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Stéphane Caut, Elodie Guirlet, Marc Girondot. Effect of tidal overwash on the embryonic development of leatherback turtles in French Guiana. *Marine Environmental Research*, 2010, 69 (4), pp.254. 10.1016/j.marenvres.2009.11.004 . hal-00564783

HAL Id: hal-00564783

<https://hal.science/hal-00564783>

Submitted on 10 Feb 2011

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Accepted Manuscript

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PII: S0141-1136(09)00148-2

DOI: [10.1016/j.marenvres.2009.11.004](https://doi.org/10.1016/j.marenvres.2009.11.004)

Reference: MERE 3397

To appear in: *Marine Environmental Research*

Received Date: 12 June 2009

Revised Date: 2 November 2009

Accepted Date: 6 November 2009



Please cite this article as: Caut, S., Guirlet, E., Girondot, M., Effect of tidal overwash on the embryonic development of leatherback turtles in French Guiana, *Marine Environmental Research* (2009), doi: [10.1016/j.marenvres.2009.11.004](https://doi.org/10.1016/j.marenvres.2009.11.004)

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1 **Effect of tidal overwash on the embryonic development of leatherback**
2 **turtles in French Guiana**

3

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5

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17 **ABSTRACT**

18 In marine turtles, the physical conditions experienced by eggs during incubation affect
19 embryonic development. In the leatherback, hatching success is known to be low in relation to
20 other marine turtles as a result of high embryonic mortality. Moreover, the hatching success
21 on Yalimapo in French Guiana, one major nesting beach for this species, is lower compared
22 to other nesting sites. We assessed the rate of leatherback turtle embryonic mortality in order
23 to investigate the tolerance of leatherback turtle clutches laid on Yalimapo beach to tidal
24 overwash, and we highlight causes of poor hatching success. Of the 89 nests studied, 27 were
25 overlapped by tide at least once during the incubation period (of which 5 nests were lost by
26 erosion). The hatching success was on average significantly lower in overwashed nests than in
27 non-overwashed, highlighting the existence of embryonic developmental arrest linked to tidal
28 inundation. The stages of developmental arrest and their proportion are linked with time,
29 frequency and level of overwash events. In the context of global warming and associated sea
30 level rise, understanding the detrimental effect of tidal inundation on the development of
31 marine turtle nests is of interest in nesting sites where turtles are likely to be forced to nest
32 closer to the tide line, thus exposing their nests to greater risk of nest overlap with sea and
33 tidal inundation.

34

35 **Key-words:** tidal inundation; leatherback turtle; embryonic mortality; French Guiana;
36 development; site selection.

37 **1. Introduction**

38 For animals that lay their eggs in a nest, the selection of a nest site may strongly
39 influence embryo development and offspring survival and may therefore have important
40 consequences for the reproductive fitness of the adult. Indeed, for most oviparous species, the
41 most vulnerable part of the life cycle is often the embryo stage, since eggs are typically left in
42 fixed locations throughout their development without parental care (Wood and Bjorndal,
43 2000). Hatching success for organisms that lay eggs in a nest, such as sea turtles, is believed
44 to be influenced by numerous biotic and abiotic factors such as predation, type of substrate,
45 porosity, temperature, moisture content, salinity, slope of the beach, nest elevation, rainfall
46 and tidal inundation (Mortimer 1990; Horrocks and Scott, 1991; Ackerman, 1997; Wood and
47 Bjorndal, 2000; Allen et al., 2001; Bilinski et al., 2001; Donlan et al., 2004; Foley et al.,
48 2006). In many oviparous reptiles, however, environmental factors not only influence embryo
49 survivorship (Horrocks and Scott; 1991; Resetarits, 1996), but also hatchling size (Packard
50 and Packard, 1988), performance (Janzen, 1993), growth (Bobyne and Brooks, 1994),
51 behaviour (Burger, 1991), and sex determination (Spotila et al., 1994). After the emergence of
52 hatchling turtles, their survival may be strongly related to the distance at which the nest is laid
53 from the sea and from supra-littoral vegetation behind the beach (Mrosovsky, 1983).
54 Placement of nests close to the sea increases the likelihood of inundation and egg loss to
55 erosion, whereas placement of nests farther inland increases the likelihood of desiccation,
56 hatchling misorientation, and predation on nesting females, eggs, and hatchlings (Bustard and
57 Greenham, 1968; Fowler, 1979; Whitmore and Dutton, 1985; Spencer, 2002).

58 Leatherback turtles (*Dermochelys coriacea*), classified as critically endangered by the
59 Species Survival Commission (IUCN, 2006)), often place their nests in the open sand near the
60 water, but rarely in vegetation (Whitmore and Dutton, 1985; Kamel and Mrosovsky, 2004;
61 Caut et al., 2006a). For this reason, researchers have investigated possible strategies and cues

