The climatic debt of loggerhead sea turtle populations in a warming world

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Abstract :

Phenological shifts, by initiating reproductive events earlier, in response to advanced seasonal warming is one of the most striking effects currently observed in wild populations. For sea turtles, phenological adjustment to warming conditions could be the most effective short-term adaptation option against climate change. We calculated future phenological changes required in seven important loggerhead (Caretta caretta) nesting populations to continue achieving a high hatching success and a sex ratio that lies within current ranges. Considering temperature-mediated phenological changes, we found that most populations (six out of seven) will not be able to keep pace with a warming climate. Under an optimistic climate warming scenario (RCP4.5), these populations will face a climatic debt, that is, a difference between required and expected phenological changes, and warming will substantially reduce hatching success and induce a feminization of hatchlings, which may jeopardize their reproductive sustainability. Our approach offers the possibility to quantify the efficiency of phenological shifts in oviparous reptiles by considering physiological, developmental and phenological processes.

Highlights

► We assess the adaptive potential of phenological shifts in 7 sea turtle populations. ► Few populations may be able to stay synchronized with suitable thermal conditions. ► Hatchling survival may be substantially reduced in important populations. ► Nearly 100% female-biased hatchling sex ratios are expected in important populations.

INTRODUCTION

Current climatic changes affect species' abundance, distributions, phenology, physiology and behavior (Bellard et al., 2012; Parmesan, 2006; Root et al., 2003). Such modifications at population- and species-levels will undoubtedly scale toward community and ecosystem levels, for example by disrupting trophic interactions (Walther, 2010). Assessing the vulnerability of species under different climate scenarios is challenging yet it is a prerequisite

52 for developing and prioritizing conservation management strategies. Species with highly

53 heritable variability and short generation time are expected to respond rapidly to selection by

54 microevolution of determinant traits, provided that they benefit from sufficient genetic

55 diversity (Bradshaw and Holzapfel, 2006; Nogués-Bravo et al., 2018; Visser, 2008). In

56 contrast, species with long generation times might be limited in their ability to keep up with

57 the current rate of biotic and abiotic changes.

58   For these species, plasticity in behavior and physiology has the potential to

59 compensate for rapid environmental shifts, allowing them to effectively track of their climate

60 envelope (Chevin et al., 2010; Huey et al., 2012; Refsnider and Janzen, 2012). Many species

61 are already shifting spatially (to higher latitudes or altitudes) and temporally (initiating

62 reproductive events earlier or later in the season) (Parmesan, 2006; Root et al., 2003). For

63 instance, several species of birds are laying their eggs 8.8 days earlier in 25 years in the

64 United Kingdom (Crick et al., 1997). Such phenotypic plasticity may be adaptive if it enables

65 a species to match with its resources or maladaptive if it creates a mismatch with available

66 resources (Charmantier et al., 2008; Visser et al., 2012). Ectotherms are expected to be

67 especially vulnerable to changes in their thermal environment because virtually all their life

68 history traits depend on ambient temperatures, which in turn, affects fitness of individuals

69 (Deutsch et al., 2008; Tewksbury et al., 2008). Temperature can even be viewed as an

70 ecological resource for ectotherms (Magnuson et al., 1979) and especially for oviparous

71 reptiles with temperature-dependent sex determination (TSD), such as sea turtles, because it

72 allows or constrains embryonic development and directs sex ratio, which influence population

73 viability (Hulin et al., 2009; Mitchell et al., 2010).

74   Six out of the seven sea turtle species are already endangered (IUCN, 2016) and may

75 be under further threat as climate change progresses (Fuentes et al., 2013; Hamann et al.,

76 2013). In their life history, like in all oviparous reptiles, the incubation stage is particularly

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77   sensitive to temperatures. Once the eggs are laid, the development of embryos is submitted to

78   environmental factors that are highly dependent on climatic conditions experienced during the

79   incubation period, without any possibility to avoid detrimental conditions. In sea turtles, both

80   the hatching success and the sex of hatchlings depend on incubation temperatures. Constant

81   temperature experiments shown that hatching occurs within a narrow thermal range (roughly

82   25-35°C) (Howard et al., 2014), with a steep threshold at lower temperatures under which

83   development fails and at higher temperatures over which embryos die. Predicting the hatching

84   success of nests in natural conditions remains challenging because temperature varies during

85   the whole incubation period. Current temperature regimes may already reach or exceed the

86   upper limit for successful development as evidenced by low incubation success observed at

87   several nesting beaches (Horne et al., 2014; Rafferty et al., 2017; Valverde et al., 2010).

88   Warming temperatures are thus expected to put the reproduction of many populations at risk.

89   In addition, sea turtles exhibit Temperature-dependent Sex Determination (TSD),

90   producing females at high incubation temperatures and males at low incubation temperatures

91   (Yntema and Mrosovsky, 1980). Many nesting sites already produce predominantly females,

92   with a bias increasing toward nearly 100% females in some of them (Hays et al., 2017; Jensen

93   et al., 2018). A further increase in incubation temperatures could dramatically jeopardize the

94   production of males, and, in turn, these populations' long-term reproductive success. An

95   adaptation to increasing temperatures could be achieved the microevolution of the pivotal

96   temperature (i.e., the temperature at which 50% of each sex may occur). However, this

97   scenario seems unlikely because (i) this trait is relatively conserved among populations (Hulin

98   et al., 2009), which suggests strong genetic constraints, (ii) long generation times should

99   hamper rapid genetic selection of individuals that might deviate, and (iii) the effective

100   heritability of pivotal temperatures in turtles is low in natural conditions (Bull et al., 1982;

101   McGaugh and Janzen, 2011; Refsnider and Janzen, 2015). Sea turtles are also known for natal

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102   homing behavior and a high degree of nest site fidelity (Bowen et al., 1994b; Bowen and Karl,

103   2007; Miller, 1997). The latter trait may constrain rapid large-scale spatial shifts toward more

104   suitable thermal conditions for egg development. Without such plasticity in nest site choice,

105   low rates of embryo survival and highly female-biased sex ratios may arise in the context of

106   global warming (Fuentes et al., 2011; Poloczanska et al., 2009). Therefore, shifting the

107   nesting season might be the most efficient short-term option for sea turtles to adapt to the

108   current rate of thermal changes.

109   Earlier nesting in response to warmer environmental temperatures has been observed

110   in a fresh water turtle (*Chrysemys picta*) (Schwanz and Janzen, 2008), in loggerhead sea

111   turtles (*Caretta caretta*) (Hawkes et al., 2007; Lamont and Fujisaki, 2014; Mazaris et al.,

112   2008; Monsinjon et al., 2019; Patel et al., 2016; Pike et al., 2006; Weishampel et al., 2004;

113   Weishampel et al., 2010) and in green sea turtles (*Chelonia mydas*) (Weishampel et al., 2010).

114   However, whether this phenotypic plasticity in nesting behavior will enable sea turtles to

115   overcome warming impacts at nesting beaches remains to be investigated. Here we address

116   this issue by applying the concept of "climatic debt", previously applied to the spatial

117   distribution of bird and butterfly communities (Devictor et al., 2012), to seven loggerhead

118   nesting populations. Briefly, the theoretical poleward range shift that a species should

119   undertake to track its thermal niche is calculated and compared to a measured real-world

120   response. In other words, a "climatic debt" can be viewed as the lag between environmental

121   changes and the species' or population's response, depending on its ability to stay

122   synchronized with previous conditions (i.e., the difference in time between required and

123   observed or expected phenological shifts). Given that sea turtle populations are unlikely to

124   fully track of suitable thermal conditions at nesting beaches by shifting spatially, we applied

125   this concept at a temporal scale by addressing the following questions: What would be the

126   "climatic prices", that is, the phenological shifts required in the future for sea turtle

127 populations to continue producing a hatching success and a sex ratio that lie within current

128 ranges? Would expected temperature-induced phenological shifts be sufficient to reach this

129 goal (i.e., to pay the "climatic prices") or would populations still face a "climatic debt", that

130 is, a positive difference between the "climatic price" and the expected phenological shift?

131   Combining physiological, developmental and phenological processes, we developed

132 two indices: A Hatching Success Index (HSI) that accounts for the number of nests

133 successfully laid and a Sex Ratio Index (SRI) that accounts for the number of nests

134 successfully laid and the proportion of surviving embryos. We forecasted the hatching success

135 and the sex ratio of seven important loggerhead nesting populations at a global scale (Figure

136 1) within four Regional Management Units (RMUs) (Wallace et al., 2010) under current

137 conditions and under two warming scenarios (RCP4.5 and RCP8.5) (IPCC, 2014). We first

138 assumed the timing of nesting seasons will remain unchanged until 2100 and we explored

139 how phenological shifts could buffer detrimental effects of rising temperatures by shifting the

140 nesting seasons from 0 to 365 days earlier. Finally, we calculated the climatic debts by

141 comparing the climatic prices to realistic expected phenological changes (7 days earlier per

142 degree Celsius increase in sea surface temperature) (Weishampel et al., 2004).

