Running head: leatherback hatchling response to lighting

Leatherback hatchling sea-finding in response to artificial lighting: interaction
between wavelength and moonlight.

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Abstract

Over the last decades, growing human populations have led to the rising occupation of coastal areas over the globe causing light pollution. For this reason, it is important to assess how this impact threatens endangered wildlife. Leatherback turtles (*Dermochelys coriacea*) face many threats of anthropogenic origin including light pollution on nesting beaches. However, little is known about the specific effects. In this study we studied the effect of different light wavelengths (orange, red, blue, green, yellow and white lights) on hatchling orientation under the presence and absence of moonlight by analyzing: (i) the mean angle of orientation, (ii) crawling duration, and (iii) track patterns.

Hatchling orientation towards the sea was always better under controlled conditions. In the absence of moonlight, leatherback hatchlings were phototaxically attracted to the experimental focus of light (misoriented) for the colours blue, green, yellow and white lights. Orange and red lights caused a lower misorientation than other colors, and orange lights produced the lowest disrupted orientation (disorientation). On nights when moonlight was present, hatchlings were misorientated under blue and white artificial lights. Crawling duration was low for misoriented hatchlings and high for the disoriented individuals. Our conclusion to this is that hatchlings can detect and be impacted by a wide range of the light spectrum and we recommend avoiding the presence of artificial lights on nesting beaches. Additionally, actions to control and mitigate artificial lighting are especially important during dark nights when moonlight is absent.

KEY WORDS: Costa Rica, conservation, misorientation, light pollution, sea turtles, tourist development

Introduction

Sea turtles nest on sandy beach ecosystems. These habitats are severely threatened by global climate change and anthropogenic effects (Schlacher et al. 2007). Light pollution associated with coastal development is one of the important anthropogenic alterations that can reduce the reproductive success of sea turtles (Verheijen, 1985; Witherington, 1996). Artificial illumination on nesting beaches alters both the nest site selection by females, hatchling behaviour and also has a direct impact on hatchling survival (Witherington, 1996; Kamrowski et al., 2012). After emergence, sea turtle hatchlings crawl rapidly from the nest towards the sea to avoid predation (Salmon and Wyneken, 1987; Santidrián Tomillo et al., 2010). Sea-finding seems to be mainly visual as sea turtle hatchlings are proven to be attracted to the brightest area within their field of vision and is also related to the brightness and lower elevation of the sea. Moreover, sea-finding abilities can also be affected by the presence of dark silhouettes that are cast by dunes and other objects (Mrosovsky, 1970; Salmon et al., 1992, Bartol et al., 2003; Tuxbury and Salmon, 2005; Limpus and Kamrowski, 2013) that continue to be important even after they enter the aquatic environment (Bartol et al., 2003). However, a hatchling's ability to detect these natural cues is reduced in the presence of artificial lights (Lorne and Salmon, 2007). As a result, beach lighting disrupts the orientation of hatchlings, which will eventually lead to exhaustion, dehydration, entanglement in dune vegetation, and/or an increase of the risk of predation (Salmon, 2003; Zheleva, 2012).

The effects of artificial light on hatchling disorientation (when they crawl in circuitous paths and are not able to find a cue) and misorientation (when they direct themselves to the artificial source) have been previously documented (McFarlane, 1963; Philibosian, 1976; Verheijen, 1985; Salmon and Witherington, 1995). However, the effect on the behaviour of the turtles varies among species and depends on the light's characteristics such as its intensity, wavelength, polarization and periodicity (Witherington, 1985).

