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1 **Potential male leatherback hatchlings exhibit higher fitness and might balance sea**  
2 **turtle sex ratios in the face of climate change**

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4  
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14 period, marine turtles, reproductive output.

15 **Running head:** Higher fitness of male hatchlings

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25 **Abstract**

26 Sea turtles are vertebrates with temperature-dependent sex determination (TSD). Rising  
27 temperatures (as a results of climate change) cause biased female sex ratios. Here we  
28 assess the influence of depth and shading conditions on nest temperatures and hatchling  
29 fitness of leatherbacks. We relocated 48 clutches into a hatchery from 2013 to 2015. 24  
30 clutches were placed under shade and 24 under sun at 3 depths (50, 75, 90 cm).  
31 Leatherback hatchling fitness (as measured by greater length, width and weight) and  
32 locomotion performance (faster crawling and shorter righting responses) was improved in  
33 clutches from cooler, shaded treatments. At 50 cm depth, hatching success was higher for  
34 shaded clutches ( $78.6\% \pm 14.6$ ) than unshaded ( $49.2\% \pm 36.4$ ). Our results showed that  
35 shaded conditions produced hatchlings with higher fitness and a high likelihood of being  
36 males. Therefore, it may be used to inform conservation policies to decrease the current  
37 female-skewed sex ratio production caused by rising temperatures at most nesting  
38 rookeries around the world.

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41 **1. Introduction**

42 It is predicted that human activities will cause an increase of over 1.5 °C in the global average  
43 temperature by the end of the 21st century (Intergovernmental Panel on Climate Change  
44 (IPCC), 2013). This rapid and significant increase in mean temperature could exacerbate the  
45 extinction risk of species exhibiting temperature-dependent sex determination by  
46 feminizing their populations. However, climate change episodes might vary among places  
47 and some populations might be more affected by climatic events than others (Fernández-  
48 Chacón et al. 2011; Wernberg et al. 2013; Santidrián Tomillo et al. 2015). For example,  
49 temperatures are predicted to increase at higher rates in tropical locations than in the  
50 temperate zones with an associated effect on sea turtle hatchling production (Pike et al. 2013,  
51 2015).

52 Sea turtles are temperature-dependent sex determination species (TSD) (Mrosovsky  
53 and Pieau 1991), with female production at high temperatures and males at low ones (Yntema  
54 and Mrosovsky 1980). Hence, increasing temperatures produce biased female sex ratios  
55 (Godfrey et al. 1996; Hawkes et al. 2007; Fuentes et al. 2009; Woolgar et al. 2013) and  
56 mortality of embryos and hatchlings within the nest (Santidrián Tomillo et al. 2012, 2014).  
57 In addition, increases in storm intensity may cause consistent precipitation during incubation  
58 in some places (Webster et al. 2005) that might increase the moisture content of the sand,  
59 decreasing the optimum conditions required for embryonic development (McGehee 1990;  
60 Van Houtan and Bass 2007; Patino-Martinez et al. 2014), and consequently, increasing  
61 mortality of embryos (Rivas et al. 2018). Rises in water table level due to sea level rise could  
62 also induce clutch mortality by prolonged tidal inundation, suffocation (Kraemer and Bell  
63 1980; Rivas et al. 2016a) and decrease optimal incubation temperature.

64 Incubation conditions of turtle clutches depend on nest depth and the shading level of  
65 the sand surface over the nest (Patiño et al. 2012; Jourdan and Fuentes 2013; Wyneken and

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66 Lolavar 2015). Cooler nests will have longer incubation periods and embryos will have more  
67 time to develop which might affect their future phenotype (Glen et al. 2003). Phenotypical  
68 hatchling characteristics may play an important role in their survivorship (Janzen et al. 2000)  
69 (i.e. increases in nest temperature decreases swimming abilities of hatchlings) (Booth and  
70 Evans 2011). Some studies have identified that hatchling morphological characteristics and  
71 locomotor performances such as righting response and crawling time (Delmas et al. 2007)  
72 could be correlated with survival.

73 Besides the effect of climate change on the female productivity due to temperature  
74 (Matsuzawa et al. 2002; Santidrian et al. 2012, 2017; Pike et al. 2013) and precipitation  
75 (Houghton et al. 2007; Saba et al. 2012; Rivas et al. 2018), hatchling success and fitness can  
76 also be influenced by other physical and environmental conditions such as vegetation  
77 (Standora and Spotila 1985; Rivas et al. 2016b), partial pressures of oxygen, pO<sub>2</sub> (Garrett et  
78 al. 2010) and moisture (Wyneken and Lolavar 2015). Considering that climatic models  
79 predict increases in mean temperature, intense tropical cyclone activity, and heavy  
80 precipitation events for the next decades (IPCC 2013), research that is focused on studying  
81 the effect of these climatic variations is important to predict how they might affect the  
82 reproductive output and hatchling fitness of TSD species such as leatherback sea turtles,  
83 *Dermochelys coriacea*.

84 Here, we present the results of a coordinated experiment to examine the influence of  
85 incubation temperature on the fitness of hatchlings from leatherback turtle clutches relocated  
86 to a hatchery. We recorded (i) mean temperature (ii) hatching success and (iii) hatchling  
87 fitness of nests incubated in different environmental conditions. We evaluated hatchling  
88 fitness by measuring their morphological characteristics and locomotor performance (righting  
89 response and crawling behaviour). Hatchling fitness could be an important estimator of

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90 survivorship during early life-history stage as well as to assess hatchling survival under future  
91 scenarios of climate change.

