Effects of temperature and demography on the phenology of loggerhead sea turtles in Brazil

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ABSTRACT: Climate change affects the spatial distribution and timing of seasonal events (i.e. phenology) of species. The phenology of ectotherms, such as sea turtles, is strongly influenced by rising temperatures associated with climate change, since most of their life history traits are dependent on temperature. Most studies on the phenology of sea turtles report changes in the duration and an earlier onset of the nesting season in response to warmer temperatures. However, inconsistencies remain among and within species in the direction and the strength of their responses. Some authors suggested that sea turtles' nesting phenology is triggered by a cue perceived before migration, whereas others suggested that environmental conditions at nesting sites are more important. Here, using nesting data collected over 26 nesting seasons, we tested whether the nesting phenology of loggerhead turtles *Caretta caretta* in Brazil is triggered by either temperature or demography, and if this occurs at nesting or foraging sites. We found that the onset of the nesting season was triggered by temperature at an important foraging site, while the duration of the nesting season was linked to the size of the nesting population. Our results suggest that loggerhead turtles respond to an environmental cue perceived at foraging sites before they start migrating. This finding will allow future research to assess the vulnerability of sea turtles in the context of climatic change by considering environmental conditions at foraging sites.

KEY WORDS: Climate change · Phenotypic plasticity · Migratory species · Ectotherm · Marine turtle · *Caretta caretta*

1. INTRODUCTION

Species may respond to a changing environment by shifting their spatial distribution or temporal occurrence, or by modifying their physiology (Bellard et al. 2012). Indeed, shifts in geographical range (e.g. towards either higher latitudes or — in the terrestrial case — upward in elevation) in response to warmer temperatures have already been observed in marine and terrestrial ecosystems (Walther et al. 2002, Parmesan & Yohe 2003, Root et al. 2003, Poloczanska et al. 2013). Changes in phenology may be driven by genetic adaptation (Bradshaw & Holzapfel 2006) or phenotypic plasticity (Charmantier et al. 2008, Chevin et al. 2010). If modifications to physiology or genetic adaptation are not possible, then phenological shifts are the only remaining responses. These changes may be adaptive when it allows species to align with periods of high resource availability or maladaptive when it creates a mismatch between the species' period of activity and the occurrence of its main resources (e.g. McCarty 2001, Walther et al. 2002, Visser & Both 2005, Walther 2010). Thus, the resilience of individuals is closely related to their ability to track environmental changes and adapt accordingly (Fuentes et al. 2013).

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The extent to which species are able to shift their phenology (genetically or phenotypically) and whether it allows for tracking suitable conditions in a changing environment (adaptive or maladaptive) is an urgent issue to address in the context of contemporary climatic change (Fuentes et al. 2013, IPCC 2014). The main trend currently observed in response to warmer temperatures is an earlier initiation of reproduction events in some species of birds, amphibians, reptiles and insects, and an earlier initiation of the growing season for some species of plants (albeit the opposite response has also been documented) (Walther et al. 2002, Parmesan & Yohe 2003, Root et al. 2003).

Ectothermic organisms, such as reptiles, amphibians, fishes and insects, are expected to be strongly affected by climate change (increases in ambient temperatures) since most of their life history traits are related to environmental temperatures (Deutsch et al. 2008, Huey et al. 2009, 2012, Angilletta et al. 2010, Sinervo et al. 2010). Species with short generation times, such as insects, may be able to cope with a rapid change in thermal regimes through genetic adaptation (microevolution) if populations have sufficient genetic variation (Bradshaw & Holzapfel 2006). Conversely, species with long generation times might struggle to keep pace with a similar rate of change solely by microevolution, even if their temperature-dependent traits are heritable (Nussey et al. 2007). For those long-lived organisms, and especially for reptiles with temperature-dependent sex determination (Bull & Bulmer 1989), phenotypic plasticity might be the best strategy to compensate for rapid, unpredictable changes in their thermal environments (Chevin et al. 2010, Huey et al. 2012, Refsnider & Janzen 2012). For oviparous species, such as sea turtles, embryo survival is closely related to temperature during incubation, and some species are probably already at the edge of their thermal limits (Deutsch et al. 2008, Doody & Moore 2010). Therefore, those species could be more vulnerable as temperatures rise (Mitchell & Janzen 2010, Fuentes et al. 2011, Hamann et al. 2013). Nevertheless, if environmental temperatures are spatially or temporally heterogeneous, those species may buffer the effect of warming temperatures through maternal behavioural plasticity such as nest-site choice and the timing of nesting (Doody et al. 2006, Schwarz & Janzen 2008, Refsnider & Janzen 2012).