74 Previous field experiments conducted on loggerhead (*Caretta caretta*) and green
75 turtles (*Chelonia mydas*) show that both short and long light wavelengths at any intensity
76 influence hatchling orientation. The effect of artificial lighting on hatchling orientation was
77 reduced in the presence of moonlight and its effects on hatchlings varied depending on the
78 characteristics of the luminaries (Witherington and Bjorndal, 1991a; Witherington, 1991;
79 Witherington and Martin, 1996; Witherington and Salmon, 2005). There are differences in the
80 behavioral response between species (Witherington and Bjorndal, 1991b). Green turtles show
81 phototactic spectral sensibility (phototaxis or light attraction) for the wavelength of the visible
82 light region 440-700 nm, and show signs of slight ultraviolet discrimination (Levenson et al.,
83 2004). Loggerhead turtles show positive phototaxis (misorientation) for blue (450 nm), green
84 (500 nm) and yellow (580 nm) colors (Young et al., 2012). Likewise, olive ridley
85 (*Lepidochelys olivacea*) (Karnad et al., 2009), hawksbill (*Eretmochelys imbricata*) (Eckert
86 and Horrocks, 2002) and flatback turtles (*Natator depressus*) (Pendoley, 2005; Fritsches,
87 2012) show preferential orientation towards low wavelengths.

88 The disorientation of hatchling leatherback turtles (*Dermochelys coriacea*) as a
89 consequence of light pollution has been documented in Gabon. This important nesting site
90 was highly contaminated by light pollution and hatchlings showed a higher attraction to
91 artificial lights than to silhouettes (Bourgeois et al., 2009). Although leatherback turtles
92 respond to a wide range of light wavelengths and are capable of color vision (Horch et al.,
93 2008), no experimental studies have analyzed the effect of the presence of artificial lights of
94 different wavelengths (colors) on the sea-finding behaviour of hatchlings under natural
95 conditions. This type of studies is important not only because of the increasing number of
96 artificial lights on beaches, but also because of the use of lights by tourists and observers on
97 the nesting beaches. Given the increasing pressure of coastal development on nesting beaches
98 and the critical situation of some leatherback populations, it is important to assess the impacts

99 of artificial lighting on hatchling behaviour and therefore on the overall reproductive success
100 of the species. Consequently, the aim of this study was to characterize the effects of both
101 artificial lights (different wavelengths) and natural lights (the presence or absence of
102 moonlight) on hatchling behaviour. Studying the impact of light sources on leatherback turtles
103 provides the basis for understanding the effects of this growing environmental threat. This
104 information is essential to characterize the threat and prioritise responses and mitigation
105 strategies in sea turtle conservation efforts (Hamann et al., 2010; Wallace et al., 2011).

106 **Methods**

107 **Study site**

108 The study was conducted at Pacuare beach, located in the Pacuare Nature Reserve
109 (PNR) (10°10 '00" N, 83°14 '00" W), an important leatherback nesting beach on the
110 Caribbean coast of Costa Rica (Rivas et al., 2014). The experiment was done during the
111 leatherback hatchling season (May through August) in 2013. Between March and May, 39
112 clutches laid by nesting turtles were relocated to a protected fenced hatchery. These clutches
113 were laid on the first kilometer of the beach and were relocated due to the high risk of
114 inundation in this area. After hatchlings emerged from the nest, seven hatchlings were
115 randomly taken to run the experiments. Experiments with lights were conducted during the
116 night (between 18:00h and 02:00h), immediately after hatchlings emerged from the nest. Each
117 hatchling was immediately released from the experimental area located close to the hatchery
118 after the experiment was completed.

119 **Natural beach light**

120 Experiments with light in the turtle's natural beach conditions (in the presence and
121 absence of moonlight) were conducted in June and July 2013. Before conducting each
122 experiment, the level of natural sky light was measured on the beach with a portable

123 photometer, the Sky Quality Meter (SQM) by Unihedron. This photometer measures average
124 luminance from a relatively wide solid angle (1.5 steradian; the Half Width Half Maximum
125 (HWHM) of the angular sensitivity is $\sim 42^\circ$) and measurements are displayed in astronomical
126 units of magnitude per square arcsec (mag/arcsec^2). The SQM is temperature calibrated and
127 gives the luminance with the precision of 0.1 mag/arcsec^2 , which is equivalent to 10 percent
128 in linear (cd/m^2) units. Sky brightness was converted to the standard luminance scale (SL)
129 (cd/m^2) using the formula $(\text{SL}) = 10.8 \times 10^4 \times 110^{(-0.4 \times [\text{mag/arcsec}^2])}$
130 (www.darkskiesawareness.org/sqm-zlpa.php) (increasing luminance values correspond to
131 lower brightness levels). Measurements were taken by pointing the device at the horizon on
132 the seaside at 1.0 meter above the sand, always from the same place and before each
133 experiment was conducted. Light readings were recorded during the absence of moonlight
134 (during the new moon, before moonrise or after moonset, and/or with total cloud cover) and
135 presence of moonlight (any lunar phase). Considering the fact that cloud coverage amplifies
136 sky luminance (Kyba et al., 2011), cloudy nights were defined as with or without moonlight
137 depending on luminance recordings: absence of moonlight (more than $500 \mu\text{cd/m}^2$) and
138 presence of moonlight (until $500 \mu\text{cd/m}^2$).