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## 93 **2. Methods**

### 94 *2.1 Study site*

95 The study was conducted at Pacuare beach located in the Pacuare Nature Reserve (PNR)  
96 (10°10'00"N, 83°14'00"W) on the Caribbean coast of Costa Rica, which hosts one of the  
97 highest density of nests per km in Central America (Rivas et al. 2016c). Leatherback turtle  
98 nesting season at PNR is March-July where recent population trends have been stable (Rivas  
99 et al. 2016c) similar to other Caribbean populations (Dutton et al. 2005; Girondot et al. 2007;  
100 Stewart et al. 2011).

### 101 *2.2 Experimental treatments – hatching success and incubation temperature*

102 To determine the effect of the incubation temperature on hatchling success and fitness, we  
103 relocated 48 nests per year to a beach hatchery during 3 nesting seasons (2013-2015). The  
104 hatchery was located close to the coastal vegetation in the same location each year with  
105 dimensions of 10 x 8 m on a 0° slope, delimited by 1 m depth and 1 m high fence. To obtain  
106 different incubation temperatures, 50% of the hatchery (10 x 4 m) was shaded and 50% was  
107 fully exposed to the sun. Shade was created using a black plastic mesh installed at 1.5 m  
108 height, allowing 40% sun radiation at 1.5 m above the sand. Clutches were placed at three  
109 depth treatments at 50, 75 and 90 cm of depth in a block design considering depth range of *in*  
110 *situ* nests at PNR ( $74.6 \pm 7.2$  cm, Min = 40, Max = 97.3 cm, n = 368) in 2012. Eight clutches  
111 were randomly assigned to each depth and shade treatments. Nests were relocated to the  
112 hatchery immediately after female oviposition. The maximum distance of transportation of  
113 nests was 800 m within an hour after laying. A random sample of 20 eggs per clutch was

114 measured with calipers. Egg clutches were buried in the hatchery in nests mimicking the  
115 shape of natural excavation chambers. Clutches of eggs were covered by returning sand in the  
116 same order as it was removed to maintain original sand moisture and grain size.

117 To record sand and incubation temperatures, data loggers Hobo StowAway Tidbit v2  
118 ( $\pm 0.2$  °C) or Hobo Pendant 8K-UA-001-08 ( $\pm 0.5$  °C) were used. A data logger was placed in  
119 the middle of each clutch for every depth and shading treatment to record incubation  
120 temperature. A second logger was buried at the same depth 1 m from each clutch to record  
121 sand temperature. All loggers recorded temperature every 30 min during the entire incubation  
122 period. Temperatures from 2015 were not included in the analysis because clutches at 75 and  
123 90 cm depths did not hatch due to inundation.

124 The incubation period was considered as the number of days elapsed between egg burial and  
125 emergence of the first hatchling. Before hatching, a cylindrical metal net was located on  
126 every nest to keep emerged hatchlings. All clutches were excavated two days after hatchling  
127 emergence to determine the number of dead eggs and dead hatchlings within the nest  
128 chamber. Hatching success was estimated as the proportion of eggs that produced hatchlings  
129 in a clutch using the equation:  $H = S/(S + U)$ , where  $S$  = number of eggshells and  $U$  =  
130 number of unhatched eggs. Eggshell fragments that represented  $\geq 50\%$  of the egg were  
131 considered as one hatched egg (Miller 1999).

132 The mean nest temperature during the middle trimester (the thermosensitive period) (Rimblot  
133 et al. 1985) was calculated and sex ratio was estimated as the mean nest temperature in that 2-  
134 week period multiplied by the proportion of nests incubating in that period. Sex ratios were  
135 estimated using curves relating incubation temperature to sex ratio for Pacific Costa Rican  
136 leatherback turtles (Chevalier et al. 1999), the closest rookery to our study site with available  
137 data. However, temperature fluctuations might infer sex ratios in natural nests (Neuwald and

138 Valenzuela 2011), therefore, means were considered as potential indicator of sex ratio,  
139 although considering that these may create a male-bias of sex ratio estimations (Girondot et  
140 al. 2018).

### 141 *2.3 Hatchling fitness: phenotype and locomotor performance*

142 Immediately after emergence, hatchlings were taken from cylindrical nets and placed in  
143 buckets for measurement and assessment of locomotor performance. To assess the effect of  
144 the incubation temperature on hatchling fitness, we measured size and mass of hatchlings,  
145 body temperature, and locomotor performance. A sample of 20 hatchlings was randomly  
146 selected and measured from each successful clutch. Hatchling straight carapace length (SCL)  
147 and straight carapace width (SCW) were measured with callipers to the nearest 0.1 cm.  
148 Hatchling mass was weighted using a microbalance (PK401 Denver Instrument, accuracy  $\pm$   
149 0.1 g). The index of physical condition was determined as the ratio between hatchling masses  
150 to the length of the carapace ( $\text{g mm}^{-1}$ ) (Van de Merwe et al. 2005). The body temperature of  
151 the plastron surface of hatchlings ( $n = 10$ ) from each nest was measured by an infrared laser  
152 thermometer (FLUKE, 561, laser  $< 1\text{mW}$  Clase II, 630-670 nm,  $-40^{\circ}$ -  $550^{\circ}\text{C}$ , accuracy  $\pm 1.0^{\circ}$   
153 C) from a distance of  $\pm 20$  cm.

