1   **Neglecting low season nest protection exacerbates female biased sea turtle hatchling**
2   **production through the loss of male producing nests.**
3
4

5   *Catherine E. Hart[a,b]*, Luis Angel Tello-Sahagun[c], F. Alberto Abreu-Grobois[d], Alan A. Zavala-*
6   *Norzagaray[c,a,b], Marc Girondot[f], Cesar P. Ley-Quiñonez[c,a,b]*
7

8   *[a]Grupo Tortuguero de las Californias A.C., La Paz, Baja California Sur, Mexico. E-mail:*

9   *cehart03@gmail.com*

10   *[b]Investigación, Capacitación y Soluciones Ambientas y Sociales A.C. Tepic, Nayarit, Mexico.*

11   *[c]Instituto Politécnico Nacional, CIIDIR Unidad Sinaloa, Juan de Dios Bátiz Paredes No. 250,*
12   *Col. San Joachin, C.P. 81101, Guasave, Sinaloa, Mexico.*

13   *[d]Laboratorio de Genética, Unidad Académica Mazatlán, Instituto de Ciencias del Mar y*
14   *Limnologia, Universidad Nacional Autónoma de México, Mazatlán, Sinaloa C.P. 82000, Mexico*

15   *[e]Laboratoire Écologie, Systématique et Évolution, Faculté des Sciences d'Orsay, Université*
16   *Paris-Sud, 91405 Orsay, France*

17
18   *Corresponding author
19

20   **Abstract**

21

22   In the eastern Pacific, peak olive ridley sea turtle (*Lepidochelys olivacea*) nesting occurs
23   during the warmest months which coincide with the rainy season, yet as nesting takes
24   place year-round, the small proportion of the nests laid during dry-low season are exposed
25   to contrasting environmental conditions. Most of the studies on Pacific coast sea turtles
26   have estimated sex ratios produced during the rainy-high season when the majority of
27   conservation activities take place. Thus, dry-low season nests have on the whole been
28   overlooked. Here we compared sex ratios and hatchling fitness for offspring produced
29   during the dry and rainy seasons during 2015. We found that protected olive ridley
30   clutches incubated during the dry-low season were exposed to lower temperatures, yielded

31 higher hatchling success, produced 100% male offspring and larger, heavier hatchlings
32 with better locomotor abilities. Our results highlight the critical value of monitoring and
33 protecting sea turtle nests beyond the peak season (when nests can be protected more
34 efficiently) to include low season nests, albeit at much lower densities, but which by
35 yielding higher proportions of males and with greater locomotor capacities may be the key
36 to population viability and adaptation to anthropogenic climate change.
37

1. Introduction

39

40 Reproductive seasonality is present across species and phyla. Even in tropical regions
41 where climatic variations may be less apparent, species maintain some level of seasonal
42 pattern. In marine species, reproductive seasonality may be linked to marine productivity
43 (Afán et al. 2015), local environmental features and large-scale environmental cues.

44

45 In the eastern Pacific, peak olive ridley sea turtle (*Lepidochelys olivacea*) nesting occurs
46 during the warmest months which coincides with the rainy season. However, nesting can
47 and does take place year-round, exposing the comparatively small number of nests laid in
48 the dry and cold months to environmental conditions that contrast with those of the
49 majority of nests incubating during the summer. For example, incubation temperature and
50 humidity are markedly different between peak and low season. Temperature is one of the
51 critical factors for the successful embryonic development of sea turtles (Miller 1985), in
52 part because these species exhibit temperature-dependent sex determination (Mrosovsky
53 and Pieau 1991; Broderick et al. 2000; Charruau and Hénaut 2012). Turtle embryos can
54 develop a thermal tolerance range of between 25°C and 35°C (Howard, Bell, and Pike
55 2014). However, olive ridley clutches can survive higher temperatures (>37.9°C) but only
56 over short durations but with detrimental effects on overall emergence success (Maulany,
57 Booth, and Baxter 2012). Olive ridley turtles also present latitudinal variation in reported
58 pivotal temperatures which produce 50 per cent of each sex within a clutch (Costa Rica:
59 31°C (Wibbels, Rostal, and Byles 1998); Mexico: 29.9°C (Sandoval, Gómez-Muñoz, and
60 Porta-Gándara 2017). As incubation temperature rises above the pivotal within a sea turtle

61 clutch, the proportion of females increases to a point of producing all females. The opposite
62 is true as temperature falls below the pivotal and all-male production can occur in the
63 lower viable temperature scale. Additionally, rainfall is a factor that varies greatly between
64 seasons, especially in the tropics. Humidity within the nest environment influences
65 moisture uptake by embryos, resulting in longer incubation durations and larger hatchlings
66 (Delmas et al. 2007) and may also affect the sex ratio (Godfrey, Barreto, and Mrosovsky
67 1996; Wyneken and Lolavar 2015).

68

69 These factors make sea turtles particularly vulnerable to climate change (Fuller et al. 2013;
70 Refsnider and Janzen 2016) which is predicted to not only cause increased incubation
71 temperatures but also in sea level (IPCC 2007). Additionally, storms which are expected to
72 become stronger and more frequent will further impact and modify turtle nesting habitat
73 (L. Hawkes et al. 2009; L. A. Hawkes et al. 2013; Fuentes, Hamann, and Limpus 2010;
74 Fuentes, Limpus, and Hamann 2011). Nonetheless, a female turtle can influence
75 reproductive success through the choice of nesting location and depth at which she lays her
76 eggs (David T. Booth and Freeman 2006; Santidrián Tomillo et al. 2017). However, even
77 with the existence of female plasticity, sea turtles may have difficulty adapting to rapid
78 climate change (L. Hawkes et al. 2009; Tilley et al. 2019). Olive ridleys may be the most
79 adept of sea turtles to cope with environmental change due to their multiple reproductive
80 strategies and observed flexibility in their degree of nesting site fidelity (Tripathy and
81 Pandav 2007) and therefore may be able to choose sites that are less impacted by
82 environmental change and which result in healthy offspring.

83

84 In recent years, phenotypical variation has been used to study the way changes in abiotic
85 conditions affect hatchling fitness (Fisher, Godfrey, and Owens 2014; Liles et al. 2019). In
86 warmer nests, hatchlings hatch sooner and consequently are smaller as less yolk is
87 converted into tissue. Smaller hatchlings are slower during the crawl towards the ocean
88 and during initial displacement from coastal zones (David T. Booth and Evans 2011) when
89 compared with their larger counterparts. Larger hatchlings have the advantage of being too
90 large a prey for certain predators. Furthermore, hatchlings must be able to maintain a 24-
91 72 hour frenzied swimming period upon entering the ocean. Larger hatchlings which are

92   stronger swimmers than smaller individuals could be more capable of avoiding the large
93   aggregations of predators offshore of the nesting beach. Turtles in poor condition upon
94   hatching have a reduced probability of avoiding predation (D. T. Booth et al. 2004;
95   Wyneken and Salmon 1992; D. T. Booth 2009). The phenotype has also been used to
96   evaluate the practice of nest relocation to hatcheries (Liles et al. 2019).