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144 **MATERIALS AND METHODS**

145 **Field data**

146 Nest temperature was recorded at several nesting sites within the following Regional

147 Management Units (RMUs) (Wallace et al., 2010) of the loggerhead sea turtle:

148 Mediterranean, Northwest Atlantic, Southwest Atlantic and Southwest Indian (information

149 summarized in Supplementary material Table A1). Some data are presented here, while the

150 remaining are already published. For the latter, we used only temperature data recorded in

151 natural conditions. Temperatures were recorded within several nests for each site

152 (Supplementary material Table A1) using temperature data loggers placed in the middle of the

153 clutches while females were laying their eggs (≈ 45 cm deep). Data loggers were excavated

154 when hatchlings emerged from the nest or several days later. Temperature data recorded

155 outside the incubation period (i.e., before the laying date or after the emergence date) were

156 omitted.

157   The number of nests was surveyed daily by patrols at the seven nesting beaches during

158 a period of the year specific to each monitoring program (information summarized in

159 Supplementary material Table A2). We omitted nest attempts (false crawls) if the data set

160 contained such information. Nests were counted at Dalyan Beach, Turkey, at Blackbeard

161 Island and Wassaw Island, Georgia, at Boca Raton, Florida, at Praia do Forte and Rio de

162 Janeiro, Brazil, and at Bhanga Nek, South Africa (Figure 1).

163 **Overview of the modeling approach**

164 For the seven nesting populations studied (Figure 1, see section "Field data"), we predicted a

165 hatching success index and a sex ratio index according to scenarios for future area-specific

166 changes in air temperature and global changes in ocean temperature (IPCC, 2014)

167 (Supplementary material Table A3). Those indices were first calculated assuming that the

168 timing of nesting seasons will not shift until 2100 (Figure 2). Thereafter, we shifted nesting

169 seasons each day from 0 to 365 days earlier and we calculated the resulting hatching success

170 and sex ratio indices, which enabled quantifying respective climatic prices (i.e., phenological

171 shifts, in number of days earlier, required for projected indices to reach the lower limit of

172 current ranges, Figure 2). Finally, we calculated the climatic debts (in number of days) by

173 subtracting expected future temperature-induced phenological shifts from climatic prices. To

174 project future temperature-induced phenological shifts, we assumed that a 1°C increase in sea

175 surface temperature will shift a nesting season 7 days earlier (Weishampel et al., 2004). Based

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176   on this linear relationship, +1.19°C and +2.89°C increases in ocean temperature (two

177   warming scenarios: respectively, RCP4.5 and RCP8.5) (IPCC, 2014) (Supplementary material

178   Table A3) would advance the whole nesting seasons 8.3 and 20.2 days earlier, respectively.

179   Negative climatic debts indicate that phenological shifts can effectively offset detrimental

180   effects of warming temperatures whereas positive climatic debts indicate that phenological

181   shifts do not allow populations to track of their thermal niche (Figure 2). Hatching success

182   and sex ratio indices resulting from future temperature-induced phenological shifts were

183   calculated (Figure 2).

184   Following an elaborate modeling approach, it is possible to predict the temperature

185   within the nest, the incubation duration, the hatching success, and the sex ratio (Figure 3).

186   First, nest temperature was reconstructed based on a correlative model that links the

187   temperature recorded within natural nests and environmental temperatures, such as air

188   temperature and sea surface temperature, at nesting beaches (Figure 3.1). This step enables

189   production of long-term time series of nest temperatures using projections from global climate

190   models. We accounted for metabolic heating (i.e., the temperature difference between the nest

191   and the adjacent incubation substratum), which is a characteristic of sea turtle nests due to

192   their large clutch sizes (Booth and Astill, 2001; Broderick et al., 2001; Godfrey et al., 1997;

193   Godley et al., 2001), and we reconstructed natural daily thermal fluctuations because they

194   affect sex determination (Georges, 2013; Georges et al., 2005; Georges et al., 1994). Second,

195   embryonic growth (in terms of carapace size) was modeled based on the Thermal Reaction

196   Norm (TRN) for growth rate inferred from nest temperatures, incubation durations and

197   hatchling measurements (straight carapace length of hatchlings), combined with a growth

198   function (Figure 3.2). When iteratively applied to time series of reconstructed nest

199   temperatures, this approach provides information about embryonic development such as the

200   incubation period and the location of the ThermoSensitive Period (TSP) of development for

201 sex determination (i.e., the period during which temperature influences sex determination).

202 Third, hatching success was estimated by a model linking the average nest temperature to the

203 Thermal Tolerance Curve (TTC) inferred using constant temperature experiments (Figure

204 3.3). Fourth, Constant Temperature Equivalents (CTEs) were converted into sex ratio

205 estimates based on the TRN for sex ratio inferred using constant temperature experiments

206 (Figure 3.4). Fifth, the dynamics of nesting activity was inferred based on the number of nests

207 counted during monitoring surveys (Figure 3.5), which enabled including the temporal

208 window within which nests are incubating. Finally, we calculated hatching success and sex

209 ratio indices per season by including the number of nests laid per day (Figure 3.6).

210 **Reconstructing nest temperatures**

211 We modeled past Nest Temperatures (NT) based on a previously published method (Girondot

212 and Kaska, 2014b; Monsinjon et al., 2017a; Monsinjon et al., 2017b). Nest temperature

213 correlates with Air Temperature (AT) and Sea Surface Temperature (SST) in front of the

214 beach (Girondot and Kaska, 2014b). We collected such data from the European Centre for

215 Medium-Range Weather Forecasts (ECMWF) data sets, which provide temperature every 6

216 hrs (UTC) for several decades at 0.125° resolution (Dee et al., 2011). Sea Surface

217 Temperature (SST) and Air Temperature (AT) at a height of 2 m were extracted from the 1st

218 January 1979 to the 31st December 2016 at geographic coordinates closest to the location of

219 nesting sites (distances between these geographic coordinates and the exact position of

220 nesting sites ranged from 1.2 to 19 km, Supplementary material Table A4). We modeled the

221 daily mean temperature and the metabolic heating using a generalized linear mixed model

222 with Gaussian distribution and identity link function (Monsinjon et al., 2017b) with the mixed

223 effect being the nest identity. Natural daily thermal fluctuations were reconstructed as they

224 can strongly affect sex determination (Georges, 2013; Georges et al., 2005; Georges et al.,

225 1994). We calculated the average daily amplitudes of temperatures (AmpT) using daily

226   maximum (from noon to noon) and daily minimum (from midnight to midnight) (Eccel, 2010)

227   for all days and all nests, independently for each nesting sites. We also calculated the average

228   time of the day when daily maxima and daily minima occur (respectively, Ti.Max and

229   Ti.Min). After site-specific long-term time series of mean nest temperatures were

230   reconstructed, we replaced daily mean by daily maximum (mean+AmpT/2) and daily

231   minimum (mean-AmpT/2) that we set at Ti.Max and Ti.Min respectively. Site-specific

232   parameters used to predict NT are presented in Supplementary material Table A4 (see also

233   Supplementary material Note A1). This modeling approach allowed for an accurate prediction

234   of nest temperature (Supplementary material Note A1, Figure A1).

235   We forecasted NT based on region-specific scenarios of changes in air temperature

236   and a global scenario of changes in ocean temperature (IPCC, 2014) (Supplementary material

237   Table A3). We chose an optimistic scenario of Representative Concentration Pathway (RCP)

238   in greenhouse gas concentration that predicts a rising radiative forcing that will stabilize at

239   +4.5 W.m^{-2} after 2100 as compared to preindustrial values, assuming a decrease in emissions

240   of CO_2 after 2040 (RCP4.5) (Moss et al., 2010). We also chose to make predictions under a

241   more pessimistic scenario. This extreme scenario predicts a radiative forcing that will reach

242   +8.5 W.m^{-2} by 2100 as compared to preindustrial values and will keep rising afterward

243   assuming no decrease in emissions of CO_2 (RCP8.5) (Moss et al., 2010). These data were

244   extracted from the KNMI (Koninklijk Nederlands Meteorologisch Instituut) Climate Explorer

245   website (https://climexp.knmi.nl/plot_atlas_form.py). Briefly, the KNMI interface allows the

246   user to select the region (here defined by IPCC Working Group 1), the data set (here Coupled

247   Model Intercomparison Project 5 for IPCC's Fifth Assessment Report), the variable (here

248   near-surface temperature), the scenario of RCP in greenhouse gas concentration (here RCP4.5

249   and RCP8.5) and the periods to be compared to obtain anomalies (here anomalies as

250   compared with the 1979-2016 period). Projected temperature anomalies were extracted for the

251   following regions: North-East Brazil, Eastern-North-America, Southern-Africa and South-

252   Europe-Mediterranean (summarized in Supplementary material Table A3). We added

253   projected (region-specific) increases in temperature to AT time series previously extracted

254   from ECMWF data sets. We also extracted the projected increase in ocean temperature at the

255   scale of the world, which was added to SST time series previously extracted from ECMWF

256   data sets. Future NT is then reconstructed following the method described above but this time

257   using modified time series of AT and SST. These new NT time series are forecasts for the

258   2062-2100 period while considering the 1979-2016 period as a baseline.