62 that might influence nest placement. Mrosovsky (1983), at the population level, and Eckert
63 (1987), at the individual level, suggested that leatherbacks have developed a scatter nesting
64 strategy whereby nests are randomly distributed along a beach to maximize clutch survival in
65 an unpredictable nesting area. However, leatherback turtles often nest in places where their
66 eggs are destroyed by high tides. Poor nest site selection, where nests have been shown to
67 completely fail, ranges from <2.5% in Malaysia to around 40% in the Guianas and appears to
68 be related to beach topography (Mrosovsky, 1983). Leatherbacks generally have low hatching
69 success (~50%) relative to other marine turtle species (~85% or more; see Bell et al., 2004).
70 Predation could partly explain the low hatching rate, with the longer incubation period for
71 leatherbacks increasing exposure to predators (Whitmore and Dutton, 1985). But this low
72 hatching success of leatherbacks also seems to be mainly the result of nest site selection and
73 embryonic mortality (Whitmore and Dutton, 1985; Bell et al., 2004). Indeed, leatherbacks
74 generally nest nearer to the sea than other marine turtles and nests are therefore subjected to
75 erosion and inundation, sometimes leading to 50% nest loss on certain beaches in South
76 America (Patino-Martinez et al., 2008). These overwashes of nests by sea water may lead to
77 egg mortality from suffocation (lack of respiratory oxygen; Whitmore and Dutton, 1985)
78 and/or disruption of metabolism as a result of exposure to higher salinities and therefore
79 chloride toxicity (Bustard and Greenham, 1968) and/or critical cooling below minimum
80 temperature for embryonic development (Hewavisenthi and Parmenter, 2002). Moreover,
81 leatherback nests are deeper than those of others marine turtles, and water content and salinity
82 are known to increase with depth, leading to a decrease in hatching success (Foley et al.,
83 2006). The greater embryonic mortality in leatherback nests is therefore mainly due to the
84 nest-site selection resulting in more nests being overwashed.

85 However, the effect of tidal overwash on hatching success and embryonic
86 development remains poorly understood and represents an important question for the future.

87 Indeed, threats to coastal areas are increasing (Huang, 1997) with the projected rise in sea
88 level resulting from anthropogenic global warming; the increase in the number and
89 concentration of greenhouse gases in the atmosphere has the potential to cause an elevation in
90 the global mean air temperature and mean sea level of 1-4.5 °C and 31-150 cm, respectively,
91 by the year 2100 (IPCC, 2007). Therefore, many nesting beaches are particularly susceptible
92 to coastal hazards such as storm surges and coastal erosion. However, although much effort
93 has been expended over the last two decades to understand and mitigate the threats to marine
94 turtles (Watson et al., 2005), the threat of climate change on this taxon has, until recently,
95 been given little attention (for more information, see Hawkes et al., 2009). Studies of the
96 effects of global warming on sea turtle populations have focused essentially on the loss of
97 nesting beach habitat as a result of an increase in sea level and on the changes in sex ratio
98 (Daniels et al., 1993; Davenport, 1997; Nicholls, 1998; Nicholls et al., 1999; Fish et al., 2005;
99 Baker et al., 2006; Jones et al., 2007; Fish et al., 2008; Mazaris et al., 2009). Most of these
100 studies examined the potential effect of sea-level rise on marine turtle nesting beaches with
101 different models (e.g. elevation model, inundation flooding model), but they did not take into
102 account how life history and ecological parameters that determine extinction risks will be
103 affected by climate change (Isaac, 2009) . The recent review on climate change and marine
104 turtles (Hawkes et al. 2009) therefore indicated the importance for future research on climate
105 change effects on key habitats upon which turtles depend and factors that influence nest site
106 selection and hatchling success. The effect of inundation and, indirectly, the sea-level rise on
107 leatherback hatching success have been poorly studied (Whitmore and Dutton, 1985) to date,
108 despite the tendency of this species to lay its clutches closer to the high-tide line than other
109 sea turtle species. Results of studies concerning global warming have highlighted threats for
110 coastal zones with accelerated beach erosion and greater frequency of flooding events
111 (Kumar, 2006).

112 The beach of Yalimapo has one of the highest nesting densities of leatherback females,
113 with about 30% of the world's population of nesting females and approximately 50% of all
114 leatherbacks nesting in the region of French Guiana and Suriname (Girondot and Fretey,
115 1996); it should be noted that the exact proportion varies according to the year. However,
116 hatching success on this beach is lower than at other leatherback nesting sites (Boulon et al.,
117 1996). Depressed hatching success compounds the problem of population decline that results
118 from adult mortality caused by incidental fisheries capture (Kaplan, 2005; Martinez et al.,
119 2007), and understanding the causes of low hatching success would therefore be an important
120 conservation step towards preventing extinction in a species (Ralph et al., 2005). In this study,
121 we determined the level and frequency of tidal overwash and hatching success of leatherback
122 nests in order to investigate the tolerance of nests to tidal inundation in the context of global
123 warming and sea-level rise. We assessed the rate and stages of leatherback turtle embryonic
124 mortality in order to investigate tolerance of leatherback turtle clutches laid on Yalimapo
125 beach to tidal overwash and we highlight causes of poor hatching success.

126

127 **2. Materials and methods**

128 **2.1. Study site and data collection**

129 Research was carried out on the Awala Yalimapo beach in French Guiana (53°57W-
130 5°45'N). The beach is located within the Amana Nature Reserve, on the inshore plain of
131 coastline between the Mana and Maroni Rivers. Guyana has a semi-diurnal tide (two daily
132 high tides) with a period of approximately 12-and-a half hours. The beach is 4 km in length
133 and the width varies from a few metres to 20 m, depending on the tide line. For this study, we
134 chose a 300-m long section of beach with the same slope (approximately 10%), which was
135 sufficiently frequented by turtles but also distant from sites frequented by tourists. The width
136 of the sand beach depends on the strength of the tide (~ 5 to 30 metres).