154 Hatchling righting response was estimated as the time that it takes for an individual to  
155 return to an upright position after being placed on its carapace (Steyermark and Spotila  
156 2001). For each righting trial, a hatchling ( $n = 10$ ) from each nest was placed on a flat table  
157 and was tested for 2 min as the maximum time for self-righting. Trials were performed on 10  
158 hatchlings per clutch.

159 Crawling rate by hatchlings was estimated by releasing groups of 5 on the sand from  
160 several distances to record the time to reach a marked line at high tide level. Prior to this trial,  
161 the beach was cleared of debris or any obstacles that could affect hatchling movement. To



162 quantify crawling rates by hatchlings, immediately after the righting response test the groups  
163 of 20 hatchlings per clutch were then released on the beach in groups of 5 from distances of  
164 30, 20, 10 and 5 m to the marked line. To reach significant numbers, the remainder of  
165 emerged hatchlings were added to this trial to assess whether groups of hatchlings could  
166 influence crawling rate. However, it was considered that results could be biased since some  
167 hatchlings in the groups were subjected to two previous trials. 34 groups (each with 20  
168 hatchlings) were released at 10 m from the marked line. Time was recorded to reach the  
169 marked line for: the first hatchling ( $t_0$ ), half of the group ( $t_1$ ) and final hatchling ( $t_2$ ).

## 170 *2.4 Statistics*

171 We used general linear modelling (GLM) to investigate the effect of depth, shading and year  
172 on hatching success and hatchling fitness. To avoid pseudo replication, mean hatchling  
173 measurements were estimated per nest. We used two-way ANOVA and egg weight as  
174 covariants to assess whether shade treatments and depth determined carapace size, weight,  
175 body temperature, righting response and crawling time. Finally, multiple regression analysis  
176 was performed to correlate egg mass and hatchling fitness, which would be used to assess the  
177 influence of depth and shade treatments on hatchling fitness and locomotor performance  
178 (Booth, Feeney and Shibata 2013). The analyses were performed using Jaguar library and R  
179 commander in R, version 3.3.3 (Rcore Team 2017) and STATISTICA v. 7.0 (StatSoft, Inc.  
180 Tulsa USA).

## 181 **3. Results**

### 182 *3.1 Experimental treatments–hatching success and incubation temperature*

183 The temperatures recorded in the centre of the clutch and the sand at the same depth and  
184 close to the nest differed on an average of  $1.1 \pm 0.2$  °C (Mean  $\pm$  SD) due to the embryonic

185 metabolic heating. The mean clutch temperature was of  $28.7 \pm 0.5$  °C in shaded clutches and  
186  $31.4 \pm 0.6$  °C in unshaded clutches (Table 1). The mean clutch temperature during the  
187 thermosensitive period (the second trimester of embryonic development) under shade  
188 treatment was  $28.0 \pm 0.4$  °C and  $31.0 \pm 0.67$  °C under the sun. A mean incubation temperature  
189 of  $28.0$  °C corresponds to an estimated sex-ratio highly biased toward males (100%), while a  
190 mean incubation temperature of  $31.4$  °C corresponds to an estimated sex-ratio highly biased  
191 to females (100%) (Chevalier et al. 1999). We also found significant differences in the  
192 incubation period between both treatments ( $F = 6.5$ ,  $p < 0.001$ ). The average incubation  
193 duration of unshaded clutches was shorter ( $61 \pm 2.1$  days,  $N = 29$  clutches than shaded  
194 clutches ( $74.8 \pm 5.3$ ,  $N = 26$  days) (Table S1). The mean size and weight of eggs were of  
195 ( $53.1 \pm 2.0$  mm,  $n = 143$ ) ( $49.0 - 65.6$ ) and ( $92.4 \pm 6.9$  gr,  $n = 143$ ) ( $74.6 - 111.2$ )  
196 respectively. Significant differences were found on egg size among years (GLM test,  $F =$   
197  $34.7$ ,  $p < 0.001$ ). Significant differences were also found in hatching success among depths  
198 (GLM test,  $F = 10.13$ ,  $p = 0.006$ ), years ( $F = 38.98$ ,  $p < 0.001$ ) and shade treatments ( $F =$   
199  $12.02$ ,  $p = 0.002$ ) (Fig. 1). The Tukey post-hoc analysis showed a higher survival on clutches  
200 at 50 cm depth compared with nests at deeper treatments. Inundation by groundwater caused  
201 a very high mortality in clutches buried at 75 and 90 cm depth. At 50 cm, where the impact of  
202 inundation was very low, shaded clutches had a higher survival than unshaded ( $78.6 \pm 14.6$   
203 %,  $49.19 \pm 36.4$  %, respectively). In contrast, at 90 cm, in 2013-2014 was ( $20.2 \pm 23.19$  %  
204 shaded,  $30.04 \pm 31.75$  % unshaded).