97

98   Since Mexico's 1990 ban on sea turtle use and consumption, multiple nesting beach
99   conservation programs have been created to protect clutches from illegal take and
100   predation. However, due to limited resources, many sea turtle conservation projects are
101   not able to continually monitor nesting beaches year-round. For species such as the olive
102   ridley that nest along the Mexican Pacific, limits in resources forces conservation programs
103   to focus on the rainy season months when nesting is significantly higher (García, Ceballos,
104   and Adaya 2003), leaving nests laid during the dry season without protection. Dry season
105   nests are often not monitored or counted leading to an impression from regional reports
106   that nesting does not occur or is insignificant during this period. Registering dry season
107   nesting is extremely important as their different abiotic conditions may affect hatchling sex
108   ratio, phenotype, and fitness. Also, as sea turtle nesting seasons have been shown to shift in
109   response to changes in temperatures (Weishampel et al. 2004; Pike et al. 2006; Witt et al.
110   2010), corresponding changes in phenology may be an adaptive strategy used by nesting
111   turtles as a response to temperature increases due to climate change.

112

113   Nesting at Majahuas beach is part of the Playón de Mismaloya rookery which is notable for
114   being the only known *arribada* rookery to collapse in the late 1970s due to high harvests of
115   nesting females. The rookeries collapse resulted from a 99% reduction in nesting females
116   (Abreu-Grobois and Plotkin 2008), which also resulted in the loss of genetic diversity
117   (Rodríguez-Zárate, Rocha-Olivares, and Beheregaray 2013). Despite conservation efforts,
118   there has been no *arribada* since the collapse. That said, solitary olive ridley nesting
119   density is high in the area (García, Ceballos, and Adaya 2003).

120

121   Our goals were to 1) monitor nesting during a 12-month period; 2) compare incubation
122   temperatures for nests incubated during the dry and rainy season; 3) determine if hatching

123   success varied between these two seasons; 4) estimate sex ratios produced in monitored

124   nests; 5) determine if incubation season had an effect on hatchling fitness and phenotypes;

125   and, 6) discuss the conservation implications of the results.

126

127   ## 2. Materials and methods

128   ### 2.1 Study site

129   Majahuas beach is located in Jalisco between 19°50'41"N 105°22'40"W and 19°46'14"N

130   105°19'38"W on the Pacific coast of Mexico. Majahuas is southernmost 11 km of the Playón

131   de Mismaloya sea turtle sanctuary. A RAMSAR mangrove wetland backs the beach.

132

133   The dry season lasts up to 8 months from November to June with a rainy season between

134   July to October. Mean annual rainfall varies between 748 to 1000 mm with a mean

135   temperature of 25°C (Bullock 1986).

136

137   ### 2.2 Nest collection and incubation

138

139   We analyzed data collected by the fishing cooperative Roca Negra recorded during beach

140   monitoring activities in 2015. Nests were protected via relocation to a hatchery (see

141   below). We selected 71 nests at random (dry season: N = 37; rainy season: N = 34) for

142   monitoring of incubation temperature and hatching success. Of these nests, 38 hatched and

143   we conducted fitness tests on the hatchlings from these nests (dry season: N=28 nests;

144   rainy season: N=10 nests).

145

146   Nests were collected during nightly beach patrols by either locating the recently laid nest

147   via tracks or by encountering the nesting turtle. On encountering a female, we waited until

148   she entered a trance-like state before taking morphometric measurements. Curved

149   carapace length (CCL) and curved carapace width (CCW) were taken using a metric tape

150   marked in 0.1 cm intervals. CCL was defined as the distance measured between the nuchal

151 scute and the outer border of the post-central scutes and CCW was taken from the widest
152 part of the carapace with the tape following the curvature of the carapace.
153
154 On locating a nest, the eggs were carefully removed from the egg chamber and counted.
155 Nest depth was measured by placing a pole across the top of the mouth of the nest and the
156 distance as taken from the pole to the bottom of the nest chamber. For each nest, we
157 recorded the beach section and zone where it was laid (Intertidal (beach face to the berm)
158 = A, Open beach (the berm to the vegetation line) = B and Beach (vegetation line to the
159 dune) = C). Eggs were transferred to a plastic bag and transported to the hatchery using a
160 quad bike located at km 2 of Majahuas beach. Each nest was reconstructed using a manual
161 tree planter to achieve a standardized depth of 45cm and then the nest chamber was
162 formed by hand to imitate the shape of a natural nest made by a female turtle. Eggs were
163 transferred into the artificially dug chamber and a temperature logger (HOBO UA-001-08,
164 Onset USA) was placed in the center of each clutch before being covered with sand.
165 Temperature loggers measured 5.8 x 3.3 x 2.3 cm and were programed to measure the
166 hourly temperature (accuracy of ± 0.5°C). Meteorological observations (daily maximum,
167 minimum and mean air temperature) were obtained from the Universidad Autonoma de
168 Mexico's Biological Research Center in Cuixmala, Jalisco from 1 January 2015 to 31
169 December 2015.
170
171 **_2.3 Hatchling phenotype and fitness_**
172
173 We selected 20 hatchlings at random upon emergence to partake in fitness tests and for
174 phenotype measurements. When hatching success was too low to provide a total of 20
175 hatchlings, we conducted phenotype and fitness tests on those that were available.
176 Hatchlings were weighed using an electronic balance (±0.1 g) and their straight carapace
177 length (SCL), straight carapace width (SCW) and carapace depth were measured using an
178 electronic calliper (±0.1 mm). Crawling speed (cm s^{-1}) was recorded by measuring the time
179 taken by each hatchling to crawl along a raceway of 3 m, 100 mm wide dug into the
180 hatchery's sand. We assigned hatchlings that failed to move within 300 s of being placed on
181 the raceway to a failed to crawl category. We installed a LED light at one end of the raceway

182   and care was taken to ensure that the track was flat. The time taken for hatchlings to self-
183   right themselves was measured by placing the turtle upside down on their carapace and
184   taking the time it took to right itself. This was repeated six times for each hatchling. If an
185   individual took more than 60 s for any righting attempt, they were given a 5 s rest period
186   on their plastron before the next attempt. After the tests, hatchlings were returned to the
187   container with their siblings and then released into the ocean.
188
189   **2.4 Sex ratio estimation**
190

191   We used the R package ***embryogrowth*** v.6.4 (Girondot and Kaska 2014) to account for the
192   effects of varying field temperatures on the dynamics of embryonic development and
193   correctly identify the dates of the thermal sensitive period (TSP) when gonad
194   differentiation occurred. With this, mean incubation temperatures during the true TSP
195   were estimated for each nest and sex ratios derived using the thermal reaction norm for
196   the species (Abreu-Grobois et al., in review). Sex ratio estimates are presented as mean ±
197   SD unless stated otherwise.