137 The nests analysed in the study were laid from 20 May to 4 June 2002. At the time of
138 oviposition or later, during nest covering, we measured the minimum straight carapace length
139 of the nesting female (SCLmin) (Bolten, 1999) and the female identity was recorded (Passive
140 Integrated Transponder (PIT) tags). For each freshly laid nest encountered, we measured the
141 minimum distance from the nest to the last high-tide line and to the vegetation line (sparse
142 creeping vegetation (*Ipomoea pes-caprae*), sand still visible) with a plastic measuring tape.
143 All nest locations were localized to within 1 m by triangulation using numbered stakes placed
144 every 10 m along the vegetation of the beach. To locate specific nests after incubation, we
145 placed a numbered ring of plastic-insulated copper in the sand above the clutch during the
146 covering of the nest by the female. We used a metal detector that captured signals from probes
147 in the copper at the end of incubation.

148

149 **2.2. Embryonic development**

150 Nest status was checked each day for signs of emergence, predation by dogs or
151 erosion. We waited sufficient time for any live embryos to hatch and leave the nest before
152 analysing the remaining embryos. All nests were excavated 48 hours after the first signs of
153 emergence; in the absence of evidence, we expected a period of 70 days of incubation, so no
154 live embryos were excavated or sacrificed (authorization no. 1516 1D/1B/ENV of 27 August
155 2001, DIREN Guyane). We recorded the total number of yolked eggs (noted *YE*, including
156 hatched and unhatched yolked eggs) and shelled albumin globs (noted 'yolkless' eggs). We
157 dissected unhatched yolked eggs in situ and staged them in category using these criteria:

158 - Category 1: Egg with no visible signs of development or dead embryo < 10 mm in length.

159 - Category 2: Egg with dead embryo \geq 10 mm and < 30 mm in length.

160 - Category 3: Egg with dead embryo \geq 30 mm and < 60 mm in length.

161 - Category 4: Egg with dead embryo \geq 60 mm (including dead hatchling in a pipped egg).

162

163 **2.3. Embryonic size and time of incubation**

164 To analyse the effect of tidal overwash on embryonic development, we determined for
 165 each category of embryonic size a corresponding time of incubation. Renous et al., (1989)
 166 presented a stage-by-stage description of leatherback development and reported that many
 167 measurements of embryonic growth could be related to developmental time (incubation
 168 period). We used Renous' stage description to estimate rates of growth. These growth curves
 169 were performed by Renous et al. (1989) on the same beach (Awala Yalimapo, French Guiana)
 170 with a random sampling of nests in natural environment and between the end of May and the
 171 beginning of August. We fitted these data using an exponential function: $y = 2.85 \exp(0.05x)$
 172 $R^2 = 0.99$, with the embryonic size on the y axis (mm, with maximum 110 mm) and the time
 173 of incubation on the x axis. We determined the incubation period for each size class of each
 174 category:

175 Category 1 corresponded to the period¹ 0 to 23 days; Category 2 to the period² 24 to 43 days;

176 Category 3 to the period³ 44 to 56 days; Category 4 to the period⁴ 57 to 67 days.

177

178 **2.4. Percentage of embryos and hatchling success**

179 We estimated the percentage of embryos for each category ($p(E)$) as:

$$180 \quad p(E_n) = E_n / YE.$$

181 Where: n = the category 1 to 4; E = Number of embryos in the category n ; YE = Total number
 182 of Yolked Eggs

183 We also estimated the percentage of embryos for categories 2 to 4 of the total yolked eggs
 184 that can continue their development at each corresponding period ($pc(E)$) as:

$$185 \quad pc(E_2) = E_2 / (YE - E_1)$$

$$186 \quad pc(E_3) = E_3 / (YE - E_1 - E_2)$$

187
$$pc(E_4) = E_4 / (YE - E_1 - E_2 - E_3)$$

188 Hatching success was estimated by the number of large shell fragments divided by the
 189 total number of yolked eggs. When eggshells were fragmented, pieces were grouped together
 190 to represent one egg. The use of shell fragments to estimate hatching success had been
 191 previously validated in an open-air hatchery study (Caut et al., 2006b)

192

193 **2.5. Measurements of overwash**

194 During each day of incubation time, we measured the minimum distance from each
 195 nest to the daily high-tide line (represented by the high-water mark of the two daily highs,
 196 noted *DDHTL* (Daily Distance to the High Tide Line; “+” positive for distance non overwash
 197 and “-“ negative for distance overwash), see Figure 1). To define the characteristics of
 198 overwash for each of the four specific periods (period¹: 0 to 23 days, period²: 24 to 43 days,
 199 period³: 44 to 56 days, and period⁴: 57 to 67 days), we define four different parameters (see
 200 Fig. 1):

- 201 - The Total Distance (*TD*): corresponding to the sum of *DDHTL* (positive or negative), the
 202 total overwash history of nest for one period;
- 203 - Overwashed Distance (*OD*): the absolute value of the sum of daily distances, in metres,
 204 between the nest and the high-tide line for overwashed days (negative values in Fig. 1), index
 205 of the level of tidal overwash;
- 206 - The Number of Overwashed Day (*NOD*): the sum of overwashed days, index of the
 207 frequency of tidal overwash;
- 208 - The First Overwashed Day (*FOD*): the first day of the incubation for which an overwash
 209 was recorded for each specific period.