### 206 *3.2 Hatchling fitness: phenotype and locomotor performance*

207 The mean SCL of hatchlings was of  $60.0 \pm 2.0$  mm ( $N = 94$ , range=  $55.2 - 63.9$ ) and showed  
208 significant differences among shade treatments (Table 1) and year ( $F = 10.5$ ,  $p = 0.005$ ) (Fig.  
209 2). The Tukey post-hoc analysis showed differences between 50 cm depth clutches between

210 shade treatments in 2013 and 2014 ( $p < 0.001$ ). The mean SCW of hatchlings was  $41.3 \pm 2.3$   
211 mm ( $N = 94$ , range= $38.2 - 59.2$ ) with no significant differences between treatments  
212 (depth\*shade treatments;  $p = 0.14$ ) but the Tukey post-hoc analysis showed differences in  
213 SCW between clutches at 50 cm depth and clutches at 75 and 90 cm ( $F = 82.0$ ,  $p < 0.001$ ).  
214 The mean weight of hatchlings was  $48.9 \pm 6.4$  g ( $N = 94$ , range =  $24.4 - 59.2$ ) and varied  
215 among shade treatments (Table 1) (Fig. 2). Post-hoc analysis showed differences between 50  
216 and 75 and 90 cm depth clutches ( $F = 34.4$ ,  $p < 0.001$ ). Overall, the mean SCL, SCW and  
217 weight of hatchlings in shaded clutches were higher than without shade ( $F = 236.6$ ,  $p < 0.001$ ;  
218  $F = 122.5$ ,  $p < 0.001$ ;  $F = 52.8$ ,  $p < 0.001$ ), respectively (Fig. 3). The egg mass and the  
219 physical condition index were positively correlated ( $p = 0.004$ ). The hatchling physical  
220 condition index (mean of  $0.8 \pm 0.1$ ) did not vary significantly among depths and shade  
221 treatments (Table 1; Fig.4). The body temperature of hatchlings did not vary significantly  
222 among depths and shade treatments ( $F = 2.13$ ,  $p = 0.34$ ;  $F = 2.32$ ,  $p = 0.470$ , respectively).

223 The analysis of locomotor performance of hatchlings revealed significant differences  
224 in the righting response between the shading treatments ( $F = 6.7$ ,  $p < 0.001$ ). Post-hoc  
225 analysis showed differences at 50 cm with respect to 75 and 90 cm depth ( $F = 4.8$ ,  $p < 0.001$ )  
226 (Fig. 5). The crawling time of hatchlings was significantly different between the shade  
227 treatments ( $p < 0.001$ ), but not between depths ( $F = 0.87$ ,  $p = 0.650$ ). Post-hoc analysis  
228 showed differences between 50 and 75 and 90 cm ( $F = 4.4$ ,  $p < 0.001$ ). Hatchlings emerging  
229 from shaded clutches were faster than those from unshaded clutches ( $5.9 \pm 3.9$ ;  $7.2 \pm 4.6$   
230 respectively) (Fig.6, Table 1), but there were no differences among distances ( $F = 7.0$ ,  $p =$   
231  $0.07$ ). Finally, the results comparing crawling time over 10 m distance by groups of  
232 hatchlings ( $t_0$ :  $2.5 \pm 1.0$ ,  $t_1$ :  $3.4 \pm 1.3$ ,  $t_2$ :  $5.4 \pm 2.1$  min,  $n = 33$ ) did not show significant  
233 differences among depths and between shade treatments ( $P = 0.02$ ;  $P = 0.13$ ;  $P = 0.86$ ,  
234 respectively).

235 **Discussion**

236 This study highlights that hatchlings from cooler nests have a higher fitness in terms of  
237 locomotor performance and ability to right themselves. In the last years many studies have  
238 shown an increased concern on the potential effects of global warming to many TSD species  
239 such as reptiles (Hulin et al. 2009; Hawkes et al. 2009; Pike et al. 2014; Santidrian et al.  
240 2015), fishes (Ospina-Alvarez et al. 2010) and birds (Mitchell et al. 2010; Grayson et al.  
241 2014) across the globe. The correlation between warm incubation temperatures and female-  
242 biased hatchling production has been widely reported in sea turtle populations (Janzen et al.  
243 1994; Hawkes et al. 2007; Laloë et al. 2016), heightening concerns that climate warming may  
244 lead to the production of female-only populations and eventual extinction (Hays et al. 2014). ,  
245 Additionally, species determined by (TSD) such as sea turtles could also be potentially  
246 threatened by mortality of eggs and hatchlings due to high incubation temperatures (Bell et  
247 al. 2003; Santidrian Tomillo et al. 2012, 2014; Laloë et al. 2017).

248 Extremely warm incubation conditions (> 30 °C) were recorded in unshaded sites  
249 during the current study on the Caribbean coast of Costa Rica. These conditions are likely to  
250 produce a female-biased sex ratio, similar to results from other Caribbean sites during the  
251 past decades (Laloë et al. 2016). In contrast, the hatchling sex ratio emerging from shaded  
252 clutches is likely to be male-biased due to lower temperatures (< 28.5 °C), Longer incubation  
253 periods were recorded in shaded rather than unshaded conditions, which corroborate that  
254 lower incubation temperatures prolong the incubation period and embryonic development of  
255 sea turtle species (Van de Merwe et al. 2005; Hays, Mazaris and Schofield 2014; Laloë et al.  
256 2014, 2016). Mean hatching success was significantly higher from shaded clutches  
257 supporting results from other studies of leatherback populations (Rivas et al. 2018; Patiño et  
258 al. 2012; Hill et al. 2015). This may be the result of lower incubation temperatures in shaded  
259 conditions and a consequent decrease in embryonic mortality linked to high temperatures

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260 (Bell et al. 2004; Santidrian et al. 2012, 2014; Howard et al. 2014). Mortality is higher in  
261 warm incubation conditions (i.e. female-producing nests) so it is logical that there are sub-  
262 lethal effects of warm, female-producing temperatures (Hays et al. 2017).