139 The anthropogenic lights from the town of Limón are visible from Pacuare ($\sim 45 \text{ km}$)
140 and therefore the mean angle of Limon from the emplacement of release was recorded (angle
141 between Limon and hatchling releasing emplacement, Fig. 1) to assess the effect of these
142 lights on the sea-finding orientation of hatchlings.

143 **Experiments with artificial light**

144 The experiments were conducted ten meters away from the hatchery and ten meters
145 away from the highest tide line. A 2-meter radius circle was drawn in the sand around the
146 point of release. The light source was located 5 meters away from the center of the circle in

147 the direction opposite to the sea and the light was focused towards the center of the circle
148 (Fig. 1). The light source was fixed to a stick at 1.0 meter above the surface of the sand.
149 Seven treatments were used, one being a control in dark conditions and six using colours of
150 the visible spectrum: orange, red, blue, green, yellow, and white. Conventional LED
151 headlamps were used as artificial light sources (28 - 35 lumens), as they are frequently used
152 by conservationists on sea turtle nesting beaches (Nichia, PETZL and Nebo brands).
153 Polycarbonate filters were used for the yellow light. Seven hatchlings from each nest were
154 randomly assigned to one light treatment. Hatchlings were placed in the center of the circle
155 and were allowed to crawl by themselves. Information was collected on the following
156 parameters under two natural light conditions (presence or absence of moonlight):

157 (1) Orientation. Previous methodology described by Salmon and Witherington (1995)
158 and Salmon (2003) was followed. The point where hatchlings crossed the circle perimeter was
159 considered to define the angle of orientation. The source of light was at 270° and the ocean at
160 90° (Fig. 1).

161 (2) Crawling duration. The time that it took the hatchling to move from the light
162 emplacement to leave the circle was recorded. The maximum time allowed was four minutes.
163 After four minutes we considered the test as a “no exit” result.

164 (3) Track pattern. Two types of track patterns were defined based on the hatchling's
165 movements: “S” when the hatchling left the circle following a straight path regardless of the
166 direction and “W” when the hatchling left a wavy track or moved in circles.

167 Due to the fact that hatchlings can react to artificial lights by a) becoming disoriented
168 (they crawl in circuitous paths and are not able to find a cue to orient themselves) or b)
169 misoriented (they direct themselves to the artificial source; Salmon and Witherington, 1995),
170 hatchling orientation was further classified into four groups depending on the exit point from

171 the circle: group 1 (45° to 135°), group 2 (315° – 45°), group 3 (135° – 225°) and group 4
172 (225° – 315°) (Fig. 1). This classification allowed us to assess the relationship between
173 crawling duration and disorientation/misorientation.

174 **Statistical analysis**

175 Multiple regression analyses and nonparametric tests were used to analyze the effects
176 of natural beach luminance on hatchling orientation. Circular statistics were also used to
177 determine the mean angle of orientation (α) and r-vector (r) as a measure of angular dispersion
178 with a range of 0-1 (Zar, 1999; Lorne and Salmon, 2007). For these tests, we used Oriana
179 version 4. Rayleigh tests were used to assess differences in hatchling orientation among light
180 experiments and a General Linear Model was used to analyze the effects of lunar phases,
181 color treatments, track patterns and orientation groups on crawling duration. Bonferroni Post-
182 hoc tests were used to determine differences among groups for the significant variables, F –
183 tests to assess differences in hatchling orientation by color treatments in presence or absence
184 of moonlight and χ^2 – tests to test for differences between track patterns. We used Statistica
185 Release 10 program (Stata Corp 2007) and SPSS v. 20.0 (IBM Corp 2011) to conduct
186 statistical analyses.