210

211 **2.5. Statistical analysis**

212 As all females laid only one clutch during the study period, they could be treated
 213 independently in the analysis. We decided to eliminate nests laid in vegetation and nests
 214 depredated prior to a completed period (about 67 days). First, we performed one-way
 215 ANOVAs using either SCLmin, the number of yolked eggs or the number of yolkless eggs as
 216 the dependent variable, and the state of nest (overwashed or non-overwashed) was treated as
 217 the independent variable. Generalized linear models (GLM) were also performed to assess the
 218 effect of overwash on (1) hatching success and (2) percentage of dead embryos (corrected or
 219 not) in the different categories 1 to 4. Nests were considered as overwashed when they were
 220 covered by tide at least once during the incubation time. Second, GLM were performed to
 221 assess the effect of *TD* of each different period on the corrected percentage of corresponding
 222 dead embryos for overwashed and non-overwashed nests. Finally, GLM were performed
 223 among overwashed nests to investigate variables responsible for developmental arrest through
 224 incubation periods (*OD*, *FOD*, *NOD*). Preliminary analysis was carried out to estimate the
 225 correlation between *OD* and *NOD*; if this correlation was significant, we selected only *OD* for
 226 the GLM. One model with first-order interactions was fitted for each period and
 227 corresponding embryonic category *n*:

$$228 \quad G^n(\text{pcE}_n) = OD^n + FOD^n + NOD^n + \text{error}$$

229 where *G* is a link function and ⁿ corresponds to one period as defined above. *OD*, *FOD* and
 230 *NOD* were treated as continuous independent variables. As dependent variables were
 231 percentages (pcE_n), we used binomial error distribution and logit link function. Computations
 232 were performed with the SAS package (procedure MIXED, v. 9.1.3, SAS Institute Inc., 2004).

233

234 **3. Results**

235 Over a period of 15 days, we marked and followed 97 nests along a 300 m stretch of
236 beach. At the end of the study, 5 nests were lost by erosion, 6 nests by dog predation and 2
237 nests by human poaching. Of the remaining 84 nests, 22 had been overwashed at least once,
238 55 nests were non-overwashed and 7 were nested in vegetation. Therefore, the remaining 77
239 nests were analysed for hatching success and the effect of overwash on embryonic mortality
240 assessed.

241

242 ***3.1. Hatching success and embryonic mortality***

243 First, we tested whether there were significant differences between the characteristics
244 of females (SCLmin) and clutch size for overwashed and non-overwashed nests. We found no
245 difference between the general characteristics in these two categories; the SCLmin and the
246 number of yolked and yolkless eggs were very similar (Table 1A).

247 However, the hatching success and the percentage of total dead embryos were
248 significantly different between nests that were overwashed or not (Table 1A). Hatching
249 success was significantly smaller for nests that were overwashed. The percentage of total dead
250 embryos was significantly higher in overwashed nests (Table 1A).

251

252 ***3.2. Embryonic arrest vs. time of overwash***

253 We calculated the percentage of nests with dead embryos for each size of embryo for
254 overwashed and non-overwashed nests and we compared this with the percentages of
255 overwashed nests for each day of incubation (Fig. 2). We observed different patterns of
256 embryo distribution:

257 - Period¹ between 0 and 23 days (corresponding to an embryo size of <10 mm) in which there
258 was the same frequency of occurrence for the overwashed and non-overwashed nests,
259 approximately 100%, meaning that all nests had embryos of <10 mm. However, the

260 percentage of dead embryos of <10 mm was significantly different between nests that were
261 overwashed or not (50.32% and 29.73%, respectively, Table 1B). During this period, the
262 overwashed nests were frequently overwashed during the 16 first days.

263 - Period² between 24 and 43 days (corresponding to an embryo size of 10 to 30 mm) in which
264 there was only one embryo. This was probably due to the fact that we had no nests
265 overwashed between the times of incubation.

266 - Period³ between 44 days and 56 days (corresponding to an embryo size of 30 to 60 mm), in
267 which there was a majority of embryos from overwashed nests. During this period 15/22 nests
268 were inundated. As tidal overwash began to occur in nests (day 44), the percentage of nests
269 with dead embryos began to increase (Fig. 2). The percentage of dead embryos 30-60 mm
270 (corrected or not) was significantly different between nests that were overwashed or not
271 (Table 1B).

272 - Period⁴ between 57 to 67 days (corresponding to an embryo size >60 mm), in which we
273 observed an important percentage of nests with dead embryos from overwashed and non-
274 overwashed nests. However, the percentage of dead embryos of >60 mm was significantly
275 different between overwashed and non-overwashed nests (pcE₄: 25.87% and 4.21%,
276 respectively, Table 1B). During this period 15/22 nests were overwashed.