259   **Modeling embryonic development**

260   The size of an embryo according to the temperature experienced within the nest can be

261   modeled based on the Thermal Reaction Norm (TRN) for growth rate using an equation that

262   describes the effect of temperature on the growth rate along with an equation that describes

263   the progression of embryo size during incubation (Girondot and Kaska, 2014a). This method

264   has been implemented to estimate the TRN for the growth rate of three loggerhead nesting

265   populations (Fuentes et al., 2017; Girondot and Kaska, 2014a; Monsinjon et al., 2017b). The

266   components form a thermodynamic description of the effect of temperature on the rate of

267   biological reactions applied to a Gompertz model for the growth of an embryo (Girondot and

268   Kaska, 2014a). Here, we applied this method following recent upgrades (Girondot et al.,

269   2018). The model requires (i) temperature time series recorded within nests from the moment

270   when eggs were laid to the moment when hatchlings emerged from the nest and (ii)

271   measurements of the Straight Carapace Length (SCL) of hatchlings (SCL data used to infer

272   TRNs are summarized in Supplementary material Table A5).

273   To detect potential differences in TRNs for growth rate among nesting populations

274   from the same Regional Management Unit (RMU), we applied a similar approach as per

275   Monsinjon et al. (2017b). Briefly, the TRN for growth rate was estimated for two populations

276   (i) independently for both populations (hypothesis 1: the populations exhibit different TRNs)

277   and (ii) after data sets of nest temperature were grouped together (hypothesis 2: the

278   populations exhibit similar TRNs). We calculated the Akaike Information Criterion corrected

279   for finite sample size (AICc) and the Akaike weight, i.e. the relative support of both

280   hypotheses (Burnham and Anderson, 2002). The sum of AICc of each model estimated

281   independently (hypothesis 1) were then compared with the AICc of the model estimated with

282   both data sets grouped together (hypothesis 2). Before comparing the populations closest to

283   one another within the same RMU, we first grouped those which belonged to the same

284   "subdivided" management unit (i.e., demographically isolated but not genetically different)

285   (Shamblin et al., 2014). The model selection procedure is presented in Supplementary

286   material Table A6.

287   Once population-specific TRNs for growth rate were estimated (Supplementary

288   material Note A2, Figure A2), we modeled embryonic development at nesting sites based on

289   long-term time series of reconstructed nest temperatures (NT). If we consider a nest being laid

290   at a date i, the progression of embryo size (SCL) is modeled until it reaches, at the date i+n,

291   the final SCL of a completely developed embryo (i.e., a freshly emerged hatchling) known for

292   the nesting population. This allowed the extraction of information such as the incubation

293   duration (n), the nest temperature within the whole incubation period, and the nest

294   temperature within the TSP (see section "Estimating sex ratio" for defining TSP boundaries

295   within incubation). The model was run again at the date i+1 and so on for the period when NT

296   is available (i.e., each day between 1979 and 2016).

297   **Estimating hatching success**

298   Here, we introduce a new mathematical description of the thermal tolerances of sea turtle

299   embryos. This model is fitted here for the loggerhead sea turtle using data obtained at constant

300   temperatures in laboratory conditions. The Thermal Tolerance Curve (TTC) is described by a

301   model composed of the product of two logistic equations and a term defining the average

302   hatching success within the optimal range of temperatures (equation 1):

303     $HS = \dfrac{1}{1+\exp\left(\frac{1}{|S_L|}(P_L-t)\right)} \times \dfrac{1}{1+\exp\left(\frac{1}{-|S_H|}(P_H-t)\right)} \times H$ equation 1

304   With S_L and P_L being the logistic parameters defining the lower part of the curve, S_H and P_H

305   being the logistic parameters defining the higher part of the curve and H being the average

306   hatching success within the optimal range of temperatures. This method accounts for both the

307   upper and the lower thermal limits for embryo survival, which is a prerequisite when making

308   projections according to extremes scenarios of thermal changes.

309   To infer the TTC, we used data for the loggerhead sea turtle from five Regional

310   Management Units (RMUs) (Supplementary material Table A7). For each constant

311   temperature experiment, the hatching success is calculated as being the number of embryos

312   that successfully hatched divided by the total number of eggs (of which we subtracted the

313   number of undeveloped embryo if specified in the original publication). The model is fitted

314   using maximum likelihood with a binomial distribution for error. As most of the data come

315   from different populations, we assessed potential similarities among RMUs. To detect

316   potential differences, we estimated the TTCs (i) independently (making the hypothesis that

317   RMUs exhibit different TTCs) and (ii) after all data were grouped together (making the

318   hypothesis that RMUs exhibit similar TTCs). Based on the AICc and the Akaike weight,

319   TTCs were found similar among RMUs (Supplementary material Note A3).

320   The model described here allows for predicting the hatching success for any nest that

321   incubated at constant temperatures (Supplementary material Figure A3). However,

322   temperature is not constant under natural conditions and it is poorly known how fluctuating

323   thermal regimes influence hatching success (Howard et al., 2014). Using published data of

324   hatching success from natural nests (Godley et al., 2001; Horne et al., 2014; Read et al.,

325   2013), we searched for an equivalent at constant temperature (i.e., the mean nest temperature

326   during incubation plus a correction parameter) that best describes hatching success in natural

327   conditions. This correction parameter aims to adjust data from natural conditions so they can

328   be compared with data from constant temperature experiments. Data were extracted from

329   figures in respective original publications using the software WebPlotDigitizer version 4.1

330   (https://automeris.io/WebPlotDigitizer/) when tables were not provided. We predicted the

331   hatching success from mean nest temperatures with a correction parameter varying from -

332   1.5°C to +1.5°C each 0.01°C and we kept the value that minimizes the dispersion (sum of

333   squares) of residuals (here +0.32°C, see Supplementary material Note A3).

334   **Estimating sex ratio**

335   The loggerhead sea turtle exhibits a cool male/warm female pattern of Temperature-

336   dependent Sex Determination (TSD) (Yntema and Mrosovsky, 1980). We inferred the

337   Thermal Reaction Norm (TRN) for sex ratio of loggerhead populations nesting in

338   Mediterranean, Northwest Atlantic, Southwest Atlantic and Southwest Indian Regional

339   Management Units (RMUs) based on constant temperature experiments previously carried out

340   in laboratory conditions. Data for Mediterranean were from Greece (Mrosovsky et al., 2002).

341   Data for Northwest Atlantic were from Florida (Mrosovsky, 1988), North Carolina

342   (Mrosovsky, 1988) and Georgia (Yntema and Mrosovsky, 1980, 1982). Data for Southwest

343   Atlantic were from Brazil (Marcovaldi et al., 1997). Data for Southwest Indian ocean were

344   from South Africa (Maxwell, 1987). We estimated TRNs for sex ratio using a logistic

345   equation (Girondot, 1999).

346   The simple mean temperature during either periods of incubation typically is a poor

347   predictor of sex ratio because the effect of temperature on sex determination may vary with

348   gonadal growth which also depends on temperature (Georges et al., 2005; Neuwald and

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349   Valenzuela, 2011). A Constant Temperature Equivalent (CTE) was developed to account for

350   such effect by calculating the temperature at which half of the development occurred

351   (Georges, 1989; Georges et al., 1994). Here, we used a recent update that accounts for a

352   nonlinear development within incubation (Fuentes et al., 2017). Basically, this CTE is the

353   mean temperature weighted by the differential growth within the TSP. We produced sex ratio

354   estimates based on population-specific TRNs for sex ratio (Supplementary material Note A4,

355   Figure A4) using this proxy.

356   The ThermoSensitive Period (TSP) of development occurs between embryonic stages

357   21 and 26 for sea turtles (Miller, 1985) which roughly corresponds to the middle third of

358   incubation at constant temperature as generally observed in most reptiles with TSD (Bull,

359   1987; Desvages et al., 1993; Girondot et al., 2018; Pieau and Dorizzi, 1981; Woolgar et al.,

360   2013). The Straight Carapace Length (SCL) at the onset of the TSP and the SCL at the end of

361   the TSP are respectively 21% and 71% of the SCL of a completely developed embryo for the

362   loggerhead sea turtle (Girondot et al., 2018).