187 **Results**

188 **Hatchling orientation**

189 There were significant differences in natural luminance between nights in which
190 moonlight was present and absent (Mann-Whitney test, $Z = 1.96$, $p = 0.006$). The mean
191 luminance values were $4899.5 \mu\text{cd}/\text{m}^2$ and $443.9 \mu\text{cd}/\text{m}^2$ in moonless and moonlit nights
192 respectively. Light pollution from the city of Limón was also detected at Pacuare beach
193 located at a mean angle of 30° , with respect to the 360 degrees of the diagram (Fig 1).

194 Luminances of light treatments used were: control ($16.47 \mu\text{cd}/\text{m}^2$), orange ($8.77 \mu\text{cd}/\text{m}^2$), red
195 ($8.45 \mu\text{cd}/\text{m}^2$), blue ($8.15 \mu\text{cd}/\text{m}^2$), green ($7.54 \mu\text{cd}/\text{m}^2$), yellow ($6.82 \mu\text{cd}/\text{m}^2$), and white
196 ($6.18 \mu\text{cd}/\text{m}^2$).

197 In the absence of moonlight, significant differences were found in hatchling
198 orientation for most light treatments (Watson-Williams F-test, $F = 45.25$, $p < 0.0001$). In
199 general terms, hatchlings in control, orange and red experiments were predominantly capable
200 of moving towards the sea. However, hatchlings exposed to blue, green, yellow and white
201 lights were predominantly misoriented and moved towards the experimental source of light
202 (Fig. 2A). Although some hatchlings exposed to orange and red lights were eventually able to
203 move towards the sea, they showed high levels of disorientation predominantly moving in the
204 direction of the sea and the town of Limon (Table 1, Fig. 2A). On moonlit nights, hatchlings
205 under control, orange, red, green and yellow lights were capable of finding the sea while
206 hatchlings exposed to blue and white lights were misoriented (Fig. 2B).

207 There were significant differences in the mean vector of hatchling orientation between
208 the control and each of the light treatments during moonless nights (Watson-Williams f-tests,
209 $F = 45.2$, $p < 0.001$) (Table 2). On the contrary, there were only significant differences
210 between the mean vectors of the control and blue, and control and white treatments during
211 moonlit nights (Table 2). Rayleigh tests showed that the mean direction and the mean vector
212 length of hatchling orientation were significantly different among all light treatments in the
213 absence of the moonlight. With moonlight present, there were significant differences among
214 light treatments with the exception of blue (Rayleigh test, $Z = 2.8$, $p = 0.054$) and white lights
215 ($Z = 0.42$, $p = 0.66$) (Table 3).

216 **Crawling duration and track pattern**

217 The general linear model showed a significant effect of track shape on crawling
218 duration ($F_{1,262} = 47.1$, $p < 0.001$), interactions between track shape and orientation group
219 ($F_{1,262} = 5.2$, $P = 0.006$) and between color treatments and track shape ($F_{1,262} = 2.3$, $P =$
220 0.03). The Bonferroni post-hoc analysis showed significant differences in crawling duration
221 between groups 1 (towards the sea) and 2, and between groups 2 and 4 (towards the light
222 treatment) ($p < 0.001$ for both). Hatchlings in groups 1 and 4 (oriented and misoriented,
223 respectively) were the fastest at leaving the circle (mean $\pm$ SD duration: 1.33 ± 0.18 min and
224 1.40 ± 0.18 min respectively), compared with hatchlings in groups 2 (1.83 ± 0.19 min) and 3
225 (1.77 ± 0.34 min). The post-hoc analyses also showed significant differences in crawling
226 duration among treatments with red and yellow lights ($p < 0.01$), and among treatments with
227 red and white lights ($p = 0.005$). The shortest mean crawling duration occurred under yellow
228 light (mean = 1.14 min, $n = 36$). Under this treatment, hatchlings were mainly misoriented.