277

278 **3.3. Sensitivity of embryos vs. parameters of overwash**

279 To study more precisely the effect of overwash on embryonic mortality, we selected
280 three different periods corresponding to the presence of embryo size: period¹ (1 to 24 days),
281 period³ (44 to 56 days) and period⁴ (57 to 67 days). First, we performed GLM to assess the
282 general effect of *TD* (sum of daily distance to the high-tide line) during two periods (period¹
283 and period⁴) on the percentage of corresponding dead embryos (pcE_n) for overwashed and
284 non-overwashed nests (Table 2A). We did not perform GLM for period² (no overwash) or for

285 period³, because the *TD* and the number of dead embryos were very low (Fig. 3). For the two
286 periods (1 and 4), *TD* was found to be significant for overwashed nests and not significant for
287 non-overwashed nest (Table 2A). The percentage of dead embryos increased with *TD*.
288 Second, GLM were performed among overwashed nests to investigate more precisely
289 variables responsible for embryonic arrest (OD, FOD, NOD). Preliminary analysis found a
290 significant correlation between OD and NOD ($R=0.87$). We selected therefore only OD for
291 the GLM ($G^1(\text{pcE}_1) = \text{OD}^1 + \text{FOD}^1 + \text{error}$ and $G^4(\text{pcE}_4) = \text{OD}^4 + \text{FOD}^4 + \text{error}$ for period¹
292 and period⁴, respectively). The GLM model for period¹: OD¹ and FOD¹ was significant
293 (Table 2B). The percentage of embryos $E_{<10}$ increased with OD¹ and when the FOD¹
294 decreased (the earlier the nest was overwashed, the more abundant were the dead embryos).
295 The GLM model for period⁴: Only OD⁴ was found to be significant. The percentage of
296 embryos $E_{>60}$ increased with OD⁴. The non-significance of FOD⁴ was probably due to the
297 short duration of this period (Table 2B).

298

299 **4. Discussion**

300 In marine turtles, the physical conditions experienced by the egg during incubation in
301 the nest have been shown to strongly affect embryonic development and hatching rate (
302 Mortimer, 1990; Ackerman, 1997; Marco et al., 2005). As female marine turtles do not
303 provide parental care to eggs or offspring, female nesting behaviour and nest site selection are
304 important factors that can largely affect the development of embryos and the survival of
305 juveniles (Kamel and Mrosovsky, 2004). Our results showed first that many nests were
306 inundated at least once during the incubation periods and that these nests were not
307 automatically associated with null hatching success, but presented a higher proportion of dead
308 embryos than in non-overwashed nests. This result highlights that overwash may affect
309 important variables for embryonic development leading to embryo mortality. Mortality in our

310 study is probably caused by fluctuations of those important physical or chemical variables for
311 embryo development, caused by overwash, rather than overwash alone. Embryonic mortality
312 (stage and proportion) also seems to be linked with the date of the overwash event during the
313 incubation, the frequency and the level of overwash.

314

315 ***4.1. Effects of overwash***

316 The effects of the hydric environment and immersion of the nest during incubation
317 have been studied in reptiles (Losos et al., 2003) but relatively little attention has been given
318 to those effects in marine turtle. Indeed, Kennett et al. (1998) studied the northern long-
319 necked turtle, *Chelodina rugosa*, the only reptile known to deposit its eggs underwater
320 (Kennett et al., 1993a). They showed that prolonged immersion of eggs in water results in
321 smaller hatchlings and shorter incubation times, but does not increase egg mortality during
322 incubation. However, other studies have shown that even short-term immersion is fatal for
323 reptilian embryos (*Tryonix muticus muticus*, Plummer, 1976; *Crocodylus porosus*, Webb et
324 al., 1977; *Alligator mississippiensis*, Kushlan and Jacobsen, 1990; *Pseudemys nelsoni*, Kam,
325 1994). Embryo death normally results from the influx of water into the egg, with consequent
326 egg swelling and rupture of shell and membranes, but these changes do not occur in *C. rugosa*
327 eggs (Kennett et al., 1993b). Moreover, for marine species the effect is more important,
328 especially due to the variation in water salinity that may be related to rainfall and tidal
329 inundation. Studies generally concern *Caretta caretta* or *Chelonia mydas* in sea turtles (Foley
330 et al., 2006; Mortimer, 1990). The effect of moisture and/or immersion on eggs of leatherback
331 turtles has, for example, been little studied, while their nests are the most likely to be
332 inundated (Whitmore and Dutton, 1985). In our study, immersion of eggs is not necessarily
333 fatal to the whole clutch, thus highlighting that the eggs can withstand flooding episodes The
334 failure of development during tidal overwash may actually be explained by the fluctuations of

335 the three most important physical variables affecting the survival of reptilian embryos:
336 temperature, water content and respiratory gases (Packard and Packard, 1988). Because
337 leatherbacks nest closer to the tide line than other marine turtles, their nest are more exposed
338 to fluctuations of these important variables. There is an optimal range of temperatures above
339 and below which hatchability decreases. Hatchability is generally known to decrease
340 significantly at lower temperature. The effects of large daily temperature fluctuations on
341 embryonic development are unknown, but prolonged exposure of reptilian eggs below
342 optimum temperature can result in developmental abnormality and embryonic mortality
343 (Packard and Packard, 1988). Moreover, local conditions such as rainfall and tidal overwash
344 may induce pronounced cooling and decrease hatchability if temperature is below minimum
345 temperature for embryonic development (Hewavisenthi and Parmenter, 2002). During
346 overwash, eggs can also be confronted with increased water content and lower gas content,
347 leading to higher moisture and limited or blocked gas exchange responsible for asphyxiation
348 and death of the embryo (Ackerman, 1981; Özdemir et al., 2008). Indeed, the hatching
349 success of loggerhead turtle nests has been shown to decrease when water content increases in
350 this way (Foley et al., 2006). Finally, eggs can be confronted with increased salinity, which is
351 known to reduce the ability of eggs to absorb water (Bustard and Greenham, 1968) and to
352 disrupt cellular metabolism as a result of exposure to higher salinities and therefore chloride
353 toxicity (Bustard and Greenham, 1968).

