 2006), to 0.2 °C for loggerhead turtles in Zakynthos, Greece (Zbinden *et al.*, 2006)).
269 Should clutch splitting be investigated further as a potential intervention, its effectiveness at these scales
270 would be worthy of investigation due to such variation.

271 Clutch splitting is of particular interest for management because it requires no funding, materials or
272 specialist skill and is well-suited for areas where such resources are scarce (as turtle rookeries often are).
273 While it may be of little use in augmenting sex ratio in areas where incubation temperatures are well above
274 the pivotal temperature, our results highlight its' effectiveness in reducing temperatures in nests near the

275 upper thermal limit for survival (Hawkes *et al.*, 2009; Fuentes *et al.*, 2011) potentially improving hatch
276 success (as may have occurred in 2014).

277 Intraspecific and interspecific variation in turtle clutch sizes exists, a key consideration for implementing
278 clutch splitting as a management intervention. Metabolic heating will hence similarly vary, and for
279 populations with smaller clutch sizes (e.g. some hawksbill and green turtles), splitting may be of little
280 value. Prior knowledge on clutch sizes is necessary to inform its implementation. For species with large
281 clutch sizes, such as leatherbacks (*Dermochelys coriacea*) (up to 130 eggs) (Ros, 2013), splitting clutches
282 may reduce nest temperatures sufficiently to alter sex ratios. Splitting clutches into thirds may further
283 reduce metabolic heating and nest temperatures, although further lowering clutch sizes may be more likely
284 to have implications on hatch success and hatchling fitness by increasing the energetic costs of emergence
285 (Rusli *et al.*, 2016). Given the variation in reproductive biology and output between species it does not
286 necessarily follow that our results will be consistent in other populations, and the feasibility of these types
287 of manipulative management strategies in the future will depend on the geographic and genetic
288 characteristics of the rookeries supporting the management unit in question.

289 The dramatic change in sex ratios in shaded nests may have only occurred because natural nests on Boa
290 Vista appeared to currently incubate within 0.5 °C of the pivotal temperature for loggerhead turtles in 2012
291 (29 °C; (Mrosovsky *et al.*, 2002); mean temperature of unshaded control nests in the present study was 29.4
292 °C in the middle third of incubation). Given the resource intensive nature of this method (daily maintenance
293 to the shading was required) and dramatic altering of nest thermal profiles it is thus perhaps reserved for
294 only the most at-risk rookeries, where it could be judiciously applied to nests that are otherwise unlikely to
295 survive, and/or are expected to produce near to 100% female hatchlings (Matsuzawa *et al.*, 2002; Hawkes
296 *et al.*, 2007; Fuentes *et al.*, 2009; Laloë *et al.*, 2014; Tanner *et al.*, 2019).

297 *Should we intervene?*

298 Reductions in carbon emissions have not yet been sufficient to stabilise atmospheric CO₂, and uptake of
299 renewable and low carbon sources of energy is slow (Hansen *et al.*, 2013). Thus, it seems unlikely that
300 climate change will cease to present a serious potential threat to biodiversity. It is therefore important to
301 continue to investigate potential management interventions. Although our results demonstrate the potential
302 for implementing these strategies successfully, such interventions remain controversial.

303 Past reviews on the effects of climate change to marine turtles have identified critical gaps in understanding
304 that should be addressed before implementation of interventionist management (Hawkes *et al.*, 2009;
305 Hamann *et al.*, 2010; Fuentes *et al.*, 2012), and a better baseline understanding of primary and operational
306 sex ratios for the population in question is a critical prerequisite before intervention to fundamentally alter
307 basic life history parameters. Whilst female-dominated sex ratios have been the focus of much of the recent

308 literature around sea turtles and global climate change, work suggests that operational sex ratios remain
309 balanced (Hays *et al.*, 2010; Wright *et al.*, 2012; Hays *et al.*, 2014; Schofield *et al.*, 2016). Thus these
310 interventions may only be considered necessary in populations at risk of nest failure due lethal
311 temperatures, rather than those producing skewed sex ratios. Furthermore, the continued production of
312 males in some nesting populations may occur around the periphery of incubating clutches, nests in the
313 intertidal and areas shaded by vegetation and those with lighter sand (Kaska *et al.*, 1998; Patino-Martinez *et*
314 *al.*, 2012). These areas that continue to produce male hatchlings should be identified and protected as a
315 priority (Hansen *et al.*, 2010; Fuentes *et al.*, 2012).

316 The adaptive potential of any species depends on both the level of phenotypic plasticity and the potential
317 for microevolutionary genetic changes (Hulin *et al.*, 2009). Recent work has suggested that phenological
318 shifts observed in loggerhead turtles are insufficient to mediate the effects of climate change on successful
319 reproduction, and called for urgent further research on population dynamics to understand the links
320 between potential population declines, genetic shifts and biased primary sex ratios (Mitchell and Janzen,
321 2010; Monsinjon *et al.*, 2019). Furthermore, whilst much of the research on climate change and sea turtles
322 has focused on climate warming, other forecasted system changes will influence incubation in combination
323 with elevated ambient temperatures, and must also be considered (e.g. Staines *et al.*, 2020). Until existing
324 knowledge gaps are addressed, researchers cannot be confident that such intervention will not undermine
325 the adaptive capacity of a population or artificially select for individuals that are in fact less suited to a
326 warmer future climate.

327 *Future actions*

328 We suggest that a robust analytical framework for assessing the need and ramifications of intervention is
329 required before any is attempted, certainly for populations of marine turtles, but probably for wider
330 biodiversity in general (e.g. Omann *et al.*, 2009). Proper and complete consideration should be given to
331 both the positive and negative ramifications, particularly whether intervention undermines or erodes the
332 adaptive capacity of a population to cope with the negative effects of climate change. To carry out any
333 intervention or mitigation without such an analysis would risk compounding one of the most severe
334 stressors known to modern biodiversity with potentially calamitous management.

335 **Acknowledgements**

336 The authors would like to acknowledge the Worldwide Fund for Nature (Dr Carlos Drews) and the WAVE
337 Foundation of Newport Aquarium in funding this work, the National Directorate of Environment of Cabo
338 Verde for authorising the field work, and the help and hospitality of the volunteers and staff of the Natura
339 2000 group (for work in 2012) and BIOS.CV (for work in 2014) on Boa Vista.

340 **Authors' Contributions**

341 L.J.C, R.L.E. and L.A.H. designed the experiment and carried out fieldwork, data analysis and manuscript
342 preparation. E.A-P., S.M, A.M and S.R.J. contributed to fieldwork and manuscript revisions.