229 The longest mean crawling duration occurred under red light (mean = 1.83 min, $n =$
230 41). Under the red light and without the presence of moonlight, 22% of hatchlings ($n = 41$)
231 were disoriented and unable to leave the circle, or took more than 4 minutes to acquire the
232 capacity to leave the circle. On the other hand, all hatchlings under the orange light were able
233 to leave the circle. In this case, the percentage of hatchlings that were within orientation group
234 2 were 41.4% and 46.5% for red and orange lights respectively (Table 1).

235 On moonless nights, the frequency of track patterns was affected by light treatment
236 ($X^2 = 51.51$; $gl = 6$; $p < 0.0001$, $n = 234$) (Fig. 3). Red and orange lights resulted in the highest
237 number of hatchlings moving in a wavy zig-zag pattern. The frequency of wavy crawls was
238 significantly higher under the red light (70.3%) than under the orange light (35%) ($X^2 = 9.58$;
239 $gl = 1$; $p = 0.002$; $n = 87$). However, in the presence of moonlight, there was not a significant
240 influence of the light treatment on track pattern although results were close to being
241 significant ($X^2 = 12.11$; $gl = 6$; $p = 0.06$; $n = 96$).

Discussion

Hatchling orientation and interactions with natural beach lighting

Color light treatments had a negative effect on hatchling orientation but the overall effect depended on the presence or absence of moonlight. Absence of moonlight resulted in misorientation under blue, green, yellow and white light, and disorientation under orange and red lights; hatchling disorientation was greater under the red than under the orange light. Crawling duration was low for hatchlings that were oriented or misoriented, and high when hatchlings were disoriented.

Our results confirm that leatherback hatchlings are less sensitive to long wavelengths (~700 nm) near red than to shorter wavelengths such as short deep blue (~380 nm). Although some hatchlings still found the ocean on moonless nights under red and orange treatments, orientation was impaired as shown by the long crawl durations. Studies that used electroretinography confirmed that both loggerhead and leatherback turtles can see from wavelengths near to UV, showing a maximum sensitivity or phototaxis at 500 - 580 nm (blue–green) and a second peak at 380 nm near UV (Witherington and Bjorndal, 1991; Constantino and Salmon, 2003; Levenson et al., 2004; Horch et al., 2008). Most studies on the spectral sensitivity of sea turtles have been conducted on loggerhead and green turtles in the laboratory. Although the capacity for color vision in leatherback turtles had also been previously described, there was little information on ranges of discrimination and behavioral responses to different wavelengths in natural conditions. Leatherback hatchling spectral sensibility seems to be similar to that of loggerhead hatchlings (Witherington and Bjorndal, 1991; Levenson et al., 2004; Horch et al., 2008) and other sea turtle species (Eckert and Horrocks, 2002; Pendoley, 2005; Karnad et al., 2009; Fritsches, 2012). However, behavioral responses to the same wavelengths can differ among populations of a single species. For

266 example, loggerhead hatchlings show an orientation aversion to yellow light in the US
267 (Witherington and Bjorndal, 1991a,b), but not in Australia (Fritsches, 2012). Therefore, light
268 sensitivity could also differ among hatchlings from different populations in other sea turtle
269 species.

270 Although leatherback turtle hatchlings are less sensitive to the longest wavelengths of
271 the human visual spectrum (Horch et al., 2008), hatchling orientation was still affected by red
272 light stimuli during sea-finding orientation, increasing crawling times and increasing the
273 frequency of circling movements in comparison to the control. Additionally, there was less-
274 frequent circling and a higher percentage of hatchlings left the circle under the orange light
275 than under the red light experiment (Fig. 3A). Orientation circles are more commonly
276 displayed while crawling to the ocean in leatherback hatchlings than in other species
277 (Mrosovsky and Shettleworth, 1975). We found that the frequency of circling was also
278 affected by the colour of the light source and among hatchlings that were capable of orienting,
279 frequency of circling was the lowest under control, followed by orange and then by the red
280 treatment. The orange light source emitted the lowest luminance value among colors tested.
281 Hatchling disorientation under the red light could also result from higher brightness of this
282 source in comparison to the orange one.