354 Mortality during inundation may be related to the stage of development at which
355 inundation occurs. Our results showed a relationship between time of incubation and
356 embryonic arrest. Early and late embryonic stages were identified as the critical periods in the
357 embryonic development of turtles (Whitmore and Dutton, 1985; Girondot et al., 1990,
358 Özdemir et al., 2008). The present study is consistent with these results, since embryonic
359 mortality was higher in both of these stages than during the middle stage. However, there

360 were few inundation events during the middle stages of incubation in our study nests. This
361 study is the first to analyse the daily situation of the nest, and we found a relationship between
362 overwash event and mortality of embryo, with a clear match between days of overwash and
363 embryonic development arrest, judging by the size of dead embryos (see Fig. 2). More
364 research is needed to determine precisely whether the middle stages of incubation are more
365 resilient to the negative impacts of overwash. Bell et al., (2004) studied the development of
366 leatherback embryos in the laboratory and showed that the early stages appeared to be critical.
367 The late stage seems to be a sensitive period for the development for all nests in general. We
368 found this stage of arrested development in each nest (overwashed or not), although the rate
369 was higher for overwashed nests. This sensitivity appears to result from an increase in gas
370 exchange between the embryo and the nest environment at the end of development (higher
371 metabolism) and a period of immersion at this stage is likely to be more damaging because of
372 higher sensitivity to hypoxia (Thompson, 1993). In addition, we found that mortality during
373 overwash could also be largely dependent on the frequency and the length of overwash.
374 However, overwashed nests in this study also showed high hatching rates, which suggests that
375 nests in marine turtles have a certain tolerance to immersion and can survive a substantial
376 period of time in saltwater. However, if immersion is too long or too frequent, mortality
377 increases drastically. Calcium is another factor linked to inundation which has already been
378 shown to affect development. Calcium is a major component of the eggshell (Ewert et al.,
379 1984; Packard et al., 1984a, Packard et al., 1984b) and is leached from the shell during
380 immersion (Seymour et al., 1997). Eggshell is an important source of calcium for the
381 developing embryo (Packard, 1994), and reduced calcium availability may limit embryonic
382 growth. The loss of calcium also potentially alters eggshell permeability and leads to higher
383 rates of water exchange (water uptake by the yolk and increases in yolk mass and size,
384 Kennett et al., 1998). Finally, when nests were greatly overwashed at the very beginning of

385 the incubation (as in the nest in Fig. 1), hatching success was found to be null with
386 $pE_1=100\%$; this period of immersion is likely to have caused the death of all the eggs.
387 However, it should be noted that yolked eggs with no visible sign of development may not
388 have been fertilized, although results on the population of leatherback along the Guianas
389 (Whitmore & Dutton 1985) and Costa Rica coasts (Bell et al., 2004) showed a very low rate
390 of infertile yolked egg ~ 6%.

391 In our study, only nests that were covered once or more by tide were included in the
392 analysis of the effects of overwash on embryonic development. However, nests that have not
393 been covered by tide might also suffer from the adverse effects of inundation because of
394 immersion due to the water table below the surface of the beach. The water table is the level
395 at which the ground water pressure is equal to atmospheric pressure, and is above the mean
396 sea level (Li et al., 1997). We were unable to assess the height of the water table and it is
397 therefore likely that we underestimated the number of nests affected by the deleterious effects
398 of immersion.

399

400 ***4.2. Nesting beaches threatened***

401 Nest placement has major consequences for offspring survival and it is likely that this
402 behaviour is or has been under strong selection (Mrosovsky, 2006). If nest site selection has a
403 genetic basis, then individual females should be consistent in their particular choice of nesting
404 sites; that is, their choices should be repeatable (Boake, 1989). The significant repeatability of
405 nest-site choice with respect to distance from the high-tide line suggests that this behaviour
406 may show evolutionary potential (Kamel and Mrosovsky, 2004). In this case, it appears that
407 leatherbacks may have the opportunity for further evolution of nest-site choice in response to
408 selection. This is particularly important in the context of current environmental changes and
409 habitat destruction and alteration. Many of these areas are particularly susceptible to coastal

410 hazards such as storm surges and coastal erosion and, with the projected rise in sea level
411 resulting from anthropogenic global warming, threats to coastal areas are increasing (Huang,
412 1997). Increases in sea-level rise are thought to lead to increases in high-tide levels and the
413 frequency of storm events (Kurlle and Gudmundson, 2007). Coastal environment and nesting
414 beaches are therefore threatened with more frequent flooding events that are supposed to
415 decrease the viability of the turtles' nests. This threat is especially true for narrow beaches,
416 such as Yalimapo, on which nests are already located close to the high-tide line, thus
417 exposing them to a greater risk of nest overlap and tidal inundation. Reduction of the size of
418 nesting beaches has implications for reproduction success, especially in major nesting sites
419 such as Yalimapo where density-dependent effects have already had a detrimental effect on
420 nest development (Caut et al., 2006b).