343 **Data Availability Statement**

344 Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.3r2280gfq>. (Clarke et al.,
345 2021)

References

- Abella Pérez, E., Marco, A., & López-Jurado, L. F. (2007). Success of delayed translocation of loggerhead turtle nests. *The Journal of Wildlife Management*, 71(7), 2290-2296.
- Abella Perez, E., Marco, A., Martins, S., Hawkes, L. A. 2016. Is this what a climate change-resilient population of marine turtles looks like? *Biological Conservation*, 193: 124-132.
- Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B. & Ferrer, E.A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, 471, 51-57.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15, 365-377.
- Böhm, M., Cook, D., Ma, H., Davidson, A. D., García, A., Tapley, B., ... & Carr, J. (2016). Hot and bothered: using trait-based approaches to assess climate change vulnerability in reptiles. *Biological Conservation*, 204, 32-41.
- Bolten, A.B. (2003). *Variation in sea turtle life history patterns: neritic vs. oceanic developmental stages*. The Biology of Sea Turtles (ed. by P.L. Lutz, J.A. Musick and J. Wyneken), pp. 243-257. CRC Press, Boca Raton, Florida, USA.
- Braña, F. & Ji, X. (2000). Influence of Incubation Temperature on Morphology, Locomotor Performance, and Early Growth of Hatchling Wall Lizards (*Podarcis muralis*). *Journal of Experimental Zoology*, 286, 422-433.
- Broderick, A.C., Godley, B.J. & Hays, G.C. (2001). Metabolic Heating and the Prediction of Sex Ratios for Green Turtles (*Chelonia mydas*). *Physiological and Biochemical Zoology* 74, 161-170.
- Buckley, L.B., Hurlbert, A.H. & Jetz, W. (2012). Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography*, 21, 873-885.
- Carr, A. F., Hirth, H. F., & Ogren, L. H. (1966). *The ecology and migrations of sea turtles*. 6, The hawksbill turtle in the Caribbean Sea. American Museum Novitates; no. 2248.
- Chambers, L.E., Hughes, L. & Weston, M.A. (2005). Climate change and its impact on Australia's avifauna. *Emu*, 105, 1-20.

Clarke, L.J., Elliot, R.L., Abella-Perez, E., Jenkins, S.R., Marco, A., Martins, S. & Hawkes, L.A. (2021) Low-cost tools mitigate climate change during reproduction in an endangered marine ectotherm. Dryad Digital Repository. <https://doi.org/10.5061/dryad.3r2280gfg>.

Clusella-Trullas, S., Blackburn, T.M. & Chown, S.L. (2011). Climatic Predictors of Temperature Performance Curve Parameters in Ectotherms Imply Complex Responses to Climate Change. *American Naturalist*, 177, 738-751.

Dawson, T.P., Jackson, S.T., House, J. I., Prentice, I.C., Mace, G.M. (2011). Beyond predictions: biodiversity conservation in a changing climate. *Science*, 332, 53-58.

Dickinson, M., Prentice, I. C., & Mace, G. M. (2015). Climate change and challenges for conservation. Briefing paper, 13.

Donlan, C. J., Wingfield, D. K., Crowder, L. B., & Wilcox, C. (2010). Using expert opinion surveys to rank threats to endangered species: a case study with sea turtles. *Conservation Biology*, 24(6), 1586-1595.

Esteban, N., Laloë, J. O., Kiggen, F. S., Ubels, S. M., Becking, L. E., Meesters, E. H., ... & Christianen, M. J. (2018). Optimism for mitigation of climate warming impacts for sea turtles through nest shading and relocation. *Scientific Reports*, 8(1), 1-8.

Feeley, K.J., Stroud, J.T., Perez, T.M. (2017). Most 'global' reviews of species' responses to climate change are not truly global. *Diversity and Distributions*. 23, 231-234

Fuentes, M.M.P.B., Maynard, J.A., Guinea, M., Bell, I.P., Werdell, P.J. & Hamann, M. (2009). Proxy indicators of sand temperature help project impacts of global warming on sea turtles in northern Australia. *Endangered Species Research*, 9, 33-40.

Fuentes, M. M. P. B., Limpus, C. J., & Hamann, M. (2011). Vulnerability of sea turtle nesting grounds to climate change. *Global Change Biology*, 17(1), 140-153.

Fuentes, M.M.P.B., Fish, M.R. & Maynard, J. (2012). Management strategies to mitigate the impacts of climate change on sea turtle's terrestrial reproductive phase. *Mitigation and Adaptation Strategies for Global Change*, 17, 51-63.

Fuentes, M. M. P. B., Saba, V (2016). *Impacts and effects of ocean warming on marine turtles*. Explaining Ocean Warming: Causes, Scale, Effects, and Consequences, edited.

Hagerman, S., Dowlatabadi, H., Satterfield, T. & McDaniels, T. (2010). Expert views on biodiversity conservation in an era of climate change. *Global Environmental Change*, 20, 192-207.

Hamann, M., Godfrey, M., Seminoff, J., Arthur, K., Barata, P., Bjorndal, K., Bolten, A., Broderick, A., Campbell, L., Carreras, C., Casale, P., Chaloupka, M., Chan, S., Coyne, M., Crowder, L., Diez, C., Dutton, P., Epperly, S., FitzSimmons, N., Formia, A., Girondot, M., Hays, G., Cheng, I., Kaska, Y., Lewison, R., Mortimer, J., Nichols, W., Reina, R., Shanker, K., Spotila, J., Tomas, J., Wallace, B., Work, T., Zbinden, J. & Godley, B. (2010). Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endangered Species Research*, 11, 245-269.

Hamann, M., Limpus, C.J. & Read, M.A. (2007). *Chapter 15: Vulnerability of marine reptiles in the Great Barrier Reef to climate change*. In: *Climate change and the Great Barrier Reef: A vulnerability assessment* eds. J.E. Johnson and P.A. Marshall), pp. 465-496. Great Barrier Reef Marine Park Authority and Australia Greenhouse Office, Hobart.

Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, 8(5), 461-467.

Hansen, L., Hoffman, J., Drews, C. & Mielbrecht, E. (2010). Designing Climate-Smart Conservation: Guidance and Case Studies. *Conservation Biology*, 24, 63-69.

Hansen, J., Kharecha, P., Sato, M., Masson-Delmotte, V., Ackerman, F., Beerling, D.J., Hearty, P.J., Hoegh-Guldberg, O., Hsu, S.L., Parmesan, C., Rockstrom, J., Rohling, E.J., Sachs, J., Smith, P., Steffen, K., van Susteren, L., von Schuckmann, K. & Zachos, J.C. (2013). Assessing “Dangerous Climate Change”: Required Reduction of Carbon Emissions to Protect Young People, Future Generations and Nature. *PLoS ONE*, 8, e81648.

Haward, M., Davidson, J., Lockwood, M., Hockings, M., Kriwoken, L., & Allchin, R. (2013). Climate change, scenarios and marine biodiversity conservation. *Marine Policy*, 38, 438-446.

Hawkes, L.A., Broderick, A.C., Godfrey, M.H. & Godley, B.J. (2007). Investigating the potential impacts of climate change on a marine turtle population. *Global Change Biology*, 13, 923-932.