363   **Unraveling the dynamics of nesting activity**

364   We used a set of equations that describe the underlying dynamics of a nesting season based on

365   time series of nest counts (Girondot, 2017). Basically, a nonlinear function with seven

366   parameters was fitted using maximum likelihood with negative-binomial distribution for each

367   ordinal day of the year. These parameters describe adequately the pattern of a nesting season:

368   a minimum number of nests when turtles are not active before and after the active season and

369   a maximum number of nests at the ordinal day when the peak of activity occurs around which

370   the curve can flatten out. The dispersion around the mean was controlled by a negative-

371   binomial parameter (Girondot, 2017). Here we assumed that the curve was not flat around the

372   peak because a visual examination of nest counts showed a bell-shaped distribution. First, we

373   allowed all parameters to vary across seasons to obtain a "season-specific" description of

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374 nesting activity at any nesting site. Second, we fitted parameters without allowing them to

375 vary across seasons to obtain a "global" description of nesting activity. The global description

376 of nesting activity was used in Figure 4 to provide a visual picture of the dynamics of nesting

377 activity along with within-year variations in hatching success and sex ratio. The season-

378 specific description of nesting activity was used to capture the actual interseasonal variability

379 of current hatching success and sex ratio indices while the global description of nesting

380 activity was used to project future indices, assuming the overall pattern of nesting seasons will

381 remain unchanged until 2100.

382 **Calculating hatching success and sex ratio indices**

383 We calculated a Hatching Success Index (HSI) as being the average hatching success during a

384 nesting season weighted by the number of nests laid (equation 2).

385 $$HSI = \frac{\sum_{i=k}^{N} HS_i \times Nest_i}{\sum_{i=k}^{N} Nest_i}$$ equation 2

386 HS_i is the hatching success (survival proportion) for nests laid at the day i of the season with

387 k being the first date of the season. $Nest_i$ is the number of nests laid at the day i of the

388 season. N is the last date of the season.

389   We calculated a Sex Ratio Index (SRI) as being the average sex ratio during a nesting

390 season corrected by the hatching success and weighted by the number of nests laid, which is

391 the sex ratio of surviving hatchlings (equation 3).

392 $$SRI = \frac{\sum_{i=k}^{N} SR_i \times Nest_i \times HS_i}{\sum_{i=k}^{N} Nest_i \times HS_i}$$ equation 3

393 SR_i is the sex ratio (male proportion) for nests laid at the day i of the season with k being the

394 first date of the season. $Nest_i$ is the number of nests laid at the day i of the season. HS_i is the

395 hatching success for nests laid at the day i of the season. N is the last date of the season.

396   Current indices (between 1979 and 2016) were calculated only for seasons when nests

397   were surveyed (see Supplementary material Table A2) and using the season-specific

398   description of nesting activity. Future indices (i.e., forecasts for the 2062-2100 period) were

399   calculated for all future seasons (n = 38) using the global description of nesting activity (see

400   section "Unraveling the dynamics of nesting activity" for the descriptions of nesting activity).

401

402   **RESULTS**

403   **Current nesting activity, hatching success and sex ratio**

404   Currently, the nesting seasons occur when the hatching success is optimal at Dalyan Beach,

405   Blackbeard Island, Wassaw Island, Rio de Janeiro, and Bhanga Nek (respectively, Figure 4a,

406   b, c, f and g). A different situation is observed at Boca Raton and Praia do Forte, where the

407   hatching success decreases slightly around the peak of nesting (respectively, Figure 4d and e).

408   The nesting seasons occur when both sexes are produced in variable proportions (with

409   a peak of nesting when mostly female hatchlings are expected) at Dalyan Beach, Blackbeard

410   Island, Wassaw Island, Rio de Janeiro, and Bhanga Nek (respectively, Figure 4h, i, j, m and

411   n). A different situation is observed at Boca Raton and Praia do Forte, where the whole

412   nesting seasons occur when a nearly 100% female-biased sex ratio is expected (respectively,

413   Figure 4k and l).

414   **Warming temperatures may reduce hatching success and induce a feminization of**

415   **hatchlings**

416   Current Hatching Success Indices (HSIs) are optimal for all nesting populations studied here

417   except at Boca Raton and Praia do Forte (Figure 5a). Under an optimistic warming scenario

418   (RCP4.5), all nesting populations are expected to face a reduction in hatching success, except

at Dalyan Beach (Figure 5a). According to this scenario, the population nesting at Boca Raton should face a very low hatching success (<20%). Under a pessimistic warming scenario (RCP 8.5), all nesting populations should face a hatching success lower than 50%, except at Dalyan Beach (Figure 5a). In this extreme warming situation, expected phenological shifts can effectively buffer reductions in hatching success, except for populations nesting at Boca Raton and Praia do Forte which may face a very low hatching success (<10%) either ways (Figure 5a).

Current Sex Ratio Indices (SRIs) are highly female-biased at Praia do Forte and Boca Raton (>95% females) whereas it is less skewed toward females at other nesting sites (<85% females) (Figure 5b). Under an optimistic warming scenario (RCP4.5), the sex ratio might become increasingly female-biased in all nesting populations studied here (with only female hatchlings expected at Praia do Forte), except at Boca Raton where the proportion of males is expected to increase slightly (Figure 5b). Under a pessimistic warming scenario (RCP8.5), all nesting populations should experience a highly female-biased sex ratio (>95% females), except at Boca Raton where the proportion of males might increase substantially (Figure 5b). In both warming situations, only the population nesting at Dalyan Beach may benefit from a buffering effect of expected phenological shifts while the opposite situation is observed at Boca Raton (Figure 5b).

Most populations could face a climatic debt in the future

Phenological shifts required in the future (2062-2100 as compared to 1979-2016) for HSIs and SRIs to remain within current ranges (i.e., climatic prices) range from 0 day earlier (for HSI at Dalyan Beach under an optimistic warming scenario: RCP4.5) to 118 days earlier (for HSI at Rio de Janeiro under a pessimistic warming scenario: RCP8.5) (Table 1, Supplementary material Figure A5). Six out of the seven nesting populations studied here could face a climatic debt in the future under both warming scenarios and for both the HSI

18

444   and the SRI (Table 1). Only the population nesting at Dalyan Beach might not face a climatic

445   debt in the future for the HSI to remain within its current range and only under the RCP4.5

446   scenario (Table 1).

447

448   **DISCUSSION**

449   For ectotherms, such as fishes, amphibians and non-avian reptiles, temperature is a major

450   driver of population distribution and viability (Angilletta et al., 2010; Deutsch et al., 2008;

451   Huey et al., 2009; Maffucci et al., 2016). Our results highlight differences among loggerhead

452   nesting populations in their capacity to keep pace with the rate of thermal changes and suggest

453   that only a subset of populations may be able to offset detrimental effects by shifting their

454   nesting phenology. A growing number of studies have suggested that phenological changes

455   may, to some extent, buffer detrimental effects of warming temperatures on reptile embryos

456   (Almpanidou et al., 2018; Mitchell et al., 2008; Mitchell et al., 2016; Stubbs et al., 2014). For

457   many sea turtle populations, whether climate-induced phenological shifts confer the potential

458   to buffer detrimental effects on their progeny remains unclear. Here we took a step forward in

459   the prediction of warming impacts on sea turtles' hatching success and sex ratio using an

460   elaborate modeling approach and comparing distant populations, which should inform new

461   strategies for prioritizing conservation efforts at a global scale. Importantly, our model offers

462   a process-based framework to quantify the sex ratio of sea turtle hatchlings during a nesting

463   season by considering (i) the number of nests laid and (ii) the proportion of surviving embryos

464   under both cold and warm conditions.

465   **Nesting activity, hatching success and sex ratio**

466   Loggerhead populations nesting at the lowest latitudes of our data sets (Boca Raton, Florida,

467   and Praia do Forte, Brazil) are already at the edge of thermal limits for embryo survival

468 (Figure 4d and e) and nest during the period when mostly female hatchlings are produced.

469 Conversely, other populations studied here, which nest at relatively higher latitudes, may

470 experience optimal incubation temperatures for embryo survival and produce a more balanced

471 sex ratio. Overall, male hatchlings are more likely to hatch during the first part of the nesting

472 season while mostly females are produced during the rest of the nesting season. This may

473 explain why future sex ratio at Boca Raton is expected to be less skewed toward females,

474 because remaining male-producing clutches would experience more suitable temperatures at

475 the beginning of the nesting season than middle and late clutches that may experience 100%

476 failure, as currently suspected at female-producing nesting sites (Figure 4d and e).

477 Whether a highly female-biased primary sex ratio is likely to persist through age

478 classes may vary within and among sea turtle species (Hamann et al., 2013; Hamann et al.,

479 2010). If feminization of the primary sex ratio persists in the adult sex ratio, detrimental

480 effects at population level can occur such as (i) reduced fertility rates (Bell et al., 2009) and/or

481 (ii) loss of genetic diversity through reduction of effective population size (Hamann et al.,

482 2010). Concerning these threats, males can breed annually with multiple females while

483 females do not breed every year. This sex-specific difference in reproductive behavior can be

484 somewhat compensatory and balance the operational sex ratio, thus buffering current or future

485 negative effects of female-biased adult sex ratios on fertility rates (Hays et al., 2010; Wright

486 et al., 2012). According to some authors, temperature-dependent sex determination can confer

487 a short-term demographic advantage by producing more females at increasing temperatures,

488 which could first enhance population growth (Hays et al., 2017). However, such a positive

489 effect on population dynamics does not seem sufficient to offset the current rate of climatic

490 changes in the long term (Laloë et al., 2014, 2017; Saba et al., 2012; Santidrián Tomillo et al.,

491 2015a). A decrease in effective population size finally seems inevitable, which in turn can

492 induce genetic erosion and thus lower potential to respond to selection pressures (Hamann et

493 al., 2010). There is a strong need for further research into population dynamics, and
494 particularly modeling, that integrates genetic Allee effects linked to potential biases in sex
495 ratio (Mitchell et al., 2010).