421 However, susceptibility to storm-related threats may vary according to species (Pike
422 and Stiner, 2007); species with lower nest-site fidelity, such as leatherback turtles, would be
423 less vulnerable than those with higher site fidelity (Lahanas et al., 1994; Dutton et al., 1999;
424 Hatase et al., 2002). Moreover, highly dynamic and interseasonally variable nesting beaches
425 in the Guianas (Plaziat and Augustinius, 2004), allow turtles to maintain successful nesting
426 (Kelle et al., 2007), despite the fact that some beaches disappear between nesting years. Such
427 behavioural flexibility may offer opportunities to colonise new beaches, with nesting now
428 occurring at recently formed sites at areas opened after glacial retreats. Whether turtles can
429 colonise nesting areas made available, either thermally or geographically, by climate change
430 remains to be seen (Hawkes et al., 2009). Although it is possible that other beaches in the area
431 could be used, extensive coastal development is occurring regionally, and alternatives are
432 likely to become increasingly scarce. Until a critical habitat can be more clearly identified, it
433 is essential from a conservation standpoint that the choice of beach and new site is not limited
434 because reproductive success could be compromised.

435

436

437 **Acknowledgments**

438 We would like to thank L. Antoni, J. Bernard and S. Quetre for their help in the field, E.
439 Stanek for the design of the probe, E. Angulo for statistical analysis and Matthew Godfrey for
440 his helpful comments on this paper. We wish to thank Jacqueline Minett for improvement of
441 the English. DIREN-Guyane provided financial and legal support (1516 1D/1B/ENV of 27
442 August 2001) and the use of the facilities of the Amana Nature Reserve (Réserve Naturelle de
443 l'Amana).

444

ACCEPTED MANUSCRIPT

445 **LITERATURE CITED**

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- 655

656 **Table 1:** (A) Differences between overwashed nests and non-overwashed nests for different
 657 parameters: female size (SCLmin), clutch size (Number of yolked and yolkless eggs),
 658 hatching success (%) and the percentage of total dead embryos (pE_{Total}). (B) Percentage of
 659 dead embryos corrected (pcE_n) or not (pE_n) for different size categories corresponding to the
 660 four different periods. A nest was considered overwashed when it was overwashed during the
 661 period corresponding to the embryonic size.

	Overwashed nests			Non-overwashed nests			F/ χ^2	P
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>		
A / SCLmin	161.8	8.3	22	161.7	8.0	55	<0.01	0.958
Number of yolked eggs	90.3	21.0	22	86.9	21.7	55	0.39	0.534
Number of yolkless eggs	21.9	8.1	22	25.0	10.2	55	1.64	0.204
Hatching success	28.3	26.8	22	44.9	17.9	55	168.42	<0.001
pE_{Total}	54.5	32.1	22	33.2	17.1	55	263.75	<0.001
B / pE_1	50.3	31.0	15	29.7	16.9	62	166.69	<0.001
pE_3	2.0	3.5	14	0.4	2.1	63	29.57	<0.001
pcE_3	3.8	7.3	13	1.0	4.6	62	42.30	<0.001
pE_4	11.9	16.7	16	2.8	2.7	61	184.65	<0.001
pcE_4	25.9	29.2	16	4.2	4.0	59	238.57	<0.001

662

663 **Table 2:** Variations of the corrected percentage of dead embryos during period¹ (0-23 days)
 664 and period⁴ (57 to 67 days). (A) Effect of *TD* (Total Distance) of each different period on the
 665 corrected percentage of corresponding dead embryos for overwashed and non-overwashed
 666 nests. (B) Effect of *OD* (Overwashed Distance) and *FOD* (First Overwashed Day) of each
 667 different period on the corrected percentage of corresponding dead embryos for overwashed
 668 nests.

Variables	Predictors	Overwashed nests		Non-overwashed nests		
		χ^2	P	χ^2	P	
A /	pcE ₁	TD ¹	224.35	<0.001	1.77	0.184
	pcE ₄	TD ⁴	167.47	<0.001	0.54	0.462
B /	pcE ₁	OD ¹	126.29	<0.001		
		FOD ¹	97.22	<0.001		
	pcE ₄	OD ¹	134.70	<0.001		
		FOD ¹	0.59	0.4440		

669

670 **Figure 1:** Example of overwashed pattern in one nest during the 67 days of the study. Daily
671 Distances of the High Tide Line (*DDHTL*) to the nest are shown. Negative distance represents
672 overwashed events and is highlighted in black. The four periods were represented and for
673 period³, we have represented and calculated the different measurements of overwash for one
674 nest to illustrate: Total Distance (TD), Overwashed Distance (OD), Number of Overwashed
675 Day (NOD) and First Overwashed Day (FOD). (For information this nest has a hatching
676 success = 0%, with $pE_1 = 100\%$).