Hawkes, L. A., Broderick, A. C., Godfrey, M. H., & Godley, B. J. (2009). Climate change and marine turtles. *Endangered Species Research*, 7(2), 137-154.

Hays, G. C., Ashworth, J. S., Barnsley, M. J., Broderick, A. C., Emery, D. R., Godley, B. J., ... & Jones, E. L. (2001). The importance of sand albedo for the thermal conditions on sea turtle nesting beaches. *Oikos*, 93(1), 87-94.

Hays, G. C., Fossette, S., Katselidis, K. A., Schofield, G., Gravenor, M. B. (2010). Breeding periodicity for male sea turtles, operational sex ratios, and implications in the face of climate change. *Conservation Biology* 24:1636-1643

Hays, G. C., Mazaris, A. D., Schofield, G. (2014). Different male vs. female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. *Frontiers in Marine Science* 1:43

Hays, G. C., Mazaris, A. D., Schofield, G., Laloë, J-O. (2017). Population viability at extreme sex-ratio skews produced by temperature-dependent sex determination. *Proceedings of the Royal Society B: Biological Sciences* 284:20162576

Heller, N.E. & Zavaleta, E.S. (2009). Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation*, 142, 14-32.

Hirayama, R. (1998). Oldest known sea turtle. *Nature*, 392(6677), 705-708.

Hulin, V., Delmas, V., Girondot, M., Godfrey, M. H., & Guillon, J. M. (2009). Temperature-dependent sex determination and global change: are some species at greater risk? *Oecologia*, 160(3), 493-506.

Ihlow, F., Dambach, J., Engler, J.O., Flecks, M., Hartmann, T., Nekum, S., Rajaei, H. & Rödder, D. (2012). On the brink of extinction? How climate change may affect global chelonian species richness and distribution. *Global Change Biology*, 18, 1520-1530.

IPCC (2018) Summary for Policymakers. In: Global warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty (eds Masson-Delmotte V, Zhai P, Pörtner HO, *et al*). World Meteorological Organization, Geneva.

Jourdan, J. & Fuentes, M.M.P.B. (2015). Effectiveness of strategies at reducing sand temperature to mitigate potential impacts from changes in environmental temperature on sea turtle reproductive output. *Mitigation and Adaptation Strategies for Global Change*, 1-13.

Katselidis, K. A., Schofield, G., Stamou, G., Dimopoulos, P., & Pantis, J. D. (2012). Females first? Past, present and future variability in offspring sex ratio at a temperate sea turtle breeding area. *Animal Conservation*, 15(5), 508-518.

Kaska, Y., Downie, R., Tippet, R. & Furness, R.W. (1998). Natural temperature regimes for loggerhead and green turtle nests in the eastern Mediterranean. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 76, 723-729.

Lamont, M. M., & Fujisaki, I. (2014). Effects of ocean temperature on nesting phenology and fecundity of the loggerhead sea turtle (*Caretta caretta*). *Journal of Herpetology*, 48(1), 98-102.

Laloë, J. O., Cozens, J., Renom, B., Taxonera, A., & Hays, G. C. (2014). Effects of rising temperature on the viability of an important sea turtle rookery. *Nature Climate Change*, 4(6), 513-518.

Laloë, J. O., Cozens, J., Renom, B., Taxonera, A., & Hays, G. C. (2019). Conservation importance of previously undescribed abundance trends: increase in loggerhead turtle numbers nesting on an Atlantic island. *Oryx*, 54(3), 315-322.

Liles, M. J., Peterson, T. R., Seminoff, J. A., Gaos, A. R., Altamirano, E., Henríquez, A.V., Gadea, V., Chavarría, S., Urteaga, J., Wallace, B. P., Peterson, M. J. (2019). Potential limitations of behavioral plasticity and the role of egg relocation in climate change mitigation for a thermally sensitive endangered species. *Ecology and Evolution*, 9:1603–1622

Marco, A., Abella, E., Liria-Loza, A., Martins, S., López, O., Jiménez-Bordón, S., Medina, M., Oujo, C., Gaona, P., Godley, B.J. & López-Jurado, L.F. (2012). Abundance and exploitation of loggerhead turtles nesting in Boa Vista islands, Cape Verde: the only substantial rookery in the Eastern Atlantic. *Animal Conservation*, 15(4), 351-360.

Marco, A., Abella, E., Martins, S., López, O., & Patino-Martinez, J. (2018). Female nesting behaviour affects hatchling survival and sex ratio in the loggerhead sea turtle: implications for conservation programmes. *Ethology Ecology & Evolution*, 30(2), 141-155.

Matsuzawa, Y., Sato, K., Sakamoto, W. & Bjorndal, K.A. (2002). Seasonal fluctuations in sand temperature: effects on the incubation period and mortality of loggerhead sea turtle (*Caretta caretta*). pre-emergent hatchlings in Minabe, Japan. *Marine Biology*, 140, 639-646.

Miller, J.D. (1997). *Reproduction in Sea Turtles*. The Biology of Sea Turtles (ed. by P.L. Lutz and J.A. Musick), p. 432. CRC Press, Boca Raton.

Mitchell, N.J. & Janzen, F.J. (2010). Temperature-Dependent Sex Determination and Contemporary Climate Change. *Sexual Development*, 4, 129-140.

- Monsinjon, J. R., Wyneken, J., Rusenko, K., López-Mendilaharsu, M., Lara, P., Santos, A., ... & Nel, R. (2019). The climatic debt of loggerhead sea turtle populations in a warming world. *Ecological Indicators*, 107, 105657.
- Montero, N., dei Marcovaldi, M. A., Lopez–Mendilaharsu, M., Santos, A. S., Santos, A. J., & Fuentes, M. M. (2018). Warmer and wetter conditions will reduce offspring production of hawksbill turtles in Brazil under climate change. *PLoS One*, 13(11), e0204188.
- Mrosovsky, N., Kamel, S., Rees, A.F. & Margaritoulis, D. (2002). Pivotal temperature for loggerhead turtles (*Caretta caretta*). from Kyparissia Bay, Greece. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 80, 2118-2124.
- Omann, I., Stocker, A., & Jäger, J. (2009). Climate change as a threat to biodiversity: An application of the DPSIR approach. *Ecological Economics*, 69(1), 24-31.
- Önder, B. F., & Candan, O. (2016). The feminizing effect of metabolic heating in Green Turtle (*Chelonia mydas*). clutches in the eastern Mediterranean. *Zoology in the Middle East*, 62(3), 239-246.
- Patino-Martinez, J., Marco, A., Quiñones, L. & Hawkes, L.A. (2012). A potential tool to mitigate the impacts of climate change to the caribbean leatherback sea turtle. *Global Change Biology*, 18, 401-411.
- Panetta, A. M., Stanton, M. L., & Harte, J. (2018). Climate warming drives local extinction: Evidence from observation and experimentation. *Science Advances*, 4(2), eaaq1819.
- Pike, D. A. (2013). Forecasting range expansion into ecological traps: Climate-mediated shifts in sea turtle nesting beaches and human development. *Global Change Biology*, 19(10), 3082-3092.
- Poloczanska, E.S., Limpus, C.J. & Hays, G.C. (2009). Vulnerability of marine turtles to Climate change. *Advances in Marine Biology*, 56, 151-211.
- Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., ... & Duarte, C. M. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, 3(10), 919-925.
- Pritchard, P. C. H. (1969). Sea turtles of the Guianas. University of Florida.
- Rijnsdorp, A.D., Peck, M.A., Engelhard, G.H., Möllmann, C. & Pinnegar, J.K. (2009). Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science*, 66, 1570-1583.
- Ros, E. J. (2013). Size, clutch size and nesting distribution in leatherbacks on Playa Norte, Costa Rica.