Sea turtles are long-lived and late maturing ectotherms facing both direct anthropogenic threats (e.g. bycatch in fisheries, pollution and poaching) and climate change (e.g. sea level rise and rising tempera-

tures), with 6 out of the 7 species currently listed as Threatened (IUCN 2016). These species enter long migrations between specific foraging areas and their nesting sites, where they can lay several clutches during a single nesting season (Avise & Bowen 1994, Miller 1997). Earlier initiation of nesting and a reduction in the length of nesting seasons has been observed as a result of warmer temperatures for loggerhead turtles *Caretta caretta* nesting in Florida (Weishampel et al. 2004, Pike et al. 2006), whereas warmer temperatures were associated with longer nesting seasons in the Gulf of Mexico (Lamont & Fujisaki 2014), North Carolina (Hawkes et al. 2007), and the Mediterranean (Mazaris et al. 2013). The variability in the relationship among populations between nesting season duration and temperature suggests a complex, site-specific interplay between biotic and abiotic factors. This could also reflect the diversity of methods used among studies.

In general, 3 hypotheses have been previously formulated to explain this variability in the timing of nesting seasons: (1) foraging site hypothesis (FSH): sea turtles start migration in response to environmental cues perceived at their foraging sites and nest soon after they arrive at their nesting site (Mazaris et al. 2009); (2) nesting site hypothesis (NSH): sea turtles arrive early at the nesting site and start laying eggs in response to an environmental cue perceived at the nesting site (Pike 2009); and (3) demography hypothesis (DH): nesting phenology is affected by the number of nesting individuals (as was found to be the case for a population of the leatherback sea turtle *Dermochelys coriacea* nesting in Costa Rica; Robinson et al. 2014). We tested each of these 3 hypotheses with a population of loggerhead turtles nesting at Praia do Forte, Brazil, where we explored whether the (1) onset and (2) duration of the nesting season for this population is triggered by sea surface temperature (SST) offshore of the nesting site or at foraging sites and whether population demography (using the number of nests as a proxy for population size) better explained these 2 phenological parameters.