283 Previous studies have shown that variances in the natural beach light due to solar and
284 lunar positions significantly influence hatchling orientation. Seaward orientation depends on
285 phototaxic reactions to light and visual assessments of the brightness of the horizon
286 (Mrosovsky, 1972; Witherington, 1992; Limpus and Kamrowski, 2013). The shape and/or
287 elevation of natural cues (i.e. high silhouettes) and the slope of dunes and vegetation can
288 provide additional cues on hatchling orientation towards the sea (Mrosovsky, 1972; Salmon et
289 al., 1992). Interactions between natural cues and artificial lighting such as the presence of
290 high silhouettes and moonlight can also affect the orientation of hatchling sea turtles

291 (Tuxbury and Salmon, 2005). Our results show that there is an interaction between the
292 moonlight's presence/absence and the effects that artificial lighting has on hatchling
293 behaviour. On moonless nights, all light treatments had a negative effect on hatchling
294 orientation, which was stronger in the treatments that resulted in misorientation (blue, green,
295 yellow and white lights) than in those causing disorientation (orange and red lights). Some
296 hatchlings could still find the direction of the water under orange and red light treatments.
297 With moonlight, misorientation was only observed among hatchlings exposed to blue and
298 white lights. Overall, our results confirmed those by Salmon and Witherington (1995), who
299 suggested that natural beach light plays an important role on the effects of artificial lighting in
300 the sea-finding mechanisms used by hatchlings. Finally, it must be noted that the small
301 headlamps that are frequently used by conservationists and tourists on the beach were used as
302 light sources in this study. Therefore, it could be plausible that exposure to more intense
303 lights, such as those of buildings, can likely cause a stronger effect on hatchlings.

304 **Conservation and management implications**

305 Artificial lighting constitutes an important anthropogenic impact that has been
306 threatening sea turtle populations on their nesting beaches around the world for
307 decades (Carr and Ogren, 1960; McFarlane, 1963; Kamrowsky et al., 2012). In the
308 Caribbean region, artificial lightning can reduce reproductive success in sea turtle
309 populations, and accelerate their extinction, which can be associated with economic
310 impacts (Brei et al., 2014). Therefore, keeping nesting beaches in dark conditions is
311 the best and most highly recommended management strategy. On the nesting beaches,
312 red lights are sometimes used for beach monitoring because white light was proved to
313 produce phototaxis and disrupted orientation (Carr and Ogren, 1960; Mrosovsky and
314 Shettleworth, 1975; Mrosovsky and Carr, 1967). In this study, the orange light yielded
315 better results than those of the red treatment, but the most suitable conditions for

hatchling orientation were under the control treatment where no artificial lights were applied.

As mentioned above, coastal artificial lighting or photo-pollution is a grave threat to sea turtles especially as anthropogenic settlements are increasing along coastal areas around the globe and are determined by economic activity (Bourgeois et al., 2007; Gallaway et al., 2010; Kamrowski et al., 2014). These impacts disrupt behavioral responses in many organisms and affect their reproductive success (Kyba et al., 2011; Kamrowski et al., 2012; Brei et al., 2014). If this increasing trend of artificial lighting continues, future coastal biodiversity may be compromised (Brei et al., 2014). There was an influence of light pollution from the town of Limón on hatchling orientation at Pacuare, even though the town was relatively far from the beach (~45 km). There were more disoriented hatchlings in orientation group 2 (Limón would be located at 30° between groups 1 and 2) than in orientation group 3 (away from Limón) that had very few hatchlings. The presence and location of towns should be considered in management plans since lights from nearby towns can also affect the orientation of sea turtle hatchlings. The use of orange/red lights in unprotected areas of influence (i.e. on roads or nearby towns that are visible from the beach) is recommended when darkness is not possible. However, management strategies on the nesting beaches should prioritize dark conditions over any type of light.

In addition to the management efforts that focus on the control of light sources at many sites, other measures such as the restoration or reinforcement of natural cues could also improve the sea-finding of hatchling sea turtles (Witherington et al., 1992; Tuxbury and Salmon, 2005; Bourgeois et al., 2009). Keeping the beaches dark is essential. However, unprotected beaches often suffer the effects of lights. In these cases, we also recommend the use and reinforcement of natural vegetation fences to minimize the effects of light emissions from nearby coastal settlements on unprotected nesting beaches.