Rusli, M. U., Booth, D. T., & Joseph, J. (2016). Synchronous activity lowers the energetic cost of nest escape for sea turtle hatchlings. *Journal of Experimental Biology*, 219(10), 1505-1513.

RStudio Team. (2020). RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA
URL <http://www.rstudio.com/>.

Schofield, G., Hobson, V. J., Lilley, M. K. S., Katselidis, K. A., Bishop, C. M., Brown, P., Hays, G. C. (2010). Inter-annual variability in the home range of breeding turtles: implications for current and future conservation management. *Biological Conservation*, 143, 722–730.

Schofield, G., Katselidis, K. A., Lilley, M. K., Reina, R. D., Hays, G. C. (2017). Detecting elusive aspects of wildlife ecology using drones: new insights on the mating dynamics and operational sex ratios of sea turtles. *Functional Ecology*, 31:2310-2319

Sim, E.L., Booth, D.T. & Limpus, C.J. (2015). Incubation temperature, morphology and performance in loggerhead (*Caretta caretta*). turtle hatchlings from Mon Repos, Queensland, Australia. *Biology Open*, 4, 685-692.

Sinervo, B., Méndez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M.L., Meza-Lázaro, R.N., Gadsden, H., Avila, L.J., Morando, M., De la Riva, I.J., Sepulveda, P.V., Rocha, C.F.D., Ibarquengoytía, N., Puntriano, C.A., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J. & Sites, J.W. (2010). Erosion of Lizard Diversity by Climate Change and Altered Thermal Niches. *Science*, 328, 894-899.

Sodhi, N.S., Bickford, D., Diesmos, A.C., Lee, T.M., Koh, L.P., Brook, B.W., Sekercioglu, C.H. & Bradshaw, C.J.A. (2008). Measuring the Meltdown: Drivers of Global Amphibian Extinction and Decline. *PLoS One*, 3, e1636.

Staines, M. N., Booth, D. T., Hof, C. A. M., & Hays, G. C. (2020). Impact of heavy rainfall events and shading on the temperature of sea turtle nests. *Marine Biology*, 167(12), 1-11.

Tanner, C. E., Marco, A., Martins, S., Abella-Perez, E., & Hawkes, L. A. (2019). Highly feminised sex-ratio estimations for the world's third-largest nesting aggregation of loggerhead sea turtles. *Marine Ecology Progress Series*, 621, 209-219.

Tilley, D., Ball, S., Ellick, J., Godley, B. J., Weber, N., Weber, S. B., & Broderick, A. C. (2019). No evidence of fine scale thermal adaptation in green turtles. *Journal of Experimental Marine Biology and Ecology*, 514, 110-117.

Tittensor, D. P., Beger, M., Boerder, K., Boyce, D. G., Cavanagh, R. D., Cosandey-Godin, A., Crespo, G.O., Dunn, D.C., Ghiffary, W., Grant, S.M. & Hannah, L. (2019). Integrating climate adaptation and biodiversity conservation in the global ocean. *Science Advances*, 5(11), eaay9969.

Tomillo, P. S., Saba, V. S., Blanco, G. S., Stock, C. A., Paladino, F. V., & Spotila, J. R. (2012). Climate driven egg and hatchling mortality threatens survival of Eastern Pacific leatherback turtles. *PLoS One*, 7(5), e37602.

Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J. B., Pe'er, G., Singer, A., ... & Gonzalez, A. (2016). Improving the forecast for biodiversity under climate change. *Science*, 353(6304).

Van De Merwe, J., Ibrahim, K., & Whittier, J. (2006). Effects of nest depth, shading, and metabolic heating on nest temperatures in sea turtle hatcheries. *Chelonian Conservation and Biology*, 5(2), 210-215.

Van de Merwe, J. P., Ibrahim, K., & Whittier, J. M. (2013). Post-emergence handling of green turtle hatchlings: improving hatchery management worldwide. *Animal Conservation*, 16(3), 316-323.

Wallace, B. P., DiMatteo, A. D., Bolten, A. B., Chaloupka, M. Y., Hutchinson, B. J., Abreu-Grobois, F. A., ... & Mast, R. B. (2011). Global conservation priorities for marine turtles. *PloS One*, 6(9), e24510.

Weishampel J. F., Bagley D. A., Ehrhart L. M. (2004). Earlier nesting by loggerhead sea turtles following sea surface warming. *Global Change Biology*, 10, 1424–1427

Weishampel, J. F., Bagley, D. A., Ehrhart, L. M., & Weishampel, A. C. (2010). Nesting phenologies of two sympatric sea turtle species related to sea surface temperatures. *Endangered Species Research*, 12(1), 41-47.

Willis, K. J., & Bhagwat, S. A. (2009). Biodiversity and climate change. *Science*, 326(5954), 806-807.

Witt, M.J., Hawkes, L.A., Godfrey, M.H., Godley, B.J. & Broderick, A.C. (2010). Predicting the impacts of climate change on a globally distributed species: the case of the loggerhead turtle. *Journal of Experimental Biology*, 213, 901-911.

Wood, A., Booth, D.T. & Limpus, C.J. (2014). Sun exposure, nest temperature and loggerhead turtle hatchlings: Implications for beach shading management strategies at sea turtle rookeries. *Journal of Experimental Marine Biology and Ecology*, 451, 105-114.

Worm, B., & Lotze, H. K. (2016). Marine biodiversity and climate change. *Climate Change*, 195-212.

Accepted Article

Wright, L. I., Stokes, K. L., Fuller, W. J., Godley, B. J., McGowan, A., Snape, R., ... & Broderick, A. C. (2012). Turtle mating patterns buffer against disruptive effects of climate change. *Proceedings of the Royal Society B: Biological Sciences*, 279(1736), 2122-2127.

Yntema, C. L., & Mrosovsky, N. (1982). Critical periods and pivotal temperatures for sexual differentiation in loggerhead sea turtles. *Canadian Journal of Zoology*, 60(5), 1012-1016.

Zbinden, J.A., Margaritoulis, D. & Arlettaz, R. (2006). Metabolic heating in Mediterranean loggerhead sea turtle clutches. *Journal of Experimental Marine Biology and Ecology*, 334, 151-157.