496   Nesting phenology and hatching success both influence the number of male and
497 female hatchlings that may reach the sea. Only a few studies have attempted to account for
498 differential survival of both sexes accounting for temperature-mediated hatching success or
499 emergence rate (Hays et al., 2017; Santidrián Tomillo et al., 2014) and none have accounted
500 for the number of nests before the present study. Here we provide reliable quantitative
501 predictions of temperature-mediated hatching success based on the thermal tolerance curve of
502 loggerhead embryos, which accounts for both lower and upper critical limits. This novel
503 model should now be calibrated in other sea turtle species to make accurate predictions under
504 both cold and warm extreme conditions, which is particularly relevant for populations nesting
505 at high latitudes where seasons are more pronounced. Nevertheless, this method can still be
506 improved. In natural conditions, embryo survival depends on the magnitude of the thermal
507 stress and the time spent over a critical threshold (Howard et al., 2014, 2015). Therefore, new
508 methods to predict hatching success should be deployed to capture biologically-determined
509 thermal variation. Recent studies about heat tolerance of loggerhead embryos will probably
510 help in refining models that incorporated cellular processes underlying embryo survival in
511 response to temperature (Bentley et al., 2017; Tedeschi et al., 2016). Precipitations and
512 moisture levels within nests are other factors that influence hatching success, either directly or
513 indirectly through an evaporative cooling effect (Montero et al., 2018a; Montero et al., 2018b;
514 Pike, 2013; Santidrián Tomillo et al., 2015b). Further studies must integrate this parameter
515 into a more comprehensive model to forecast the hatching success of sea turtles as the rate of
516 precipitation is also expected to change in the future (IPCC, 2014).

517 **Phenological shifts: adaptive potential and implications for conservation**

518   Sea turtles have been around for more than 110 million years (Hirayama, 1998) and have

519   survived dramatic thermal changes (Hamann et al., 2007; Hawkes et al., 2009). However, the

520   mechanisms by which sea turtles adapted and whether they will be able to adapt in the future

521   remains an open question. Shifting the nesting season is one key response to rising

522   environmental temperatures. In a freshwater turtle, it appears that shifting the nesting season

523   may not be effective enough to offset warming impacts on sex ratio (Schwanz and Janzen,

524   2008; Telemeco et al., 2013). The opposite conclusion reached for tuataras (Nelson et al.,

525   2018). Our results highlight differences in the efficiency of phenological shifts among

526   loggerhead populations to buffer detrimental effects of warming temperatures, with

527   populations nesting at the edge of lethal thermal limits being likely at greater risks (i.e., low

528   hatching success and female-biased sex ratio). Following this, several management strategies

529   can be proposed: (i) nest relocation, artificial nest shading and watering to cool the nests

530   (Esteban et al., 2018; Hill et al., 2015), (ii) preservation, restoration and enrichment of native

531   coastal vegetation to increase available shaded areas (Kamel, 2013), (iii) assisted migration

532   (or colonization) of nesting sites by moving eggs to colder beaches (Bowen et al., 1994a) and

533   (iv) foster international collaborations and agreements for safeguarding sea turtles worldwide

534   (Carr, 1956; Wold, 2002) to allow for a better protection of resilient nesting populations, like

535   the one nesting at Dalyan Beach, Turkey, identified in the present study. The first strategy

536   requires long-term human resources, which are not always available depending on the

537   country. Moreover, this strategy could slow down or prevent potential local adaptations by

538   lowering natural selection pressures (Mrosovsky, 2006). The second strategy could be

539   sustainable but further research is needed to anticipate potential detrimental effects of highly

540   vegetated beaches on egg incubation and female nesting success (Wood et al., 2014). The

541   third strategy, here based on sea turtles' natal homing behavior, is still controversial and

542   requires, among others, an extensive ecological understanding of the species and a careful

543   characterization of new intended habitats (Dade et al., 2014; McLachlan et al., 2007). We

544   urge further research to evaluate the risks and benefits associated with assisted migration and

545   we recommend following the last proposed strategy, while further identifying other resilient

546   nesting populations and potentially suitable beaches for nesting based on the application and

547   development of our approach.

548   Here we assumed that 1°C increase in sea surface temperature will shift nesting

549   seasons 7 days earlier (Weishampel et al., 2004). However, this relationship could vary

550   among populations and whether temperature affects nesting phenology at foraging, breeding,

551   and/or nesting areas remains unclear (Mazaris et al., 2009; Monsinjon et al., 2019). One of the

552   steepest responses was found in Mediterranean where loggerheads start nesting 8.5 days

553   earlier in response to 1°C increase in sea surface temperature at breeding areas (Mazaris et al.,

554   2008). Conversely, the slope of this relationship seems to be weaker for populations nesting at

555   low latitudes (Mazaris et al., 2013), which may jeopardize even more their ability to adapt to

556   rising temperatures. Moreover, we do not know whether the general pattern of nesting activity

557   will remain the same in the future. There is limited advancement of nesting phenology in

558   some loggerhead populations but no evidence for delayed initiation of nesting in response to

559   warmer temperatures, as observed in leatherback sea turtles (*Dermochelys coriacea*) (Neeman

560   et al., 2015). Some loggerhead populations have shortened their nesting season in response to

561   warmer temperatures (Pike et al., 2006; Weishampel et al., 2010) while the opposite response

562   was also found in other populations (Hawkes et al., 2007; Lamont and Fujisaki, 2014). Better

563   understanding of the timing of sea turtle reproduction is a gap that needs further research.

564   **Thermal heterogeneity, spatial shifts and other threats**

565   In the present study, we reproduced thermal heterogeneity at a fine temporal and geographical

566   scale through modeling, but we did not account for thermal heterogeneity occurring at other

567   spatial scales: inside a nest and between nests of the same nesting beach. Within a nesting

568   beach, in the context of global warming, eggs developing at cooler temperatures could suffer

569   less mortality than those developing at warmer temperatures, such that our model could

570   underestimate the proportion of male hatchlings. Further studies are required to provide

571   biologically-relevant characterization of thermal heterogeneity at these finer spatial scales.

572   Here, we projected nest temperatures based on a correlative model that involves air

573   temperature and sea surface temperature. Nevertheless, the temperature within a nest depends

574   on soil properties (e.g., thermal conductivity, soil reflectance) and other external forcing (e.g.,

575   wind speed, solar radiation, water content) that must be considered. Much effort is warranted

576   for assessing the environmental conditions at nesting sites and the physical properties of

577   beaches to better predict nest temperatures, possibly using a (mechanistic) microclimate

578   model (Fuentes and Porter, 2013; Kearney and Porter, 2017; Mitchell et al., 2016; Porter et

579   al., 2010).

580   Such micro-environmental variability may provide reptiles with a way for buffering

581   the effects of climate change. Females might modify the placement of their nests in order to

582   compensate for rising temperatures (Doody et al., 2006; Doody and Moore, 2010). For

583   instance, shade cover may provide sufficient thermal variation for a freshwater turtle to select

584   thermal microhabitats for nesting (Refsnider et al., 2013). Variation in sand color at nesting

585   beaches can also provide thermal microhabitats (Hays et al., 2001). This adaptive mechanism

586   may be effective as long as nesting sites with different available thermal conditions remain

587   accessible (Doody and Moore, 2010; Refsnider and Janzen, 2012).

588   Rapid spatial shift of nesting sites at a regional scale is unlikely for sea turtles due to

589   their natal homing behavior and, for some species, high degree of nest site fidelity (reviewed

590   in Miller, 1997). However, a few loggerhead females were found to attempt nesting hundreds

591   of kilometers distant from their former nesting sites in Australia (Limpus, 2008) and tens of

592   kilometers in South Africa (Nel et al., 2013). These wanderers have the potential to forge

593 range extensions. Establishment of new nesting sites may compensate the loss of current

594 nesting sites (Fuentes et al., 2013; Hawkes et al., 2009), provided that other suitable nesting

595 beaches are still available (Katselidis et al., 2012; Pike, 2013). For example, the population

596 nesting at Bhanga Nek, South Africa, may benefit from the availability of suitable nesting

597 beaches farther South along the East coast of Africa which provides sandy beaches within a

598 wide range of latitudes.