2. MATERIALS AND METHODS

2.1. Nesting data

Loggerhead turtle nesting data were obtained from Praia do Forte in the state of Bahia, Brazil (Fig. 1). This area hosts the most important loggerhead nesting population in Brazil (Marcovaldi & Laurent 1996, Marcovaldi et al. 2016). Nesting occurs from Septem-
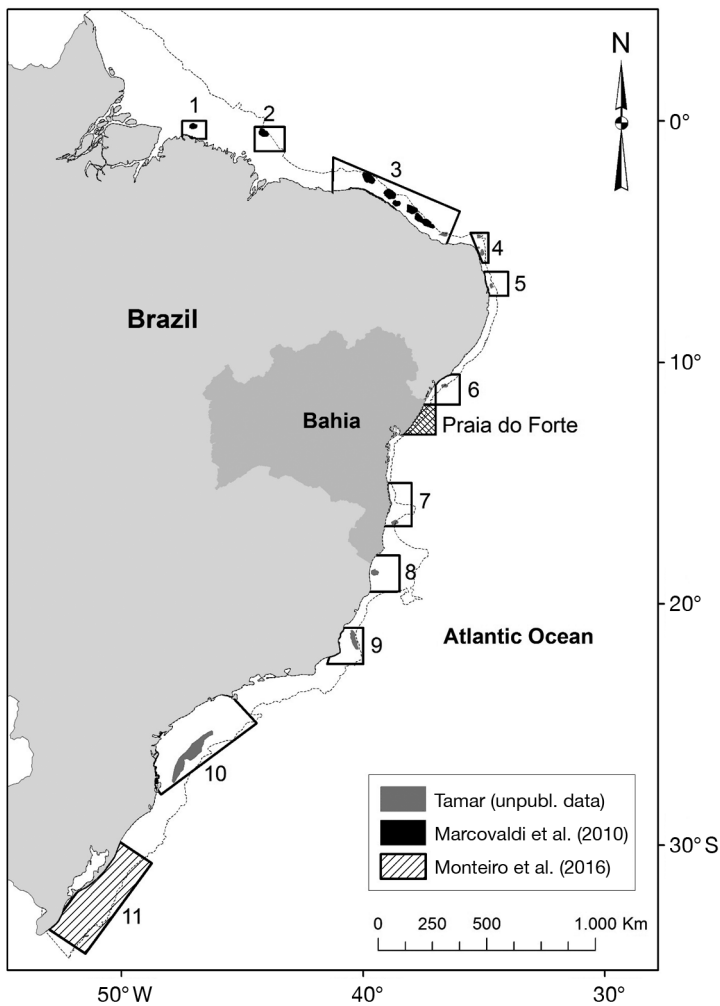
Fig. 1. Nesting and foraging sites of loggerhead turtles. Black polygons: potential foraging sites (numbered from 1–11); crossed-hatched area: area offshore of the nesting site (Praia do Forte, Bahia). Sea surface temperature time series data were extracted within these areas

ber–March, with a peak in November and December (Marcovaldi & Chaloupka 2007, Lima et al. 2012, Marcovaldi et al. 2016). Nests were monitored and counted during the 1989/1990–2014/2015 nesting seasons (26 seasons) by staff of the National Marine Turtle Conservation Program in Brazil (Projeto TAMAR; for more information about TAMAR see Marcovaldi & dei Marcovaldi 1999). Monitoring patrols were conducted daily from 1 September–31 March between 1989 and 2000 and from 1 September–30 April after 2000. Nests that were encountered outside these monitoring periods were also included in the data set.

2.2. Foraging sites

We identified 11 foraging sites used by loggerhead turtles nesting in the northern coast of Brazil (Fig. 1). Sites 1–10 were identified from 23 nesting females satellite-tracked in 2006 and during the 2013–2015 nesting seasons at Praia do Forte by TAMAR (Marcovaldi et al. 2010) (Fig. 1, information summarized in Table 1). Three of the tags stopped transmitting during their post-nesting migration and thus were not included in this study. The 50% kernel-estimated home range utilization distributions (following the method of Marcovaldi et al. 2010) of these turtles during their post-nesting movements were used to define potential foraging sites (Fig. 1). Site 11 was identified by a recent

Table 1. Data used to identify potential foraging areas for loggerhead turtles *Caretta caretta* nesting at Praia do Forte, Brazil

Foraging site no.	No. of turtles	Coasts	Method of identification	Source
1	1	Pará	Satellite tags:	Marcovaldi et al. (2010)
2	1	Maranhão	KiwiSat 101	
3	8	Ceará	(Sirtrack)	
3	1	Rio Grande do Norte (West)	Satellite tags:	This study
4	3	Rio Grande do Norte (East)	Spot/Splash Argos Tags	
5	1	Pernambuco	(Wildlife Computers)	
6	1	Sergipe		
7	1	Bahia		
8	1	Esperito Santo (North)		
9	1	Esperito Santo (South), Rio de Janeiro (North)		
10	1	São Paulo, Paraná, Santa Catarina		
11	NA	Rio Grande do Sul	Mark–recapture	Monteiro et al. (2016)

study on sea turtles strandings off the coast of Rio Grande do Sul (Monteiro et al. 2016) (Fig. 1).