Figures

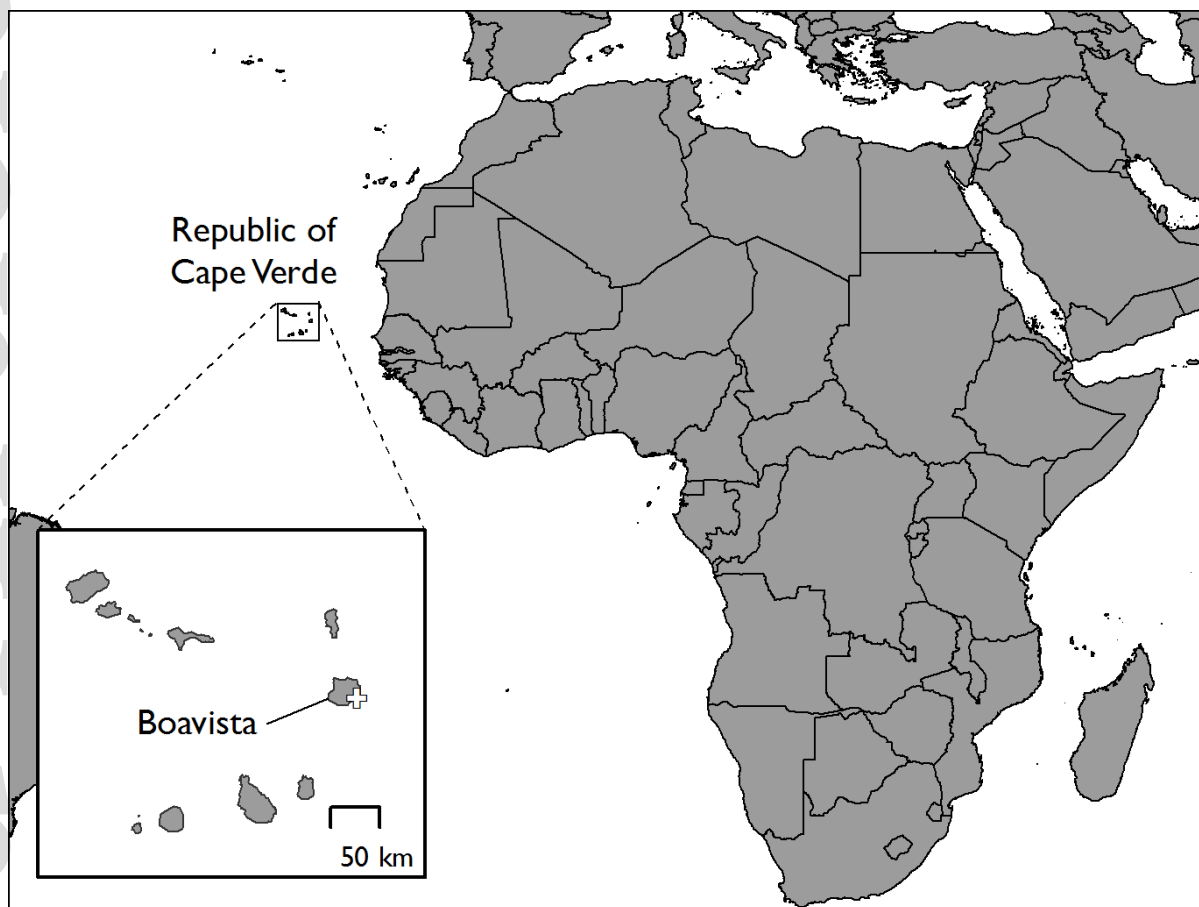


Figure 1. Map showing the location of the Cape Verde islands 600km off the West African coast and (inset) Boavista, the easternmost island of the Cape Verde islands. The approximate location of the study site is indicated as a white cross on inset.