677

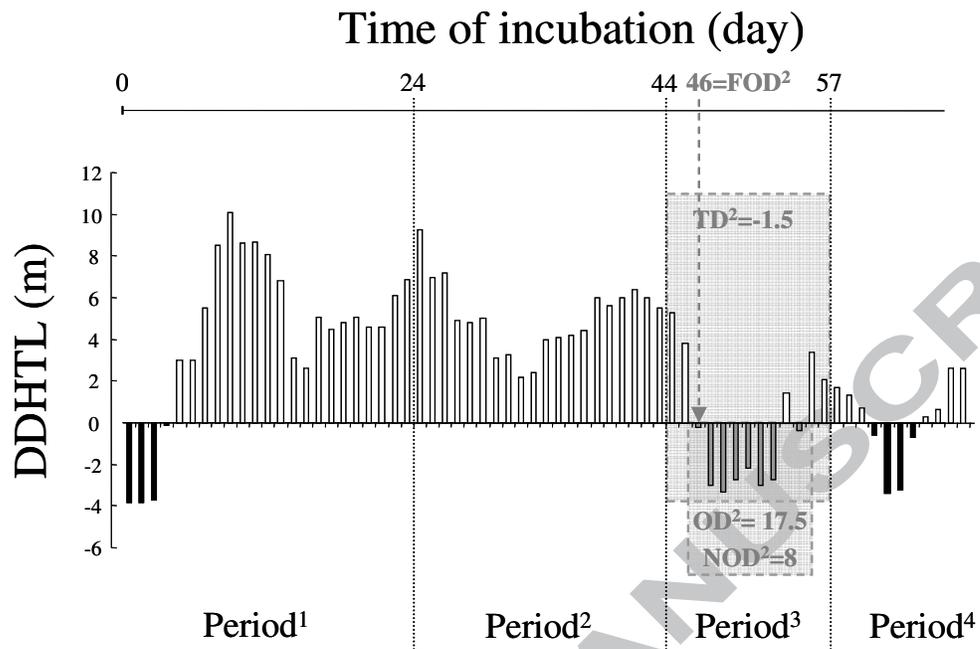
678 **Figure 2:** Percentages of nests (1) with dead embryos for each size of embryo (according to
679 nests overwashed and non-overwashed), (2) overwashed for each day of incubation. The x-
680 axis shows both embryonic size and corresponding time of incubation.

681

682 **Figure 3:** Relationships between percentage of embryos corrected (pcE_n) and the Total
683 Distance (TD) of the nest to the tide line on the Yalimapo beach. Overwashed nests are
684 represented with black circles and non-overwashed nests with white ones. Only significant
685 regressions are represented.

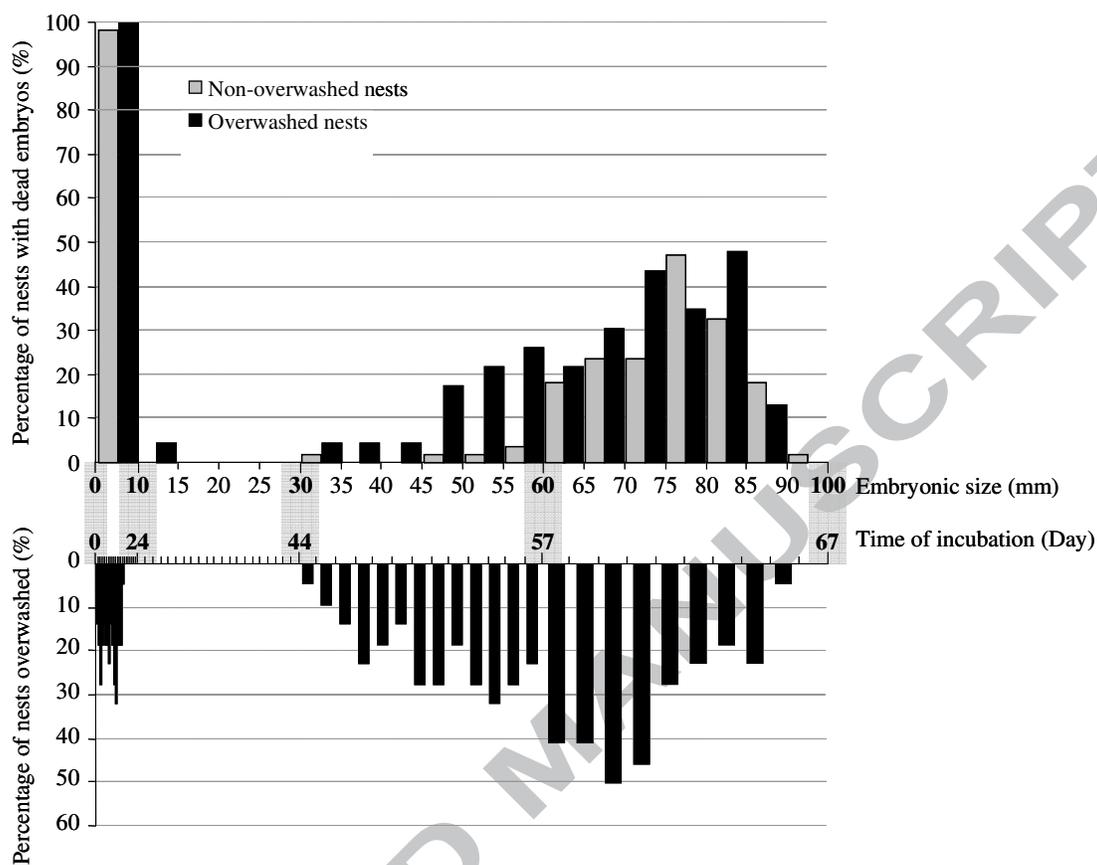
686 **Figure 1**

687



688 **Figure 2**

689



690 **Figure 3**

691