198   **2.4 Statistical analysis**

199   Reported statistics are arithmetic means ± standard deviation (SD). All statistical were
200   analyzed using Minitab® 18.1. (Minitab Inc., State College, Pennsylvania, USA).
201   Kolmogorov-Sminov test was used as a normality test. Statistical test ANOVA with Tuckey's
202   method were carried out to examine mean differences among neonate fitness data
203   obtained. A simple linear regression model for correlating the size of the adult females with
204   number of eggs, and the incubation temperature with effect hatchling morphology. The *p*
205   *values* of ≤0.05 were used to determine significant differences.

206   **2.5 Ethics Statement**
207   Permits were granted in Mexico by Dirección General de Vida Silvestre/Secretaría para el
208   Medio Ambiente y los Recursos Naturales (SEMARNAT). Field Permits:
209   SGPA/DGVS/05366/15.

3. Results

3.1 Nesting

We registered a total of 1954 nests over 12 months (1st January 2015 - 30th December 2015). Nesting occurred year-round with highest levels registered in October when the conservation project relocated 605 nests to the beach hatchery and lowest levels in May (n= 22 nests) (Fig. 1a). The majority of nests (n = 1573, 80.5%) were laid in rainy season while 19.5% of nests (n = 381) occurred during the dry season. Nesting was predominately on beach berm or zone B where 79.3% of nests were laid (n = 1547 nests) (zone A: 7.3%, 143 nests; zone C: 13.4%, 261 nests). Proportionally a greater number of nests were laid in intertidal zone C during the dry season (9.0% n=34 nests) than during the rainy season (6.9% n = 109). We measured 25 nesting females and found that the mean curved carapace length (CCL) and width (CCW) was 67.6 cm (range: 63–76 cm) and 73.8 cm (range: 68–82 cm), respectively (Supplementary table 1). There was no significant relationship between the size of the adult females and number of eggs laid ($R^2=0.26$; $p=0.36$) or size of hatchlings.

3.2 Nest Temperature

Nest temperatures presented significant seasonal differences ($F_{(1,69)}=143.26$; $p<0.001$) with those incubated during the dry season (29.09oC ± 0.52) being an mean of 3.89oC cooler than those incubated in the rainy season (32.98oC ± 0.58). Temperature within the 71 nests (Table 1) ranged between 22.8oC and 37.8oC. The most frequent temperature interval for dry season nests was 27-28oC with 24% of recorded values, while in the rainy season, the most frequent temperature interval was 33-34oC with 28% of records (fig. 1b).

Within the hatchery, mid-nest depth temperature was lower than atmospheric temperature with tropical storms and hurricanes causing a visible drop in temperature (Supplemental fig. 1). However, mean incubation temperature within nests was not found to effect hatchling morphology (SCL ($R^2=0.32964$), SCW ($R^2=0.05564$), carapace depth

241   (R^2=0.32831), weight (R^2=0.06795) or locomotor ability (righting propensity (R^2=0.01263)

242   righting time (R^2=0.01982) or run speed (R^2=0.01415)).

243

244   **3.3 Sex ratio**

245

246   We monitored the temperature inside 71 nests but were only able to estimate sex ratios in

247   57 due to 14 nests failing to hatch. All nests incubated in the dry season produced 100%

248   male hatchlings, whereas those incubated during the rainy season (hatched nests: n=31)

249   were female-biased with all but two nests producing 100% female offspring (Table 1).

250

251   **3.4 Hatchling morphology and locomotor performance**

252

253   Hatchling morphology was significantly affected by season, with dry season hatchlings

254   presenting both larger SCL, *(Dry:* 40.62 mm ± 1.82; Rainy: 40.15 mm ± 2.53; $F_{(1,758)}$=7.16;

255   *p=0.008)* SCW (Dry: 32.84 mm ± 1.714 ; Rainy: 32.12 mm ± 2.104; $F_{(1,758)}$=20.71; *p<0.001)*

256   weight (Dry: 16.23g ± 1.686; Rainy: 14.93g ± 2.317; $F_{(1,758)}$=64.55; *p<0.001)* than those

257   hatched in rainy season. Significant differences in terrestrial locomotor performance were

258   observed between seasons ($F_{(1,758)}$=60.17; *p<0.001*), with dry season hatchlings having

259   faster mean crawl speed (0.97 cm s^{-1} ± 0.594) than those hatched in the rainy season (0.55

260   cm s^{-1} ± 0.359). Rainy season hatchlings also presented slower mean righting response (3.33

261   s ± 2.11) than those hatched in the dry season (3.87 s ± 2.41) (Table 2). Overall hatching

262   success was 52.7% and presented a significant difference between dry season hatchling

263   success 74.3% and rainy season hatchling success 24.2% ($F_{(1,1952)}$=38.08; *p<0.001*). Data for

264   each nest studied can be found in Supplementary table 2.

265

266   **4. Discussion**

267

268

269   **Hatchling fitness**

270

271 Seasonal effects were present in our study with dry season hatchlings having superior
272 locomotor abilities and larger body size and weight than their rainy season counterparts.
273 This is similar to other studies which have looked at the effect of nest temperature finding
274 that cooler nests produce larger hatchlings (Booth, Freeney & Shibata 2013; Maulny et al
275 2013; Wood et al 2014) that may be better equipped (larger carapaces and flippers) to
276 crawl and swim faster than their smaller counterparts from warmer nests (Ischer et al
277 2009). The phenotype and fitness advantages received from cooler incubation
278 temperatures highlights the importance of protecting dry season nests which occur when
279 nesting levels are low, as these nests produce have higher hatching success and the
280 resulting hatchlings may have increased chance of survival as they may be quicker to exit
281 predator rich coastal waters due to their larger size and better fitness characteristics.
282
283 Temperature is not the only factor that presents seasonal changes. Hatchlings entering the
284 sea at different times of the year can encounter seasonal changes in oceanic circulation.
285 Ocean currents can change in both intensity and direction. Therefore, neonates hatching at
286 different times can end up in vastly different locations and be exposed to different
287 conditions (Mansfield et al. 2017).
288
289 **Hurricane season**
290
291 Hurricane season runs from May 15th to November 30th in the Eastern North Pacific
292 (NHC), coinciding with peak olive ridley sea turtle nesting activity. The 2015 storm season
293 was particularly active with 22 storms registered for the east Pacific of which 13 were
294 hurricanes, six were tropical storms and three were tropical depressions. Seven storms
295 (Supplementary Fig 1) affected Majahuas nesting beach during this study. This resulted in
296 the loss of hundreds of nests due to beach erosion and wash-out of hatcheries. However,
297 these storms also have the effect of lowering incubation temperatures, which help lower
298 sand temperature in some cases below pivotal temperature. During August and much of
299 September sand temperature remained above 34°C which has been identified as the lethal
300 superior incubation temperature for some olive ridley populations. For example, when the
301 effects of Hurricane Kevin and Linda occurred within the same week a fall in mid-nest

302 depth temperature of 3°C (35°C to 32°C) occurred taking incubation temperatures out of
303 lethal limits.