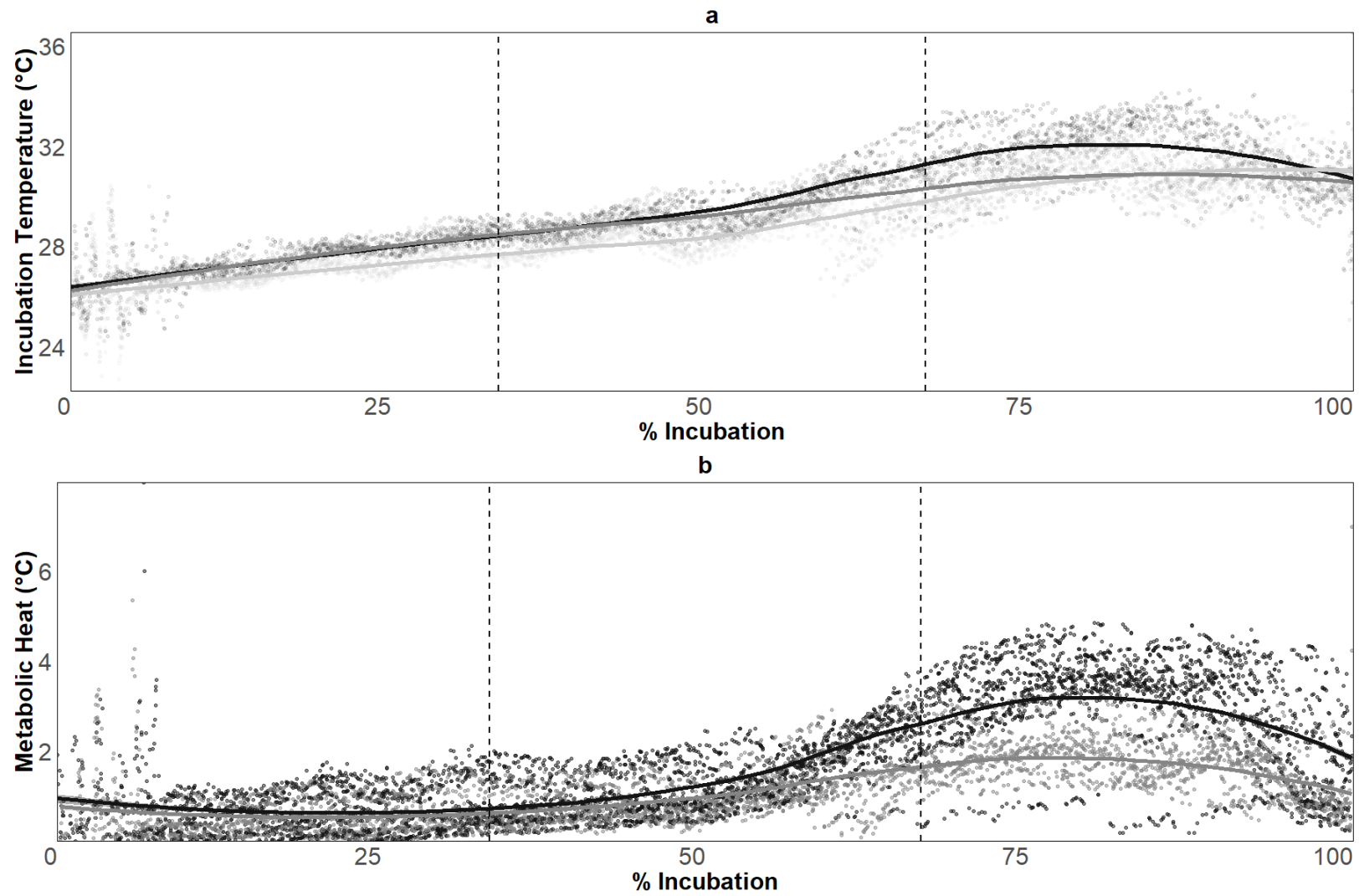


Figure 2. a) Incubation temperatures and b) metabolic heating over the course of the incubation period in each treatment (black line: control, dark grey line: split, light grey line: shaded clutches) in 2012, represented by a loess smoothing function fitted to a random subset of 10,000 temperature data points. Vertical dashed lines indicate the middle third of the incubation period.

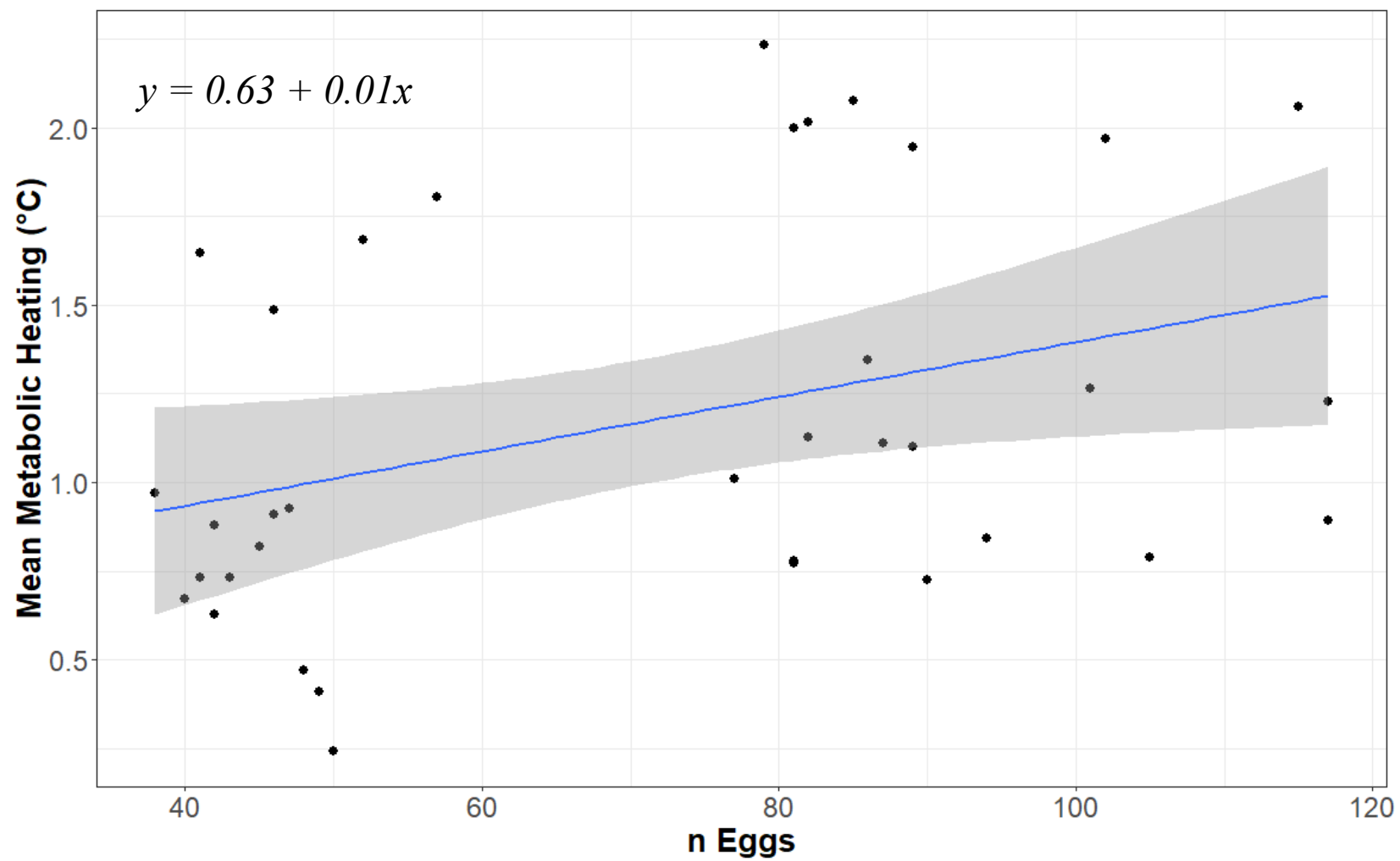


Figure 3. The relationship between the number of eggs within a clutch in 2012 and the mean amount of metabolic heat produced across the incubation period ($F(1, 34) = 5.02$, $R^2 = 0.103$, $p = 0.03$). Grey shading indicates 95% confidence intervals.