599   In any case, other environmental changes will soon threaten or are already threatening

600 the viability of sea turtles populations: (i) the availability of nesting sites may decrease as the

601 sea level rises (Fuentes et al., 2010), (ii) coastal development may further disturb these

602 nesting habitats (Fuentes et al., 2016; Sella and Fuentes, 2019), (iii) changes in precipitation

603 regimes may affect incubation success and hatchling sex ratio (Montero et al., 2019;

604 Santidrián Tomillo et al., 2015b), (iv) increasing intensity of extreme climatic events may

605 cause a high number of nest destruction (Fuentes and Abbs, 2010), and finally (v) adults can

606 be affected by other threats such as bycatch in fisheries and pollution (Hawkes et al., 2009;

607 Patrício et al., 2018).

608 **Conclusions**

609 By assessing the adaptive potential of phenological shifts under two plausible warming

610 scenarios, our study enabled the identification of loggerhead nesting populations that might

611 face detrimental thermal conditions at nesting beaches in the future. Within the locations

612 studied, we found that the population nesting at Dalyan Beach, Turkey, will be able to keep

613 track of suitable thermal conditions under an optimistic scenario of future changes in

614 environmental temperatures. Under a pessimistic warming scenario, only this population

615 nesting at Dalyan Beach would be able to buffer, but not utterly offset, the effect of warming

616 temperatures. We also identified two populations that might experience low embryo survival

617 and mostly females being produced under both warming scenarios, which are those nesting at

618 Boca Raton, Florida, and Praia do Forte, Brazil. These results show the importance of

619 modeling the long-term site-specific effects of climate change at a local scale to be able to

620 evaluate the sustainability of diverse populations. Other sea turtle species already face or will

621 soon face such warming impacts at their nesting sites and thus warrant further investigations.

622 The use and development of our approach should prove useful for assessing the

623 viability of sea turtle populations as well as other ectotherms. Combining thermal tolerances,

624 physiological and phenological processes, our conceptual approach can be applied to other

625 ectotherm species spatially-constrained by their natal homing behavior and their high degree

626 of nest site fidelity, such as salmon and other anadromous fish species, to explore the potential

627 of phenological shifts in thermal niche tracking. Species can adapt to environmental changes

628 by shifting their spatial and temporal distribution (i.e., habitat range and phenological shifts,

629 respectively) simultaneously (Chuine, 2010), so that phenological shifts can buffer or

630 neutralize range shifts (Socolar et al., 2017). Future research should now combine resource-

631 driven and climate-driven shifts in phenology and geography in a single framework to explore

632 the adaptive potential of species in response to contemporary climate change.

633

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AUTHOR CONTRIBUTIONS

J.M. initiated the project and performed the data analysis. J.W., K.R., M.L., P.L., A.S., M.A.G.d.M., M.M.P.B.F, Y.K., J.T., R.N., K.L.W., A.-M.L. and D.R. compiled the data. J.M and J.-M.G. conceived the manuscript. M.G. built mathematical models. J.M. wrote the manuscript with contributions from all authors.

CONFLICTS OF INTEREST

The authors declare no competing interests.

664 **PERMITS**

665 Data collection at Bhanga Nek took place under the Research Agreement with iSimangalio

666 Wetland Authority, with animal ethics clearance (A09-SCI-ZOO-005) and Dept of

667 Environmental Affairs Permits (RES2010/55 & 2011/41). Data collection in Georgia was

668 conducted under Georgia DNR permit Nos. 29-WMB-03-157 and 29-WMB-04-136; USFWS

669 permit No. 41620-02018; and approved by the Georgia Southern University IACUC. Data

670 collection in Florida was conducted under FAU IACUC approval, Florida Sea Turtle permit

671 073, and USFWS permits.

672

673 **SUPPLEMENTARY MATERIAL**

674 Supplementary material includes four notes, five figures and seven tables and can be found

675 with this article online. Correspondence and requests for materials should be addressed to

676 M.G. Statistical analyses were performed using R (R Core Team, 2019). Mathematical

677 models used in this study are available in the following R packages: `phenology´ (Girondot,

678 2019b) and `embryogrowth´ (Girondot, 2019a).

679

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1090   **FIGURES**

1091   **Figure 1. Location of nesting sites**
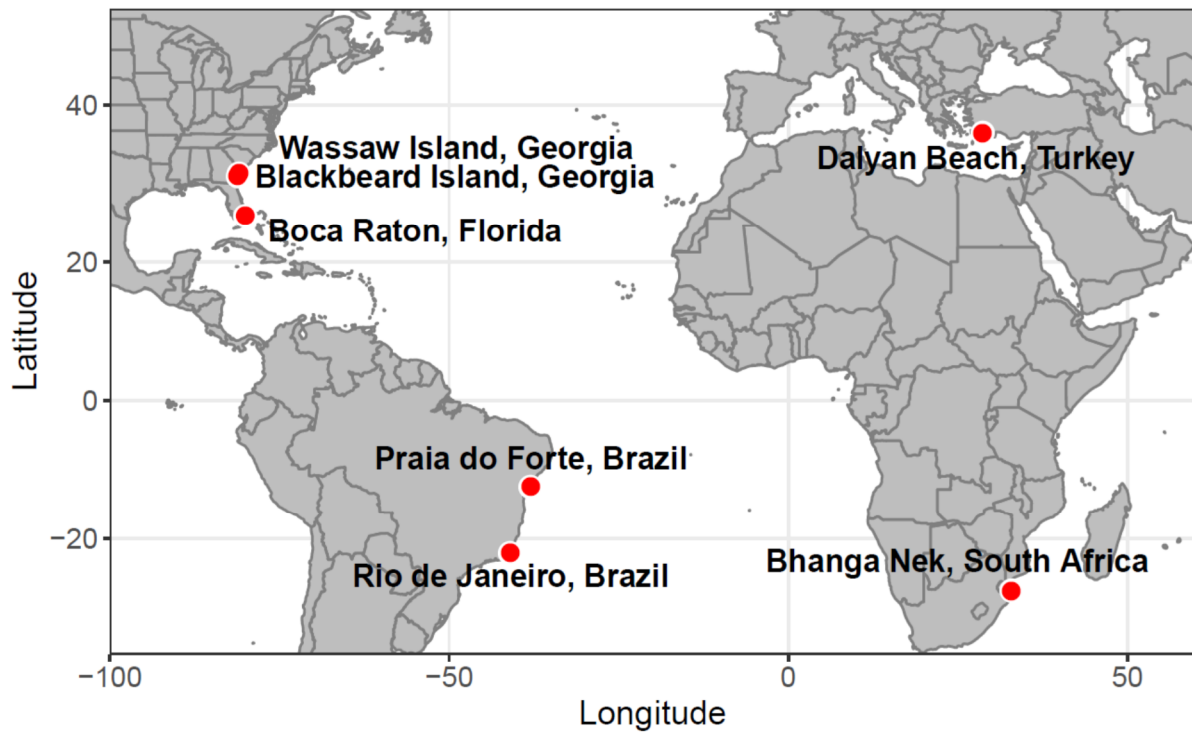
1092

Legend: Locations of the seven nesting sites studied (red dots) within four Regional Management Units (RMUs): Mediterranean (Dalyan Beach, Turkey), Northwest Atlantic (Boca Raton, Florida, USA, Wassaw Island and Blackbeard Island, Georgia, USA), Southwest Atlantic (Praia do Forte and Rio de Janeiro, Brazil) and Southwest Indian (Bhanga Nek, South Africa).