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465 **Tables**

466 **Table 1.** Number and percentage of leatherback hatchlings that did not leave the circle or took longer than four minutes (“no exit”), left the
 467 circle in orientation group 1 (45° to 135°), group 2 (315° – 45°), group 3 (135° – 225°) or group 4 (225° – 315°) under each light treatment in
 468 absence of moonlight (see Fig. 1 for a diagram of location groups).

Treatments	no exit		Group 1		Group 2		Group 3		Group 4	
	N	(%)	n	(%)	n	(%)	N	(%)	n	(%)
Control	2	5.9	22	64.7	10	29.4	0	0	0	0
Yellow	0	0	1	4.2	4	16.6	0	0	19	79.2
Red	9	22	9	22	17	41.4	2	4.9	4	9.7
Orange	0	0	14	32.6	20	46.5	1	2.3	8	18.6
Green	2	5.7	4	11.4	3	8.6	0	0	26	74.3
Blue	0	0	4	11.1	1	2.8	0	0	31	86.1
White	0	0	2	5.3	0	0	1	2.6	35	92.1

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471

472 **Table 2.** Summary of statistical results from the Watson-Williams F- tests. The Multi-sample test used comparisons of the mean vector of
 473 hatchling orientation between every light color and the control in absence or presence of moonlight. *Mean vector for the experimental group.

Variables	N		F		P		Df	df2		Mean*	
	absence	presence	absence	presence	absence	presence		absence	presence	absence	presence
Control & Yellow	(32 & 24)	(17 & 10)	139.8	0.18	<0.001	0.67	1	54	25	22.03	73.52
Control & Red	(32 & 31)	(17 & 10)	10.71	0.04	0.002	0.84	1	61	25	46.01	72.03
Control & Orange	(32 & 43)	(17 & 10)	20.04	0.34	<0.001	0.56	1	73	24	37.08	67.23
Control & Green	(32 & 33)	(17 & 10)	156.4	0.31	< 0.001	0.58	1	63	25	06.55	74.42
Control & Blue	(32 & 36)	(17 & 10)	200.0	33.02	< 0.001	< 0.001	1	66	25	354.7	52.81
Control & White	(32 & 38)	(17 & 10)	324.2	11.08	<0.001	0.003	1	68	25	330.9	71.48

474

475 **Table 3.** Summary of results from the Rayleigh (Z) tests that discriminated whether hatchlings orientated on the beach randomly or
 476 showed attraction or rejection to specific stimulus of light source. Tests were conducted in presence or absence of moonlight.

Color Source	Control		Yellow		Red		Orange		Green		Blue		White	
	absence	presence	absence	presence	absence	presence	absence	presence	absence	presence	absence	presence	absence	presence
Rayleigh (Z)	24.23	10.12	13.03	6.19	8.91	8.49	10.84	2.89	16.47	5.19	19.23	2.84	26.76	0.42
Rayleigh (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	<0.001	0.05	<0.001	0.003	<0.001	0.054	<0.001	0.666

477

Figure legends

Figure 1. Diagram of the experiment conducted on leatherback turtle hatchlings to test their orientation under different light treatments at Pacuare, Costa Rica. The light was fixed to a stick 1 meter above the sand directed toward the sea and perpendicular to the beach. A 2-meter radius circle was drawn in the sand 5 meters away from the visual stimulus. Light source was directed to the center of the circle. Hatchlings were classified based on the point of exit from the circle in orientation group 1 (45° to 135°), group 2 (315° (345°), group 3 (135° , 225°) or group 4 (225° to 315°).

Figure 2. Mean angle of orientation of hatchling leatherback turtles in response to light treatments in (A) absence of moonlight and (B) presence of moonlight. Black points represent hatchling position at leaving the circle. Black lines are mean vector and the outer circular black line represents circular variance.

Figure 3. Percentage of hatchlings in each treatment that were classified as leaving straight tracks (in grey), or wavy tracks (in light grey) after leaving the circle (A) in absence of moonlight or (B) in presence of moonlight. Only hatchlings that succeeded in leaving the circle during treatments were included.

Figure 1

Figure 2

B

Figure 3