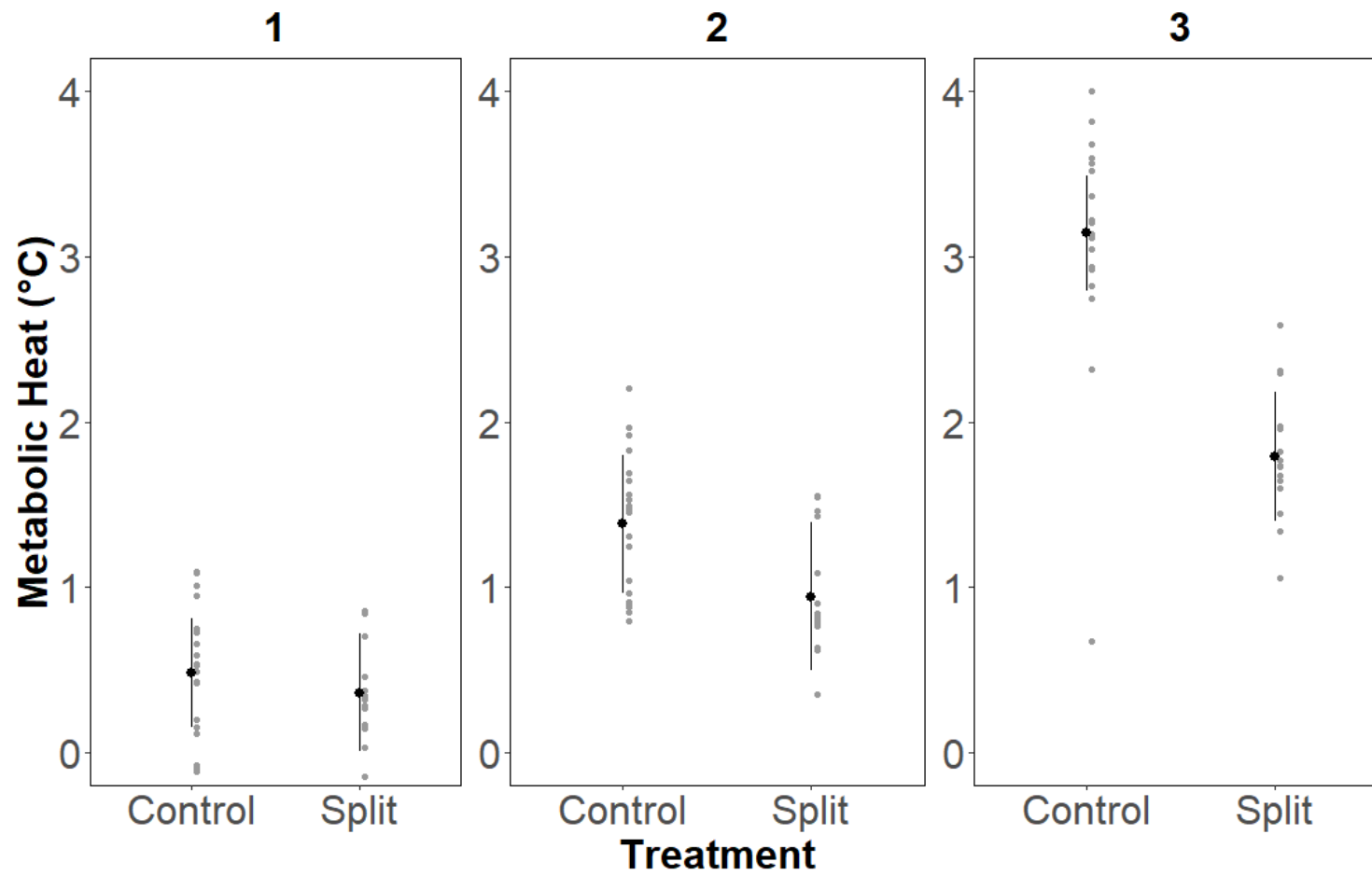


Figure 4. Metabolic heat (°C) (fitted values \pm 95% confidence intervals) produced by control and split clutches during each third of incubation in 2012. Partial residuals in grey.

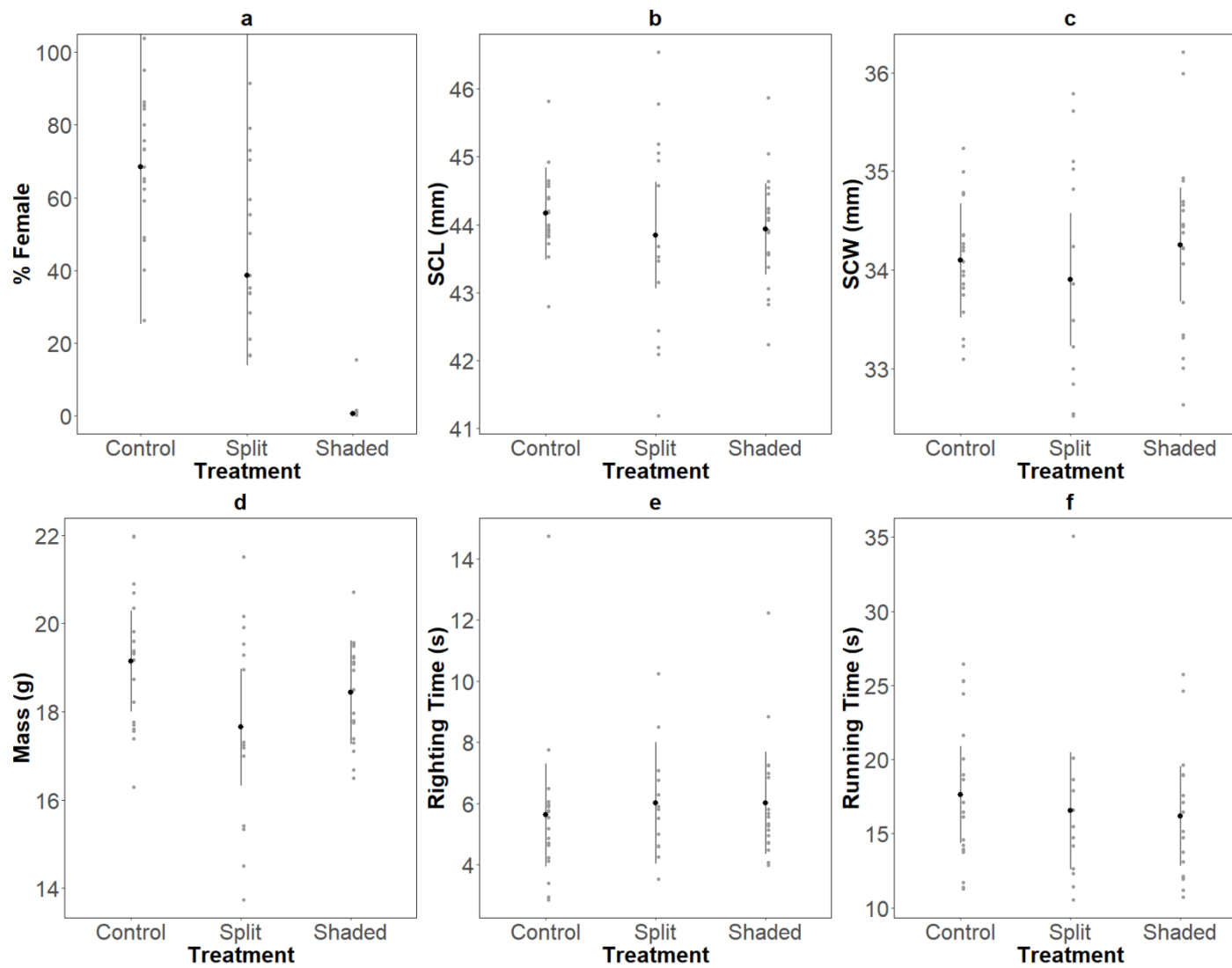


Figure 5. Treatment differences (fitted values \pm 95% confidence intervals) in a) proportion of female hatchlings, b) straight carapace length, c) straight carapace width, d) mass, e) righting speed and f) running speed of hatchlings produced in control, split and shaded clutches in 2012. Partial residuals in grey.