304

305 **Sex ratio**

306

307 Dry season nests were estimated to be produce entirely male hatchlings, the increased
308 hatch rate and survival of males may help balance out female biased sex ratios at Majahuas
309 beach. Sandoval Espinoza (2012) estimated sex ratios for olive ridleys along the Mexican
310 Pacific coast and found that ratios varied greatly with beaches in Jalisco (Chalacatepec and
311 Playon de Mismaloya) producing 23% male sex ratios. For the Mexican Pacific, they
312 estimated that temperatures would have resulted in male hatchling throughout the study
313 period (July-Dec 2010) with 31% of males in September, 11% in August, 17% in October,
314 20% in November and 19% in December. They did not monitor temperatures in dry
315 season. This is contrary to our results where the 2015 high rainy season temperatures
316 resulted in very low levels of male hatchling production.

317

318 When we compare our results with those of a study in 1993 (Valadez González, Silva Bátiz,
319 and Hernández Vázquez 2000) at a beach 5km north of Majahuas we find similar variations
320 in sex ratio with 100% females produced in October and 100% males in December.
321 However, the overall sex ratio of 7:3 in the 1993 in study is not the same as that found in
322 Majahuas during our research. Incubation period in 1993 (Valadez González, Silva Bátiz,
323 and Hernández Vázquez 2000) was 44 to 65 days, which is similar to our results where we
324 recorded the longest incubation duration in February (64.2d) and the shortest in August
325 (44.8d). However, temperature registered in the La Gloria beach hatchery ranged from
326 27°C ±0.10 (December) to 34°C ±0.36 (August) even when considering a higher
327 temperature within nests due to metabolic heat (Sandoval et al. 2011) the 1993 study nests
328 would not have experienced the extreme superior temperatures (max 37.8°C) that we
329 registered within clutches. As expected from our 12-month study period, we registered
330 lower temperatures than in the La Gloria study which did not monitor temperature during
331 the dry winter season. Although Valadez-González et al. (2000) only recorded the hatchery

332   sand temperature at 12-hour intervals at nest depth but not from within clutches, the study
333   allows us to compare our results with data taken two decades ago.
334
335   **Benefits of low season nesting for females**
336
337   Olive ridleys have been found to present the highest levels of multiple paternity in clutches
338   than in any other sea turtle species, this is especially prominent in *arribada* breeding
339   populations with 92% of nests having two or more fathers which led to the hypothesis that
340   population size has a dominant effect on multiple paternity (Jensen et al. 2006). Yet the
341   benefits of polyandry to female sea turtles have not been identified and multiple paternity
342   was found to result in smaller clutches in Green turtles (Wright et al. 2013). Females that
343   nest in times of low abundance are likely to encounter fewer males and therefore, benefit
344   by a lower chance of multiple encounters with aggressive males (Jensen et al. 2006).
345   However, small solitary breeding populations have also been found to present high levels
346   of multiple paternity (Duran et al. 2015) and this could be a result of the low breeding and
347   feeding site fidelity (Plotkin 2010) as well as a result of sea turtle females' ability to store
348   sperm for over a multiple years. During surveys in the Mexican Pacific in 2010, (Zepeda-
349   Borja et al. 2017) observed olive ridleys mating only during October (autumn).
350
351   **Implications of current conservation effort**
352
353   Concentrating effort and money on the peak nesting season may seem the best use of
354   limited funds however nests laid during peak nesting season have lower possibilities of
355   hatching than those laid in the low season due to lethally high temperatures and beach
356   erosion due to storms. When protected from predation in hatcheries, the comparatively
357   small number of nests laid in low season have higher hatch rates and produce male
358   hatchlings which are a rare occurrence during the high rainy season. Although in 2015 the
359   number of nests laid during low season represented just 19.5% of overall nesting, these
360   nests are of high conservation value as they produce the rarer sex and could help
361   population viability. It is important to note that patrols between February and May 2015
362   were limited due to mechanical problems with the projects quad bike on which patrols are

363   made of the 11 km beach. This resulted in shorter foot patrols during dry season and
364   therefore nesting levels may have been higher than those reported here. Despite this, our
365   study highlights the fact that viable nests are laid year-round and that these nests produce
366   valuable male hatchlings. The majority of these nests are left on the beach and are predated
367   by raccoons and coatis during the first night after laying.
368
369   **CONCLUSION**
370
371   Conservation projects that concentrate effort solely on peak sea turtle nesting season may
372   be inadvertently favouring the production of female hatchlings and leaving male producing
373   nests without protection from illegal take by humans as well as predation by animals.
374   Although it may be tempting to concentrate limited funds to peak season, winter nests are
375   of high value in areas such as Majahuas beach where summer nests do not produce male
376   offspring and are subject to erosion due to tropical storms and hurricanes.
377
378   **Authors' contributions.** CEH conceived the study, participated in data collection and
379   analysis and drafted the manuscript; CPLQ carried out the statistical analyses and
380   participated in writing the manuscript; LATS and CEH collected field data; MG analysed the
381   sex ratio data. All authors gave final approval for publication.
382

391
392
393

394   FIGURE LEGEND

395

396   **Figure 1.** (a) Temporal distribution of nests protected at Majahuas beach during 2015 (b)
397   Temperature frequency registered in the centre of hatched clutches during incubation.

398

399   TABLES

400   **Table 1.** Results summary for data from 71 olive ridley clutches with ranges of incubation temperatures and
401   estimated sex ratios (as proportion of males).