263 Our findings revealed that at all depths, hatchlings emerging from cooler nests had  
264 improved fitness in terms of size, weight and locomotor performance. This is the first study  
265 to record phenotype and terrestrial performance for leatherback turtles, though they have  
266 been recorded for other species, for instance green turtles *Chelonia mydas* (Booth and Evans,  
267 2011; Weber et al. 2012), loggerhead turtles *Caretta caretta* (Fisher et al. 2014; Sim et al.  
268 2015) and olive ridley turtles *Lepidochelys olivacea* (Maulany et al. 2012). Considering that a  
269 negative correlation between incubation temperature and hatchling size (Hewavisenthi and  
270 Parmenter 2001; Ischer et al. 2009; Booth and Evans 2011; Read et al. 2012; Weber et al.  
271 2012), and between incubation temperature and crawling speed have been documented in all  
272 sea turtle species (Chu et al. 2008; Ischer et al. 2009; Mickelson and Downie 2010; Maulany  
273 et al. 2012; Read et al. 2012; Booth et al. 2013; Fisher et al. 2014; Wood et al. 2014; Sim et  
274 al. 2015), the influence of incubation temperature on post-hatchling locomotion performance  
275 and growth are the traits that are likely to have the greatest effect on hatchling fitness  
276 (Burgess et al. 2006).

277 Leatherback turtles exhibit both polyandry and polygyny (Crim et al. 2002), therefore,  
278 increased frequency of male breeding would help ameliorate female-biased hatchling sex, but  
279 the effective population size in sea turtles is still unknown (Hays et al. 2010).

280 If the projections of increasing temperatures in the next decades are confirmed (IPCC 2013),  
281 the proportion of nests experiencing extremely high temperatures is likely to increase, which  
282 may affect hatchling survival rates. Based on incubation temperature assessment, this study  
283 showed that male hatchlings are likely to exhibit higher fitness than females, which could

1 284 provide higher survivorship of males than females; and consequently, might mitigate the  
2 285 female-skewed sex ratio production at most nesting populations around the world. Taking  
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4 286 into account the skewed sex ratios towards males were mainly produced under shade  
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6 287 treatment, it is recommended that new beach management strategies are considered to  
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8 288 produce balanced sex ratios. Additionally, the highest mortality of deeper clutches by  
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10 289 increasing water table levels highlighted that inundation episodes might affect all beach width  
11  
12 290 (Rivas et al. 2018), including distant locations from high tide line. Considering, nests  
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14 291 relocated at upper depths presented higher hatching success than the deepest ones, a hatchery  
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16 292 might be an effective tool to mitigate the mortality of deep nests by water table rises and  
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18 293 increase the reproductive output of sea turtle populations. However, we highly recommend  
19  
20 294 leaving *in situ* nests, urge caution when relocating nests and assessing beach microhabitat  
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22 295 conditions prior selecting hatchery locations and shading treatments by every sea turtle  
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24 296 monitoring programme.  
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## 55 306 **Author contributions**

56  
57 307 MLR and AM conceived and designed the experiments. MLR performed the experiments and  
58  
59 308 analyzed the data. MLR wrote and AM and NE revised the manuscript.  
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309 **Figures**

310 **Fig. 1.** Hatching success (%) of leatherback clutches under sun and shade treatment and depth  
311 (50, 75 and 90 cm) in 2013, 2014 and 2015. The centre point in the box represents the mean  
312 value; the whiskers represent 95% confidence interval.

313 **Fig. 2.** Straight Carapace Length (SCL) (mm), Straight Carapace Width (SCW) (mm) and  
314 weight (g) of leatherback hatchlings under sun and shade treatment and depth (50, 75 and 90  
315 cm) in 2013, 2014 and 2015. The horizontal line in the box represents the mean value; the  
316 whiskers represent 95% confidence interval. Grey points represent individual measurements  
317 and black points outliers.