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Figure 2. Conceptual approach to calculating the climatic debt
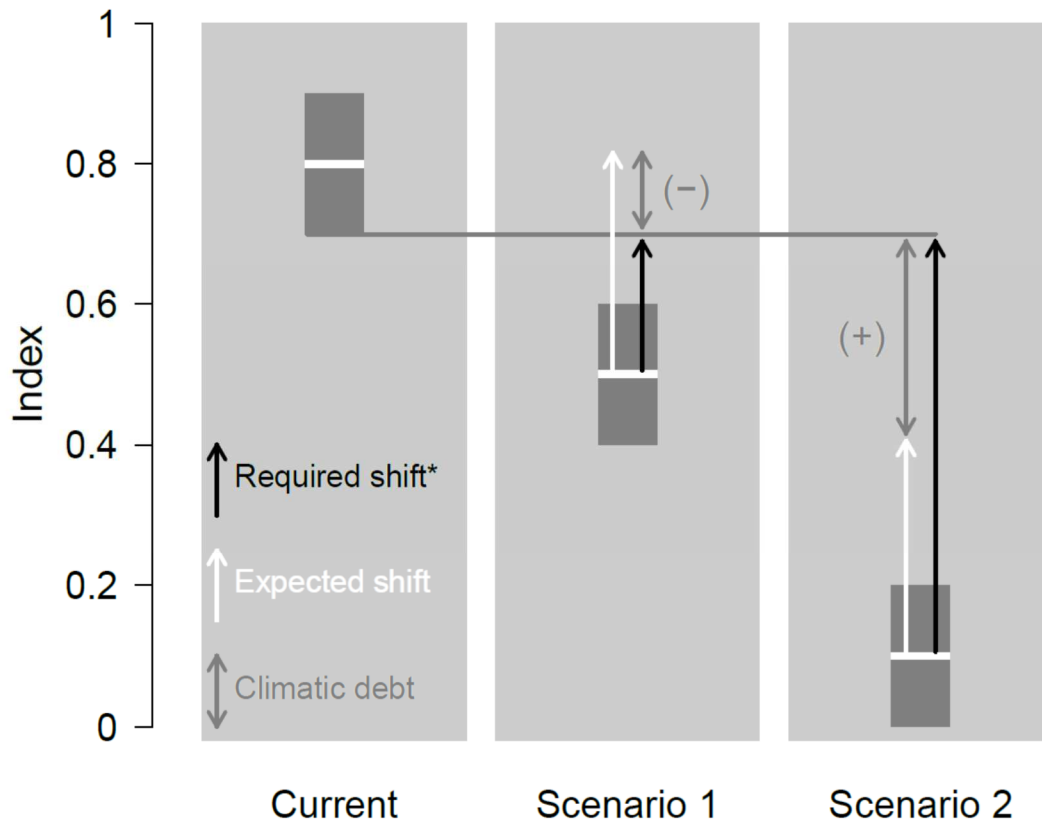
Legend: Grey bars represent the range of current and projected indices (quantiles at 25% and 75%) assuming no phenological shifts (under two warming scenarios) and white dashes represent quantiles at 50%. Black arrows represent the change in the index value required for the quantile at 50% of projected indices to reach the lower limit of current indices (*i.e., shift required to "pay" what we define as the climatic price). White arrows represent the change in the index value resulting from expected temperature-induced phenological shifts. Grey double-headed arrows represent the change in the index values according to the climatic scenario, after considering the expected phenological shift (i.e., the effect of what we define as the climatic debt). A negative climatic debt (-) is a situation where the expected phenological shift can effectively offset future climatic change, whereas a positive climatic debt (+) is the opposite situation.

1113 **Figure 3. Modeling Framework**
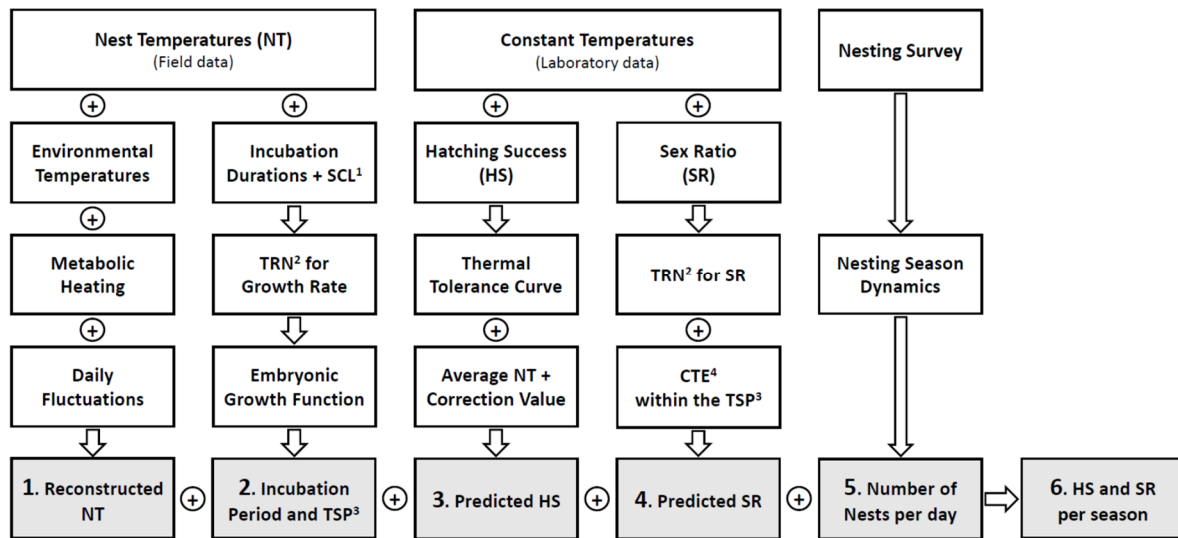
1114

1115 **Legend:** (**1**) Reconstructing nest temperature, (**2**) Modeling embryonic development, (**3**)

1116 Estimating hatching success, (**4**) Estimating sex ratio, (**5**) Unraveling the dynamics of nesting

1117 activity and (**6**) Calculating hatching success and sex ratio indices (see Methods).

1118 Abbreviations: [1]Straight Carapace Length (SCL) of hatchlings, [2]Thermal Reaction Norm

1119 (TRN), [3]ThermoSensitive Period (TSP) of development for sex determination and [4]Constant

1120 Temperature Equivalent (CTE). Plus marks (+) indicate data required to infer a model and

1121 arrows lead to a result.

1122

1123 **Figure 4. Nesting activity, hatching success and sex ratio**
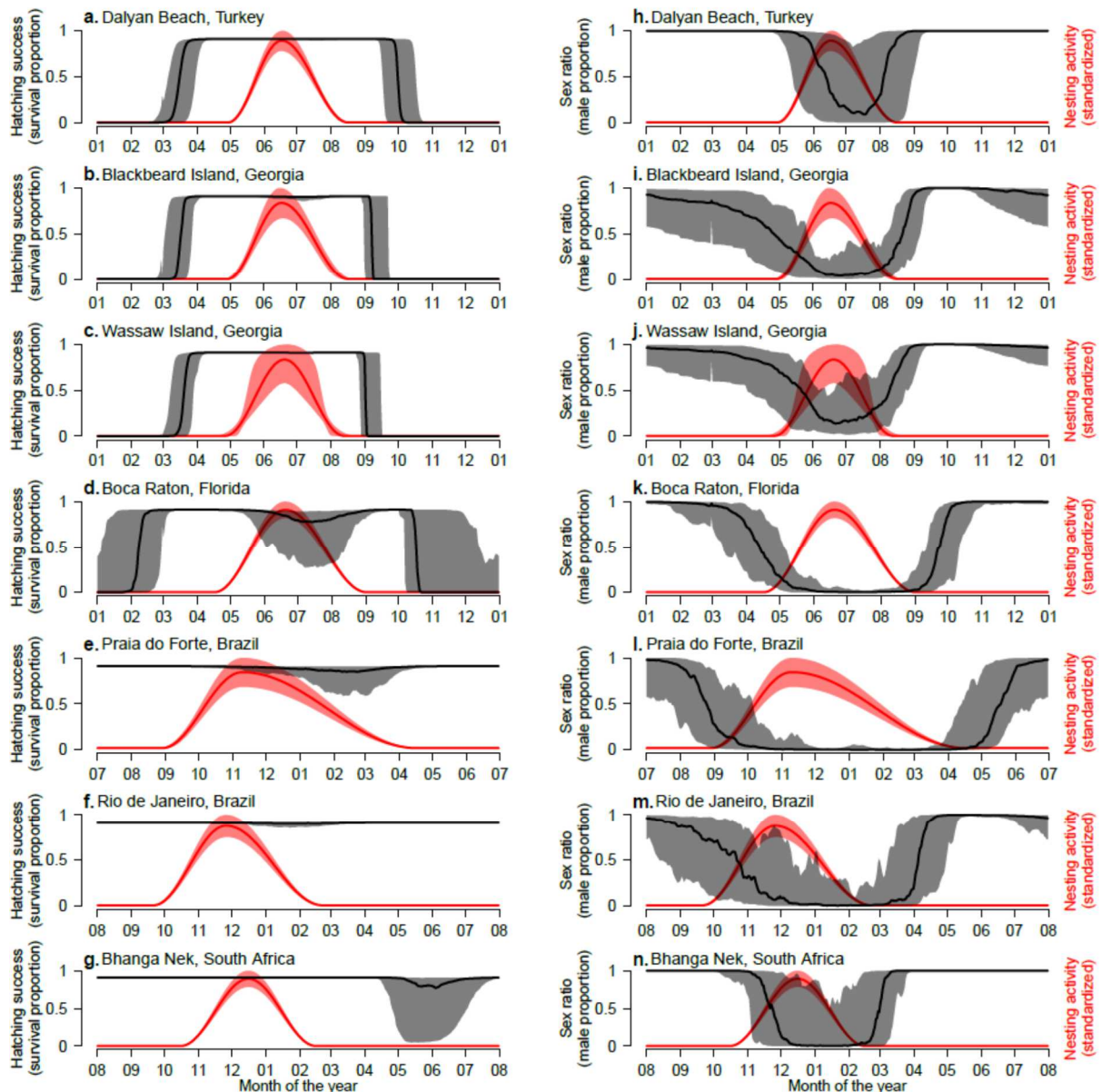
Legend: Current hatching success and sex ratio (quantiles at 50%, black lines) for any days

throughout the season with lower and upper quantiles (respectively, at 2.5% and 97.5%, grey

areas) are shown for populations nesting at Dalyan Beach, Turkey (respectively, **a** and **h**), at

Blackbeard Island, Georgia, USA (respectively, **b** and **l**), at Wassaw Island, Georgia, USA

(respectively, **c** and **j**), at Boca Raton, Florida, USA (respectively, **d** and **k**), at Praia do Forte,

Brazil (respectively, **e** and **l**), at Rio de Janeiro, Brazil (respectively, **f** and **m**) and at Bhanga

Nek, South Africa (respectively, **g** and **n**). Quantiles were calculated based on 1979-2016 time

series. Standardized nesting activity (number of nests laid throughout the season based on the

1133   global description of nesting activity) is indicated by red lines and the confidence interval at

1134   95% is indicated by red shaded areas. Note that the first month on the x-axis differs according

1135   to the nesting site.