402

Field code	Season	Starting incubation date	Incubation duration (d)	Clutch size	Hatching success	%>34ºC	%<26ºC	Mean ºC ±SD (range)	Sex ratio
MJ1	Dry	18 Feb	61.0	79	0.22	0.0	4.6	28.3 ± 1.6 (23.2-31.2)	1.0
MJ2	Dry	18 Feb	60.1	87	0.95	0.0	4.6	28.9 ± 2.1 (23.6-32.9)	1.0
MJ3	Dry	18 Feb	59.5	100	0.62	0.0	4.5	28.9 ± 2.1 (23.7-32.9)	1.0
MJ4	Dry	16 Feb	62.0	104	1.00	0.0	4.5	28.8 ± 2.3 (23.2-33.2)	1.0
MJ5	Dry	16 Feb	61.6	93	0.85	0.0	5.5	28.5 ± 2.3 (23.3-33.0)	1.0
MJ6	Dry	16 Feb	60.4	103	1.00	2.6	4.4	29.2 ± 2.5 (23.8-34.7)	1.0
MJ7	Dry	16 Feb	61.1	85	0.94	0.0	4.4	29.0 ± 2.2 (23.8-33.3)	1.0
MJ8	Dry	16 Feb	60.3	96	0.85	0.0	4.6	28.8 ± 2.4 (22.8-33.3)	1.0
MJ9	Dry	16 Feb	62.6	77	0.13	0.0	6.3	27.8 ± 1.6 (23.1-30.5)	1.0
MJ10	Dry	16 Feb	59.9	92	0.92	0.0	4.7	28.9 ± 2.1 (24.0-32.8)	1.0
MJ11	Dry	19 Feb	57.6	157	0.90	1.8	5.2	29.1 ± 2.7 (23.4-34.3)	1.0
MJ13	Dry	22 Feb	62.5	87	0.67	0.0	6.1	28.5 ± 1.9 (24.2-31.5)	1.0
MJ14	Dry	24 Feb	64.2	74	0.50	0.0	7.9	28.2 ± 1.9 (23.0-31.1)	1.0
MJ15	Dry	24 Feb	59.1	123	0.89	0.0	6.2	28.8 ± 2.5 (24.0-33.1)	1.0
MJ16	Dry	25 Feb	57.5	94	0.80	0.0	5.9	28.8 ± 2.3 (23.1-32.9)	1.0
MJ17	Dry	25 Feb	57.5	96	0.85	0.0	5.1	29.1 ± 2.3 (23.9-33.2)	1.0
MJ18	Dry	25 Feb	57.3	84	0.61	0.7	4.8	29.2 ± 2.5 (24.2-34.6)	1.0
MJ19	Dry	25 Feb	60.8	113	0.85	0.0	4.5	28.8 ± 1.9 (24.4-32.0)	1.0
MJ20	Dry	25 Feb	60.7	97	0.93	0.0	4.8	29.3 ± 2.4 (23.9-33.2)	1.0
MJ21	Dry	02 Mar	58.1	102		0.0	6.3	29.0 ± 2.2 (23.6-32.4)	1.0
MJ22	Dry	02 Mar	58.2	77		0.0	8.3	28.6 ± 2.2 (23.4-32.1)	1.0
MJ24	Dry	04 Mar	63.5	92	0.90	0.0	7.5	28.8 ± 2.1 (23.5-32.0)	1.0
MJ25	Dry	04 Mar	56.5	112	0.97	0.0	6.5	29.3 ± 2.3 (23.4-32.9)	1.0
MJ26	Dry	04 Mar	56.5	79	0.81	0.0	5.3	29.3 ± 2.1 (24.3-32.2)	1.0
MJ27	Dry	04 Mar	56.4	112	0.89	0.0	5.0	29.6 ± 2.3 (24.3-33.2)	1.0

MJ28	Dry	04 Mar	63.4	83	0.93	0.0	3.1	29.6 ± 1.9 (25.7-32.5)	1.0
MJ30	Dry	05 Mar	62.5	78	0.62	0.0	5.9	28.9 ± 1.7 (24.3-31.3)	1.0
MJ31	Dry	19 Mar	52.9	89	0.85	0.0	0.2	30.3 ± 1.6 (25.0-32.9)	1.0
MJ32	Dry	21 Mar	54.9	106	0.92	0.0	0.0	29.8 ± 1.7 (26.3-32.8)	1.0
MJ33	Dry	21 Mar	54.8	64	0.61	0.0	0.2	29.3 ± 1.3 (25.1-32.0)	1.0
MJ34	Dry	21 Mar	54.8	103	0.95	0.0	0.2	30.0 ± 2.0 (25.5-33.3)	1.0
MJ35	Dry	21 Mar	56.4	85	0.95	0.0	0.1	29.4 ± 1.8 (25.2-32.5)	1.0
MJ36	Dry	21 Mar	57.8	128	0.86	3.2	0.3	29.7 ± 2.3 (25.1-36.4)	1.0
MJ37	Dry	21 Mar	56.7	86	0.91	0.0	0.4	29.0 ± 1.9 (25.8-32.7)	1.0
MJ38	Dry	22 Mar	57.7	86		0.0	0.4	29.0 ± 1.4 (25.0-31.9)	1.0
MJ39	Dry	22 Mar	53.8	76	0.89	0.0	0.2	29.6 ± 1.7 (25.3-33.0)	1.0
MJ40	Dry	22 Mar	51.0	107	0.93	0.0	0.1	30.1 ± 1.9 (25.3-33.4)	1.0
MJ42	Rainy	02 Jun	47.7	92	0.54	41.1	0.0	33.5 ± 1.6 (29.5-36.5)	0.0
MJ43	Rainy	02 Jun	47.7	81		5.2	0.0	32.2 ± 1.1 (30.0-34.2)	0.0
MJ44	Rainy	02 Jun	47.7	98		0.0	0.0	32.0 ± 1.0 (30.2-33.6)	0.0
MJ45	Rainy	03 Jun	47.7	123	0.60	0.1	0.0	32.0 ± 1.2 (29.0-34.1)	0.0
MJ47	Rainy	10 Jun	50.8	121	0.92	8.2	0.0	32.3 ± 1.3 (29.7-35.2)	0.0
MJ48	Rainy	20 Jun	46.5	90		50.1	0.0	33.6 ± 1.5 (28.2-35.6)	0.0
MJ49	Rainy	20 Jun	46.7	109	0.93	1.5	0.0	31.8 ± 1.2 (28.3-34.1)	1.0
MJ50	Rainy	21 Jun	46.5	97	0.88	50.9	0.0	33.7 ± 1.5 (28.5-35.9)	0.0
MJ51	Rainy	26 Jun	42	80		3.1	0.0	31.9 ± 1.3 (28.4-34.3)	1.0
MJ52	Rainy	26 Jun	52.6	103		53.9	0.0	33.7 ± 1.6 (27.8-36.6)	0.0
MJ53	Rainy	02 Jul	46.1	93	0.69	40.0	0.0	33.7 ± 1.9 (28.8-37.8)	0.0
MJ55	Rainy	02 Jul	46.7	91	0.41	16.0	0.0	32.7 ± 1.5 (28.3-34.9)	0.0
MJ57	Rainy	05 Jul	47.6	98		40.4	0.0	33.4 ± 2.0 (28.1-37.7)	0.0
MJ59	Rainy	05 Jul	49.7	106		11.4	0.0	32.6 ± 1.5 (27.9-35.1)	0.0
MJ63	Rainy	14 Jul	46.2	105		17.1	0.0	33.5 ± 0.7 (30.4-34.9)	0.0
MJ67	Rainy	14 Jul	59.6	109	0.25	0.0	0.0	32.0 ± 1.4 (27.4-34.0)	0.0
MJ69	Rainy	14 Jul	59.6	111		2.8	0.0	32.5 ± 1.4 (27.9-34.4)	0.0
MJ71	Rainy	23 Aug	47.9	100		27.5	0.0	33.1 ± 1.5 (29.0-35.9)	0.0
MJ73	Rainy	24 Aug	47.8	87		28.8	0.0	33.2 ± 1.5 (29.0-36.0)	0.0
MJ74	Rainy	24 Aug	47.8	86	0.69	28.2	0.0	33.1 ± 1.6 (28.9-36.2)	0.0
MJ75	Rainy	24 Aug	44.8	56	0.88	0.4	0.0	33.9 ± 0.7 (31.2-36.1)	0.0
MJ77	Rainy	24 Aug	Did not hatch	68	0.00	0.3	0.0	33.2 ± 1.5 (29.0-36.7)	NA