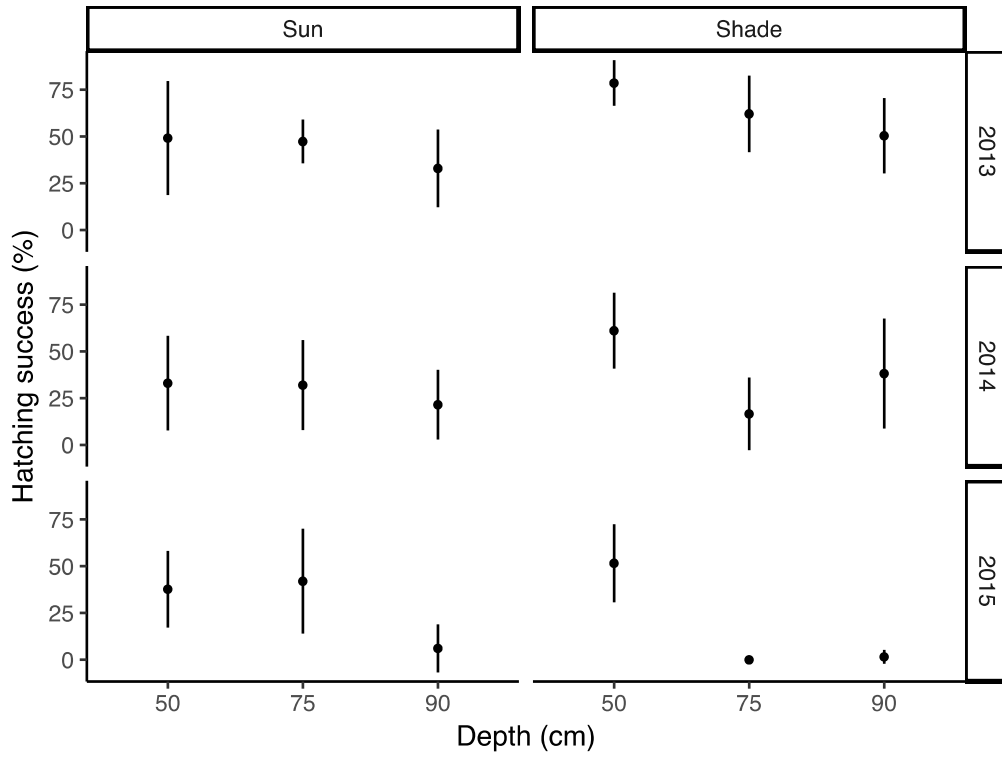
318 **Fig. 3.** A. Straight Carapace Length (SCL) (mm), B. Straight Carapace Width (SCW) (mm)  
319 and C. Weight (g) of leatherback hatchlings under sun and shade treatments in 2013-2015.  
320 The horizontal line in the box represents the mean value; the whiskers represent 95%  
321 confidence interval.

322 **Fig. 4.** Body temperature (°C) of leatherback hatchlings under sun and shade treatment and  
323 depth (50, 75 and 90 cm) in 2013, 2014 and 2015. The horizontal line in the box represents  
324 the mean value; the whiskers represent 95% confidence interval. Grey points represent  
325 individual measurements.

326 **Fig. 5.** Righting response (min) of leatherback hatchlings under sun and shade treatment and  
327 depth (50, 75 and 90 cm) in 2013-2015. The horizontal line in the box represents the mean  
328 value; the whiskers represent 95% confidence interval. Grey points represent individual  
329 measurements.

330 **Fig. 6.** Crawling time (min) of leatherback hatchlings under sun and shade treatment in 2013-  
 331 2015. The horizontal line in the box represents the mean value; the whiskers represent 95%  
 332 confidence interval.