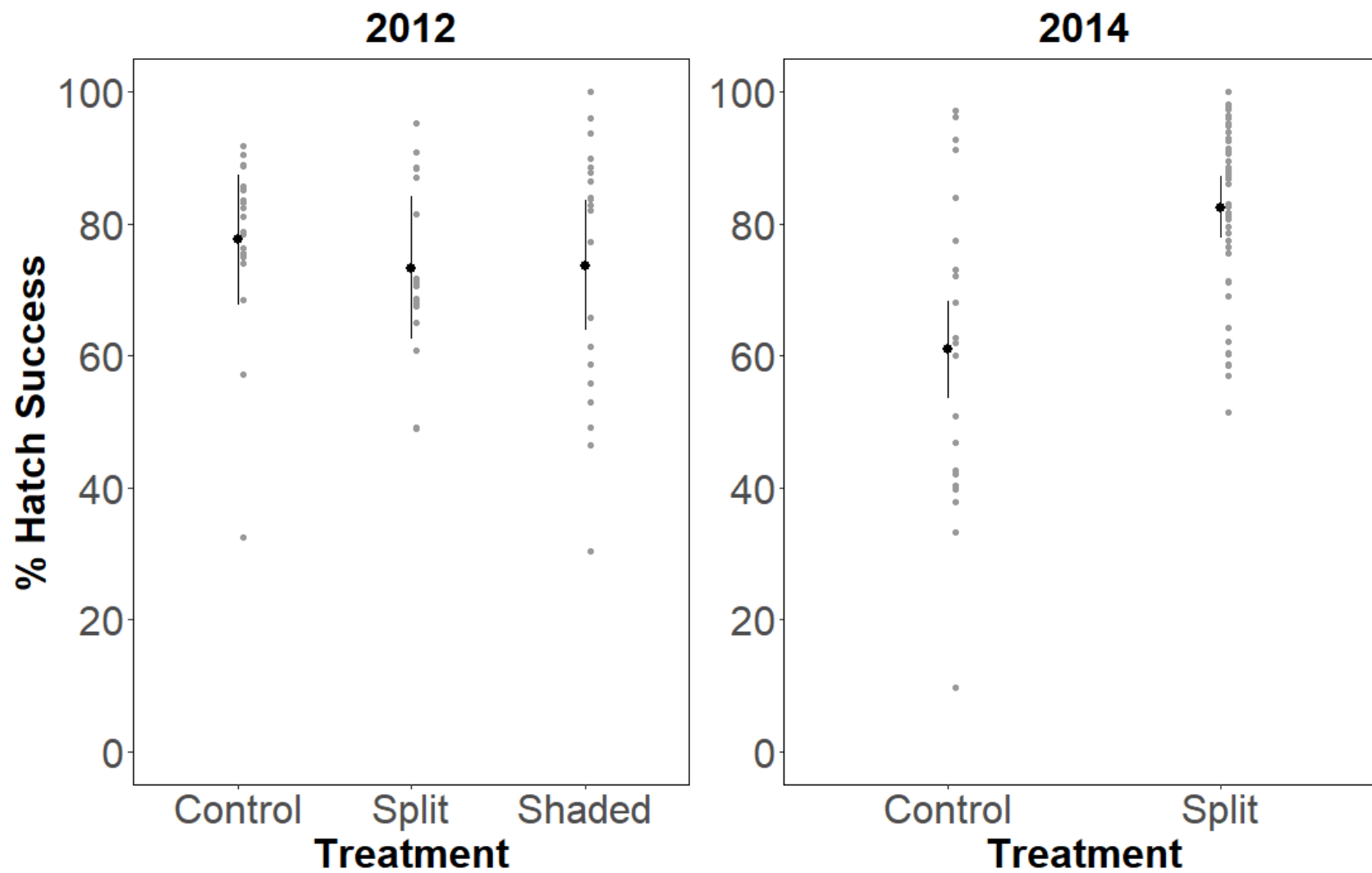


Figure 6. Hatch success (fitted values \pm 95% confidence intervals) in control, split and shaded clutches in 2012 and in control and split clutches in 2014. Partial residuals in grey.

346

Tables

347

348

Table 1. Mean (\pm S.E.) clutch and hatching parameters from control, split and shaded nests in 2012 with results of linear mixed effects models including fixed treatment effects and random effects of plot, where relevant. Means followed by a common letter are not significantly different. Hatch success data from 2014 are also presented.

Response	CONTROL	SPLIT	SHADED	TREATMENT			PLOT		
				d. f.	F	p. value	Variance	Std. Dev	
Clutch Size	92 ± 0.78	45.44 ± 0.78	88.35 ± 0.75	NA	NA	NA	NA	NA	
Incubation Duration (days)	59.35 ± 0.71 ^a	63.08 ± 0.84 ^b	66.05 ± 0.71 ^c	2, 55	22.16	< 0.001	0.56	0.75	
Incubation Temperature									
Overall (°C)	29.67 ± 0.08 ^a	29.15 ± 0.09 ^b	28.58 ± 0.08 ^c	2, 55	32.14	< 0.001	0.02	0.15	
Middle Third (°C)	29.40 ± 0.08 ^a	28.51 ± 0.09 ^b	28.32 ± 0.08 ^b	2, 55	16.09	< 0.001	0.08	0.29	
Metabolic Heating									
Overall (°C)	1.36 ± 0.19 ^a	0.89 ± 0.20 ^a	NA	1, 35	3.05	0.120	0.14	0.38	
First Third (°C)	0.48 ± 0.13 ^a	0.36 ± 0.14 ^a	NA	1, 35	0.39	0.549	0.05	0.22	
Middle Third (°C)	1.38 ± 0.16 ^a	0.94 ± 0.17 ^a	NA	1, 35	3.37	0.105	0.09	0.29	
Final Third (°C)	3.15 ± 0.14 ^a	1.79 ± 0.15 ^b	NA	1, 35	43.12	< 0.001	0.00	0.00	
Hatchling Parameters									
Hatching	2012	77.63 ± 4.91 ^a	73.34 ± 5.40 ^a	73.67 ± 4.91 ^a	2, 55	0.23	0.800	50.17	7.08
Success (%)	2014	60.98 ± 3.68 ^a	82.51 ± 2.32 ^a	NA	1, 72	24.48	< 0.001	NA	NA
% Female		69.02 ± 5.97 ^a	45.38 ± 6.6 ^a	1.46 ± 5.97 ^b	2, 55	32.89	< 0.001	54.24	7.37
SCL (mm)		44.16 ± 0.24 ^a	43.84 ± 0.28 ^a	43.93 ± 0.24 ^a	2, 51	0.42	0.670	0.02	0.12
SCW (mm)		34.10 ± 0.21 ^a	33.90 ± 0.24 ^a	34.25 ± 0.21 ^a	2, 51	0.61	0.559	0.00	0.00
Mass (g)		19.15 ± 0.41 ^a	17.65 ± 0.48 ^a	18.44 ± 0.42 ^a	2, 51	2.81	0.104	0.07	0.27
Running Time (s)		17.64 ± 1.18 ^a	16.55 ± 1.43 ^a	16.19 ± 1.21 ^a	2, 51	0.40	0.682	0.00	0.00
Righting Time (s)		5.62 ± 0.61 ^a	6.00 ± 0.72 ^a	6.02 ± 0.61 ^a	2, 51	0.13	0.877	0.51	0.71