MJ78	Rainy	24 Aug	Did not hatch	117	0.00	0.2	0.0	33.0 ± 1.5 (28.8-36.0)	NA
MJ79	Rainy	24 Aug	Did not hatch	120	0.00	0.3	0.0	33.2 ± 1.5 (29.2-36.0)	NA
MJ98	Rainy	25 Sep	Did not hatch	93	0.00	0.3	0.0	33.2 ± 1.8 (28.8-36.2)	NA
MJ99	Rainy	25 Sep	Did not hatch	66	0.00	0.4	0.0	33.3 ± 1.8 (28.6-36.3)	NA
MJ100	Rainy	25 Sep	Did not hatch	113	0.00	0.4	0.0	33.6 ± 2.0 (28.9-38.5)	NA
MJ101	Rainy	25 Sep	Did not hatch	87	0.00	0.3	0.0	33.1 ± 1.6 (29.1-35.9)	NA
MJ103	Rainy	25 Sep	Did not hatch	112	0.00	0.3	0.0	33.2 ± 1.5 (28.6-35.6)	NA
MJ105	Rainy	25 Sep	Did not hatch	92	0.00	0.2	0.0	32.8 ± 1.6 (28.3-35.3)	NA
MJ106	Rainy	25 Sep	Did not hatch	111	0.00	0.3	0.0	33.1 ± 1.7 (28.6-35.8)	NA
MJ107	Rainy	25 Sep	Did not hatch	98	0.00	0.3	0.0	33.2 ± 1.6 (28.9-35.8)	NA
MJ108	Rainy	25 Sep	Did not hatch	85	0.00	0.4	0.0	33.3 ± 1.7 (28.8-35.8)	NA
MJ110	Rainy	25 Sep	Did not hatch	93	0.00	0.4	0.0	33.5 ± 1.6 (29.5-36.0)	NA

403
404

Table 2. Mean temperature for 71 nests (37 in Dry season and 34 in Rainy season) and mean phenotype measurements (straight carapace length (SCL: mm), straight carapace width (SCW: mm) and weight (g)) and crawl speed and righting response for olive ridley sea turtle hatchlings from 38 nests at Majahuas beach by season (Rainy: n = 10; Dry: n = 28) in 2015.

	Season				
Parameter	Dry		Rainy		Statistical Test
	Mean ± SD	Min-Max	Mean ± SD	Min-Max	
Temperature (ºC)	24.94 ± 1.858 (a)	22.80-28.50	29.07 ± 0.807 (b)	27.80-32.00	$F_{(1,69)}=143.26$; $p<0.001$
Hatching Success (%)	74.2 ± 2.97 (a)	0.000-100.0	24.1 ± 3.56 (b)	0.00-92.70	$F_{(1,1952)}=38.08$; $p<0.001$
SCL (mm)	40.62 ± 1.823 (a)	34.00-47.50	40.15 ± 2.535 (b)	30.00-49.00	$F_{(1,758)}=7.16$; $p=0.008$
SCW (mm)	32.84 ± 1.714 (a)	26.40-38.00	32.12 ± 2.104 (b)	26.00-29.50	$F_{(1,758)}=20.71$; $p<0.001$
Weight (g)	16.23 ± 1.686 (a)	12.00-24.00	14.93 ± 2.317 (b)	8.020-19.88	$F_{(1,758)}=64.55$; $p<0.001$
Crawl Speed (cm s^{-1})	0.977 ± 0.594 (a)	0.132-3.600	0.550 ± 0.359 (b)	0.086-1.597	$F_{(1,758)}=60.17$; $p<0.001$
Righting Response (s)	3.870 ± 2.412 (a)	0.980-19.00	3.336 ± 2.110 (b)	0.830-18.00	$F_{(1,758)}=04.641$; $p=0.032$
Righting Propensity	4.471 ± 2.174 (a)	0.000-6.000	4.598 ± 2.139 (a)	0.000-6.000	$F_{(1,758)}=0.352$; $p=0.553$

N.B.: The statistical test used is the analysis of variance (ANOVA); statistical test data as mean ± SD followed by Tukey's test in parentheses if significant differences were found. Hatching success data in percentage.

405
406
407
408
409

410
411
412
413
414
415 **REFERENCES**
416

417 Abreu-Grobois, and Plotkin. 2008. '*Lepidochelys olivacea*'. The IUCN Red List of Threatened

418   Species. http://www.iucnredlist.org/details/11534/0.

419 Afán, Isabel, André Chiaradia, Manuela G. Forero, Peter Dann, and Francisco Ramírez. 2015.

420   'A Novel Spatio-Temporal Scale Based on Ocean Currents Unravels Environmental

421   Drivers of Reproductive Timing in a Marine Predator'. *Proceedings of the Royal*

422   *Society B: Biological Sciences* 282 (1810): 20150721.

423   https://doi.org/10.1098/rspb.2015.0721.

424 Booth, D. T. 2009. 'Swimming for Your Life: Locomotor Effort and Oxygen Consumption

425   during the Green Turtle (*Chelonia Mydas*) Hatchling Frenzy'. *Journal of Experimental*

426   *Biology* 212 (1): 50–55. https://doi.org/10.1242/jeb.019778.

427 Booth, D. T., E Burgess, J McCosker, and JM Lanyon. 2004. 'The Influence of Incubation

428   Temperature on Post-Hatching Fitness Characteristics of Turtles.' *International*

429   *Congress Series* 1275: 226–33.

430 Booth, David T., and Andrew Evans. 2011. 'Warm Water and Cool Nests Are Best. How

431   Global Warming Might Influence Hatchling Green Turtle Swimming Performance'.

432   Edited by Howard Browman. *PLoS ONE* 6 (8): e23162.

433   https://doi.org/10.1371/journal.pone.0023162.

434 Booth, David T., and Candida Freeman. 2006. 'Sand and Nest Temperatures and an Estimate

435   of Hatchling Sex Ratio from the Heron Island Green Turtle (*Chelonia Mydas*)

436   Rookery, Southern Great Barrier Reef'. *Coral Reefs* 25 (4): 629–33.

437   https://doi.org/10.1007/s00338-006-0135-4.