333 **Fig. 1.**

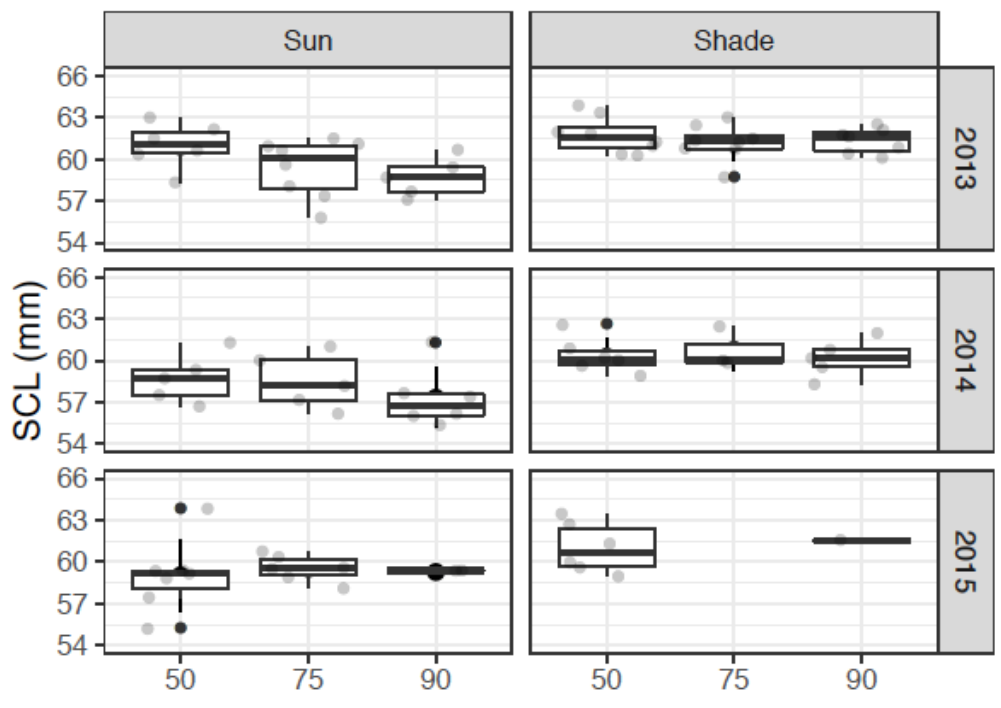


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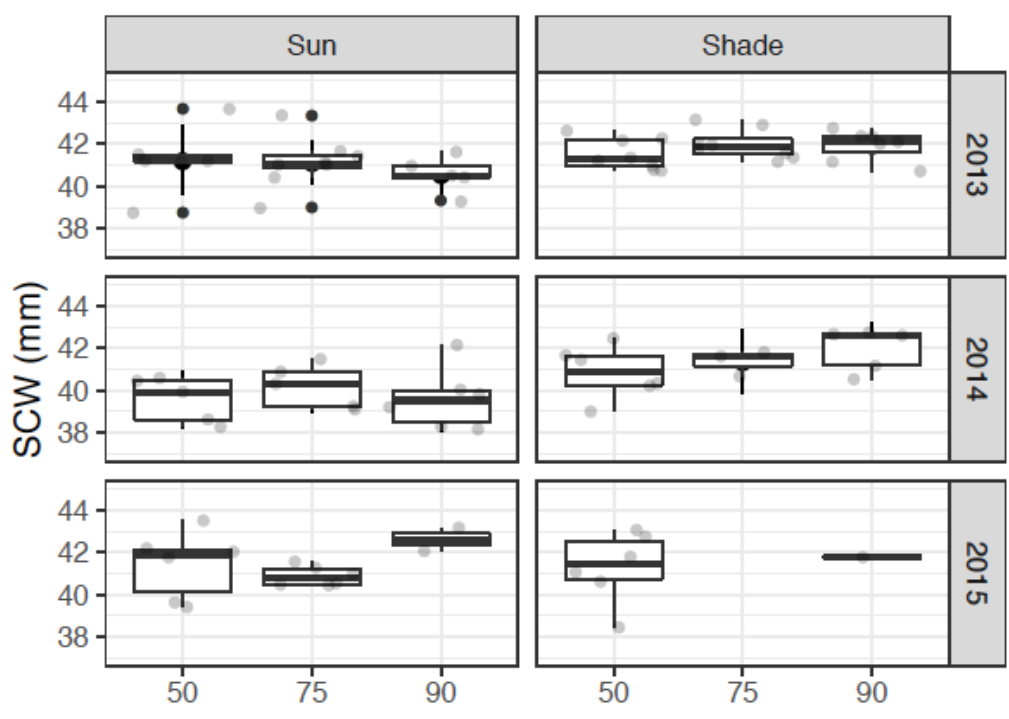
335 **Fig 2.**



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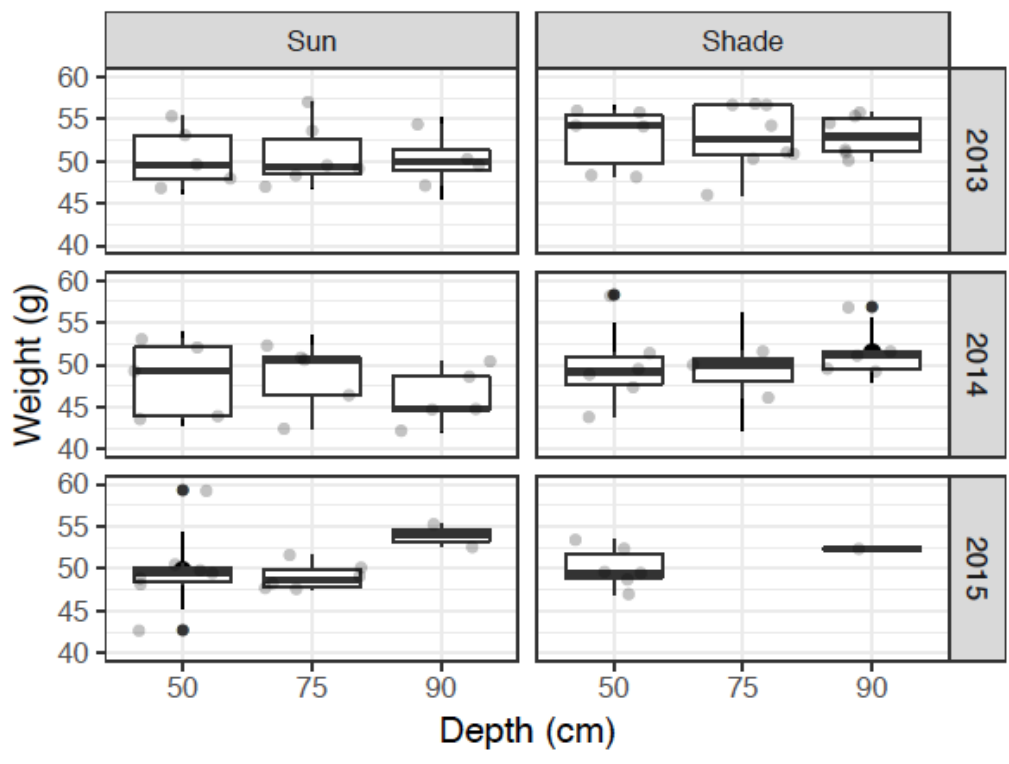