1136

1137   **Figure 5. Warming temperatures may reduce hatching success and induce a**

1138   **feminization of hatchlings**
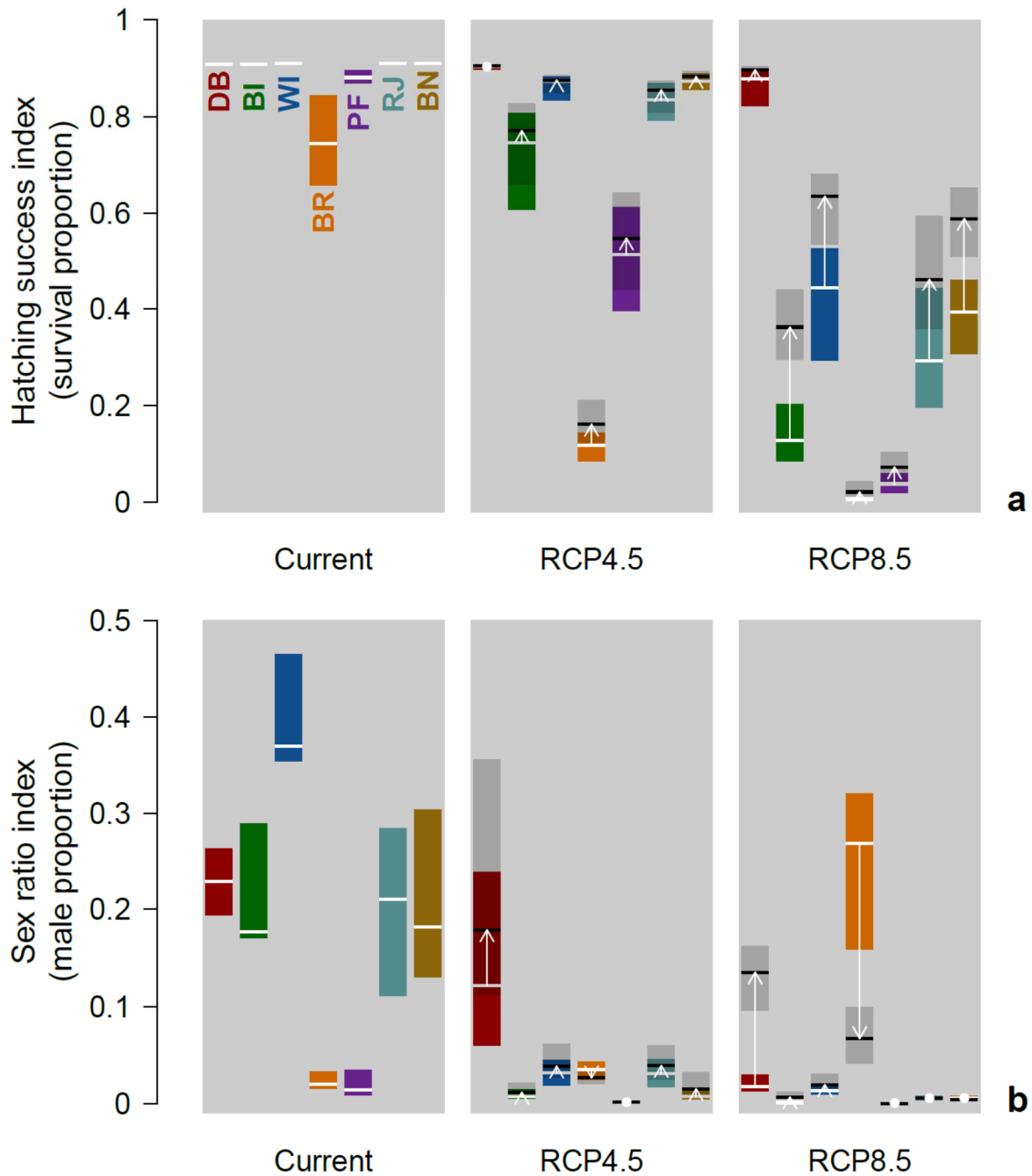
Legend: Current hatching success (**a**) and sex ratio (**b**) indices are shown (left panels) with projected ones (middle [RCP4.5] and right [RCP8.5] panels): (i) assuming no phenological shift (colored bars and white dashes) and (ii) considering expected phenological shifts (grey shaded bars and black dashes). Colored or grey shaded areas show lower and upper quantiles (respectively, at 25% and 75%), which give a measure of the interseasonal variability, and white or black dashes indicate quantiles at 50%. White arrows represent changes in the value

1146 of indices if expected phenological shifts are considered and white dots represent the situation

1147 where changes in the value of indices are <0.002. Current indices were calculated based on

1148 seasons when nests were surveyed (using the "season-specific description" of nesting activity,

1149 see Methods): n = 6 at Dalyan Beach (**DB**), n = 3 at Blackbeard Island (**BI**), n = 5 at Wassaw

1150 Island (**WI**), n = 16 at Boca Raton (**BR**), n = 26 at Praia do Forte (**PF**), n = 14 at Rio de

1151 Janeiro (**RJ**) and n = 32 at Bhanga Nek (**BN**). Projected indices (i.e., forecasts for the 2062-

1152 2100 period) were calculated under two scenarios for future Representative Concentration

1153 Pathways (RCPs) in greenhouse gas concentration (an optimistic scenario and a pessimistic

1154 scenario, respectively RCP4.5 and RCP8.5) and based on all future seasons (n = 38) using the

1155 "global description" of nesting activity (see Methods).

1156

1157 **TABLES**

1158 **Table 1. Differences between required and expected phenological shifts (climatic debts)**

Nesting site	Index	RCP4.5 (number of days)	RCP8.5 (number of days)
Dalyan Beach, Turkey	HSI	*0* - 8.3 = **-8.3**	*21* - 20.2 = **0.8**
	SRI	*10* - 8.3 = **1.7**	*26* - 20.2 = **5.8**
Blackbeard Island, Georgia	HSI	*50* - 8.3 = **41.7**	*81* - 20.2 = **60.8**
	SRI	*53* - 8.3 = **44.7**	*67* - 20.2 = **46.8**
Wassaw Island, Georgia	HSI	*52* - 8.3 = **43.7**	*76* - 20.2 = **55.8**
	SRI	*58* - 8.3 = **49.7**	*74* - 20.2 = **53.8**
Boca Raton, Florida	HSI	*54* - 8.3 = **45.7**	*90* - 20.2 = **69.8**
	SRI	*	*
Praia do Forte, Brazil	HSI	*104* - 8.3 = **95.7**	none
	SRI	*79* - 8.3 = **70.7**	none
Rio de Janeiro, Brazil	HSI	*43* - 8.3 = **34.7**	*118* - 20.2 = **97.8**
	SRI	*37* - 8.3 = **28.7**	*112* - 20.2 = **91.8**
Bhanga Nek, South Africa	HSI	*27* - 8.3 = **18.7**	*81* - 20.2 = **60.8**
	SRI	*34* - 8.3 = **25.7**	*77* - 20.2 = **56.8**

1159 **Legend:** This Table shows the shifting of nesting phenology (in minimum number of days

1160 earlier) required for projected Hatching Success Indices (HSIs in survival proportion: white

1161 rows) and Sex Ratio Indices (SRIs in male proportion: grey rows) (quantiles at 50%) to

1162   remain within current ranges (i.e., beyond quantiles at 25% of current indices) under two

1163   scenarios of Representative Concentration Pathways (RCPs) of greenhouse gas concentration:

1164   an optimistic scenario (RCP4.5) and a pessimistic scenario (RCP8.5). Climatic scenarios

1165   reflect future temperature changes (2062-2100) as compared to current thermal conditions

1166   (1979-2016). Climatic debts (values in bold) are calculated by subtracting expected

1167   phenological shifts (8.3 and 20.2 days earlier, respectively for RCP4.5 and RCP8.5) from

1168   required ones (i.e., climatic prices: values in italics). Negative values indicate that

1169   phenological shifts can effectively offset future changes, positive values indicate the opposite

1170   situation, and "none" means that no climatic price was found. *Climatic debts were not

1171   calculated because projected SRIs lie within or above the range of current indices.

1172