438 Broderick, A. C., B. J. Godley, S. Reece, and J. R. Downie. 2000. 'Incubation Periods and Sex

439   Ratios of Green Turtles: Highly Female Biased Hatchling Production in the Eastern

440   Mediterranean'. *Marine Ecology Progress Series* 202: 273–281.

441   Bullock, S. H. 1986. 'Climate of Chamela, Jalisco, and Trends in the South Coastal Region of
442   Mexico'. *Archives for Meteorology, Geophysics, and Bioclimatology, Series B* 36 (3):
443   297–316. https://doi.org/10.1007/BF02263135.

444   Charruau, Pierre, and Yann Hénaut. 2012. 'Nest Attendance and Hatchling Care in Wild
445   American Crocodiles (*Crocodylus acutus*) in Quintana Roo, Mexico'. *Animal Biology*
446   62 (1): 29–51. https://doi.org/10.1163/157075511X597629.

447   Delmas, Virginie, Emmanuelle Baudry, Marc Girondot, and ANNE-CAROLINE PREVOT-
448   JULLIARD. 2007. 'The Righting Response as a Fitness Index in Freshwater Turtles'.
449   *Biological Journal of the Linnean Society* 91 (1): 99–109.

450   Duran, N., S.G. Dunbar, R.A. Escobar, and T.G. Standish. 2015. 'High Frequency of Multiple
451   Paternity in a Solitary Population of Olive Ridley Sea Turtles in Honduras'. *Journal of*
452   *Experimental Marine Biology and Ecology* 463 (February): 63–71.
453   https://doi.org/10.1016/j.jembe.2014.10.023.

454   Fisher, Leah R., Matthew H. Godfrey, and David W. Owens. 2014. 'Incubation Temperature
455   Effects on Hatchling Performance in the Loggerhead Sea Turtle (*Caretta Caretta*)'.
456   Edited by Geir Ottersen. *PLoS ONE* 9 (12): e114880.
457   https://doi.org/10.1371/journal.pone.0114880.

458   Fuentes, M.M.P.B., M. Hamann, and C.J. Limpus. 2010. 'Past, Current and Future Thermal
459   Profiles of Green Turtle Nesting Grounds: Implications from Climate Change'.
460   *Journal of Experimental Marine Biology and Ecology* 383 (1): 56–64.
461   https://doi.org/10.1016/j.jembe.2009.11.003.

462   Fuentes, M.M.P.B., C.J. Limpus, and M. Hamann. 2011. 'Vulnerability of Sea Turtle Nesting
463   Grounds to Climate Change: VULNERABILITY ASSESSMENT FRAMEWORK'. *Global*
464   *Change Biology* 17 (1): 140–53. https://doi.org/10.1111/j.1365-2486.2010.02192.x.

465   Fuller, Wj, Bj Godley, Dj Hodgson, Se Reece, Mj Witt, and Ac Broderick. 2013. 'Importance of
466   Spatio-Temporal Data for Predicting the Effects of Climate Change on Marine Turtle
467   Sex Ratios'. *Marine Ecology Progress Series* 488 (August): 267–74.
468   https://doi.org/10.3354/meps10419.

469   García, Andrés, Gerardo Ceballos, and Ricardo Adaya. 2003. 'Intensive Beach Management
470   as an Improved Sea Turtle Conservation Strategy in Mexico'. *Biological Conservation*
471   111 (2): 253–261.

472   Girondot, Marc, and Yakup Kaska. 2014. 'A Model to Predict the Thermal Reaction Norm for
473   the Embryo Growth Rate from Field Data'. *Journal of Thermal Biology* 45 (October):
474   96–102. https://doi.org/10.1016/j.jtherbio.2014.08.005.
475   Godfrey, Matthew H., R Barreto, and N. Mrosovsky. 1996. 'Estimating Past and Present Sex
476   Ratios of Sea Turtles in Suriname'. *Canadian Journal of Zoology* 74: 267–77.
477   Hawkes, La, Ac Broderick, Mh Godfrey, and Bj Godley. 2009. 'Climate Change and Marine
478   Turtles'. *Endangered Species Research* 7 (June): 137–54.
479   https://doi.org/10.3354/esr00198.
480   Hawkes, Lucy A., Annette C. Broderick, Matthew H. Godfrey, Brendan J. Godley, and
481   Matthew J. Witt. 2013. 'The Impacts of Climate Change on Marine Turtle
482   Reproductive Success'. In *Coastal Conservation*, edited by Brooke Maslo and Julie L.
483   Lockwood, 287–310. Cambridge: Cambridge University Press.
484   https://doi.org/10.1017/CBO9781139137089.012.
485   Howard, R, I Bell, and D.A. Pike. 2014. 'Thermal Tolerances of Sea Turtle Embryos: Current
486   Understanding and Future Directions.' *Endangered Species Research* 26: 75–86.
487   https://doi. org/10.3354/esr00636.
488   Jensen, M. P., F. A. Abreu-Grobois, J. Frydenberg, and V. Loeschcke. 2006. 'Microsatellites
489   Provide Insight into Contrasting Mating Patterns in Arribada vs. Non-Arribada Olive
490   Ridley Sea Turtle Rookeries: MULTIPLE PATERNITY IN OLIVE RIDLEY SEA
491   TURTLES'. *Molecular Ecology* 15 (9): 2567–75. https://doi.org/10.1111/j.1365-
492   294X.2006.02951.x.
493   Liles, Michael J., Tarla Rai Peterson, Jeffrey A. Seminoff, Alexander R. Gaos, Eduardo
494   Altamirano, Ana V. Henríquez, Velkiss Gadea, et al. 2019. 'Potential Limitations of
495   Behavioral Plasticity and the Role of Egg Relocation in Climate Mitigation for a
496   Thermally Sensitive Endangered Species.' *Ecology and Evolution* 9: 1603–22.
497   https://doi.org/DOI: 10.1002/ece3.4774.
498   Mansfield, Katherine L., Milagros L. Mendilaharsu, Nathan F. Putman, Maria A. G. dei
499   Marcovaldi, Alexander E. Sacco, Gustave Lopez, Thais Pires, and Yonat Swimmer.
500   2017. 'First Satellite Tracks of South Atlantic Sea Turtle "Lost Years": Seasonal
501   Variation in Trans-Equatorial Movement'. *Proceedings of the Royal Society B:
502   Biological Sciences* 284 (1868). https://doi.org/10.1098/rspb.2017.1730.