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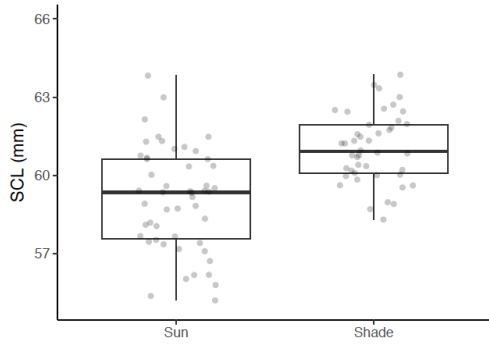
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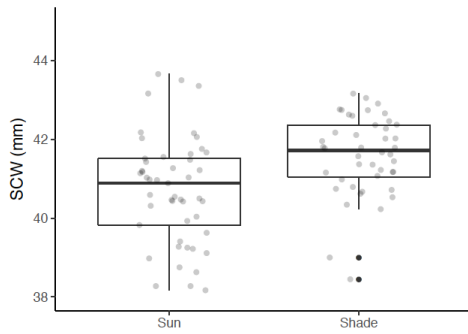
339 **Fig. 3.**

340 **A**



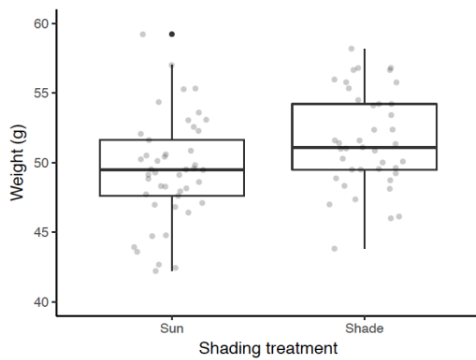
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342 **B**



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344 **C**



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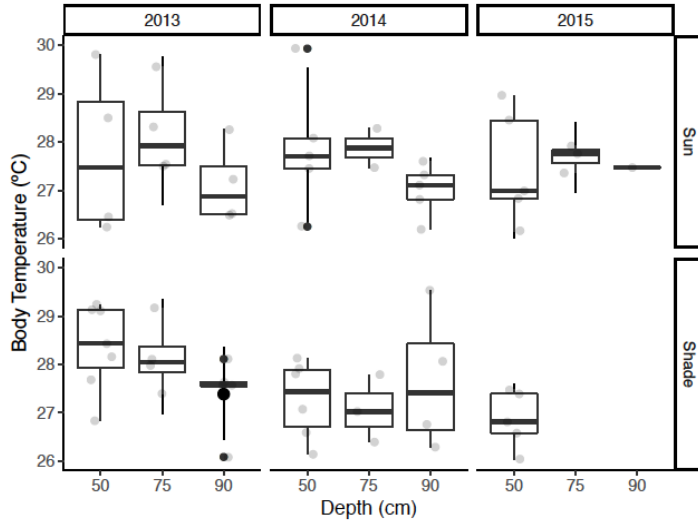
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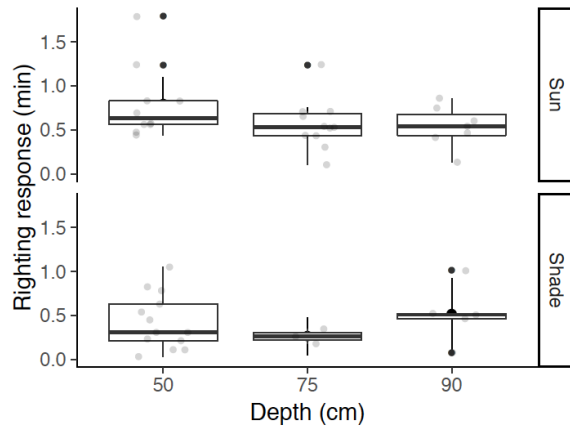
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351 **Fig. 5**



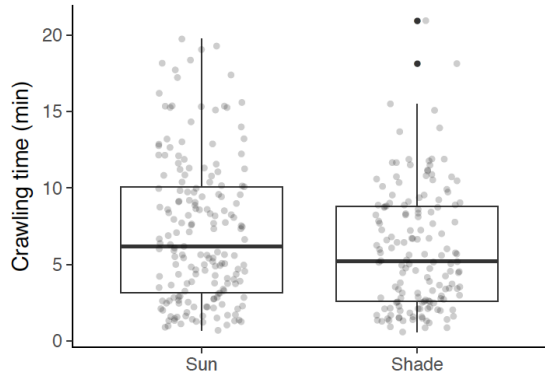
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353 **Fig. 6**

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**Table 1.** Phenotype (Straight carapace length (SCL) (mm), Straight carapace width (SCW) (mm) and weight (g)), body temperature (°C) and locomotor variables (fitness index (g mm<sup>-1</sup>), righting response (s) and crawling time (min)) of hatchlings under sun and shade treatment and depth (50, 75 and 90 cm) in 2013, 2014 and 2015.

Variables	Shade		Mean	SD	N	F	p
	treatments						
SCL (mm)	Sun		59.1	1.99	50	236.6	< 0.01
	Shade		61.0	1.33	44		
SCW (mm)	Sun		41.1	2.94	50	122.5	< 0.01
	Shade		41.6	1.01	44		
Weight (g)	Sun		47.6	6.77	50	52.8	< 0.01
	Shade		50.3	5.76	44		
Body Temperature (° C)	Sun		27.9	3.49	49	1.47	0.14
	Shade		27.3	2.91	43		
Index of physical condition (g mm <sup>-1</sup> )	Sun		0.80	0.11	50	0.95	0.34
	Shade		0.83	0.10	44		
Righting response (s)	Sun		64.0	34.20	28	6.0	< 0.01
	Shade		42.7	29.78	21		
Crawling time (min)	Sun		7.2	4.68	181	16.87	< 0.01
	Shade		5.9	3.91	152		

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