503   Maulany, Risma I., David T. Booth, and Greg S. Baxter. 2012. 'Emergence Success and Sex
504   Ratio of Natural and Relocated Nests of Olive Ridley Turtles from Alas Purwo
505   National Park, East Java, Indonesia'. *Copeia* 2012 (4): 738–47.
506   https://doi.org/10.1643/CH-12-088.
507   Miller, Jeffrey Dean. 1985. 'Embryology of Marine Turtles'. In *Biology of the Reptilia*,
508   14:269–328. John Wiley and Sons.
509   Mrosovsky, N., and C. Pieau. 1991. 'Transitional Range of Temperature, Pivotal
510   Temperatures and Thermosensitive Stages for Sex Determination in Reptiles'.
511   *Amphibia-Reptilia* 12 (2): 169–179.
512   Pike, D.A., Antworth, R.L. & Stiner, J.C. (2006). Earlier nesting contributes to shorter nesting
513   seasons for the loggerhead sea turtle, Caretta caretta. J. Herpetol. 40, 91–94.
514
515   Plotkin, Pt. 2010. 'Nomadic Behaviour of the Highly Migratory Olive Ridley Sea Turtle
516   Lepidochelys olivacea in the Eastern Tropical Pacific Ocean'. *Endangered Species*
517   *Research* 13 (1): 33–40. https://doi.org/10.3354/esr00314.
518   Refsnider, J.M., and F.J. Janzen. 2016. 'Temperature-Dependent Sex Determination under
519   Rapid Anthropogenic Environmental Change: Evolution at a Turtle's Pace?' *Journal*
520   *of Heredity* 107: 61–70. https://doi.org/10.1093/jhered/esv053.
521   Rodríguez-Zárate, Clara J., Axayácatl Rocha-Olivares, and Luciano B. Beheregaray. 2013.
522   'Genetic Signature of a Recent Metapopulation Bottleneck in the Olive Ridley Turtle
523   (*Lepidochelys olivacea*) after Intensive Commercial Exploitation in Mexico'.
524   *Biological Conservation* 168 (December): 10–18.
525   https://doi.org/10.1016/j.biocon.2013.09.009.
526   Sandoval Espinoza, Sarahi. 2012. 'Proporción sexual en crías de tortuga *Lepidochelys*
527   *olivacea* en corrales de incubación del Pacífico Mexicano'. Doctorado, La Paz, Baja
528   California Sur, Mexico: Instituto Politécnico Nacional - Centro Interdisiplinario de
529   Ciencias Marinas.
530   Sandoval, Sarahi, Victor Gómez-Muñoz, Joaquín Gutiérrez, and Miguel Ángel Porta-Gándara.
531   2011. 'Metabolic Heat Estimation of the Sea Turtle *Lepidochelys olivacea* Embryos'.
532   *Journal of Thermal Biology* 36 (2): 138–41.
533   https://doi.org/10.1016/j.jtherbio.2010.12.007.

534   Sandoval, Sarahi, Victor M. Gómez-Muñoz, and Miguel Ángel Porta-Gándara. 2017.
535   'Expansion of the Transitional Range of Temperature for Sea Turtle *Lepidochelys*
536   *olivacea* from Sex Ratio Data at Controlled Incubation Temperatures'. *Herpetology*
537   *Notes* 10: 63–65.
538   Santidrián Tomillo, Pilar, Luis Fonseca, Frank V. Paladino, James R. Spotila, and Daniel Oro.
539   2017. 'Are Thermal Barriers" Higher" in Deep Sea Turtle Nests?' *PloS One* 12 (5):
540   e0177256.
541   Tilley, D, S Ball, J Ellick, B. J. Godley, N Weber, S. B. Weber, and A. C. Broderick. 2019. 'No
542   Evidence of Fine Scale Thermal Adaptation in Green Turtles.' *Journal of Experimental*
543   *Marine Biology and Ecology* 514–515: 110–17.
544   Tripathy, Basudev, and Bivash Pandav. 2007. 'BEACH FIDELITY AND INTERNESTING
545   MOVEMENTS OF OLIVE RIDLEY TURTLES (LEPIDOCHELYS OLIVACEA) AT
546   RUSHIKULYA, INDIA'. *Herpetological Conservation and Biology*, 6.
547   Valadez González, Carmen, Francisco de Asis Silva Bátiz, and Salvador Hernández Vázquez.
548   2000. 'PROPORCIÓN SEXUAL EN CRÍAS DE LA TORTUGA MARINA *Lepidochelys*
549   *olivacea*, PRODUCIDA EN CORRAL DE INCUBACIÓN EN LA PLAYA DE ANIDACIÓN
550   LA GLORIA, JALISCO, MÉXICO'. *Boletín del Centro de Investigaciones Biológicos* 34
551   (3): 305–13.
552   Witt MJ, Hawkes LA, Godfrey MH, Godley BJ, Broderick AC (2010) Predicting the impacts of
553   climate change on a globally distributed species: the case of the loggerhead turtle.
554   213:901-911
555   Wibbels, Thane, David Rostal, and Richard Byles. 1998. 'High Pivotal Temperature in the
556   Sex Determination of the Olive Ridley Sea Turtle, *Lepidochelys olivacea*, from Playa
557   Nancite, Costa Rica'. *Copeia* 1998 (4): 1086. https://doi.org/10.2307/1447364.
558   Weishampel, J. F., Bagley, D. A. and Ehrhart, L. M. (2004). Earlier nesting by loggerhead sea
559   turtles following sea surface warming. Glob. Chang. Biol. 10, 1424-1427.
560
561   Wright, Lucy I., Wayne J. Fuller, Brendan J. Godley, Andrew McGowan, Tom Tregenza, and
562   Annette C. Broderick. 2013. 'No Benefits of Polyandry to Female Green Turtles'.
563   *Behavioral Ecology* 24 (4): 1022–29. https://doi.org/10.1093/beheco/art003.

564   Wyneken, Jeanette, and Alexandra Lolavar. 2015. 'Loggerhead Sea Turtle Environmental
565   Sex Determination: Implications of Moisture and Temperature for Climate Change
566   Based Predictions for Species Survival: ENVIRONMENTAL SEX DETERMINATION IN
567   LOGGERHEAD TURTLES'. *Journal of Experimental Zoology Part B: Molecular and*
568   *Developmental Evolution* 324 (3): 295–314. https://doi.org/10.1002/jez.b.22620.
569   Wyneken, Jeanette, and Michael Salmon. 1992. 'Frenzy and Postfrenzy Swimming Activity
570   in Loggerhead, Green, and Leatherback Hatchling Sea Turtles'. *Copeia*, 478–484.
571   Zepeda-Borja, Karen M, Christian D Ortega-Ortiz, Ernesto Torres-Orozco, and Aramis
572   Olivos-Ortiz. 2017. 'Spatial and Temporal Distribution of Sea Turtles Related to Sea
573   Surface Temperature and Chlorophyll-a in Mexican Central Pacific Waters'. *Revista*
574   *de Biología Marina y Oceanografía* 52 (2): 375–85. https://doi.org/10.4067/S0718-
575   19572017000200016.

576

a

Y-axis: Protected Nests
X-axis: Month (Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec)

b

Y-axis: Frequency (%)
X-axis: Temperature (ºC)

Legend: Dry season, Rainy season