2.3. SST data

We extracted SST (°C) at potential foraging sites and offshore of the nesting site (within the areas defined in Fig. 1). SST time series (each 6 h) were retrieved from the ERA-Interim project in the European Centre for Medium-range Weather Forecasts website (http://apps.ecmwf.int/datasets/data/interim-full-daily/levtype=sfc/), which provides a global reanalysis of climate temperature on earth at a 0.75° spatial resolution from 1 January 1979 to the present (Dee et al. 2011).

2.4. Unravelling the dynamics of nesting seasons

We estimated dates for the onset and duration of the nesting seasons following the method developed by Girondot (2017). A set of equations was used to describe the dynamics of the nesting season based on time series of nest counts. These equations were implemented in the R package 'phenology' (Girondot 2018) and used the parameters of a nonlinear function with 6 parameters fitted using maximum likelihood with negative-binomial distribution against daily nest counts. The model was built to allow the parameters to have direct biological interpretation: a minimum number of nests (Min) when turtles are not active, a maximum number of nests (Max) on the ordinal day when the peak of activity occurs (Peak), the length of the season before the peak (LengthB), the length of the season after the peak (LengthE) and the negative-binomial parameter that describes the dispersion around the mean (Theta). For a complete description of equations, see Girondot (2017). We tested for trends in the (1) onset and (2) duration of nesting seasons and (3) number of nests season^{-1} over the years using linear regressions (*F*-test), and we tested for correlations between (1) the duration of nesting seasons and (2) the onset, peak and end of nesting seasons using Pearson's product-moment correlation method.

2.5. Seeking the drivers of phenological changes

The dates for the onset of each nesting season were converted to number of days after 1 January (ordinal days) of the year the nesting season started. Duration was calculated as the number of days between the onset and end of the nesting season pattern inferred by the model described above.

The onset of the nesting season may relate to temperatures at the foraging sites (i.e. FSH) or offshore of the nesting site (NSH) (Mazaris et al. 2009). To test the FSH, we calculated the average SST at foraging sites during all periods (chosen here as 8, 16, 24 and 32 d) and for all lags (from 8 to 232 d for each 8 d period, respectively) before the onset of each nesting season. We chose to split periods this way to have both an appropriate temporal resolution (from weeks to months) and an appropriate computing speed. This resulted in 682 predictive variables. Given the high number of potential relationships, we used a machine learning algorithm, the random forest algorithm (Ho 1995, 1998), implemented in the R package 'VSURF' (Genuer et al. 2018). Random forest is a classification algorithm that performs well in discriminating among predictive variables when the number of variables is much larger than the number of observations, and gives measures of variable importance (Ho 1995, 1998). This method involves stochastic discrimination, so we ran the algorithm 100 times and counted the number of times each variable was selected. We retained only predictive variables that were selected in all 100 replicates. The resulting sets of variables were incorporated into a generalized linear model with a Gaussian link function; we applied a model selection method based on the lowest value of Akaike's information criteria corrected for finite sample size (AIC$_c$), and used the Akaike weight, which indicates relative support for each model (Akaike 1974, Burnham & Anderson 2002). To test the NSH, we calculated the average SST at the nesting site during all periods and for all lags before the onset of the nesting seasons. This resulted in 62 predictive variables. We performed the same procedure as described above to discriminate among variables.

We applied the same approach to determine the duration of the nesting season. However, nesting season duration may also relate to SSTs experienced by turtles at the nesting site while they are laying eggs, i.e. roughly from September–March (an alternative way to test the NSH). To test this hypothesis, we built a generalized linear model with a Gaussian link function using SSTs averaged during the whole nesting season.

The dynamics of the nesting season could also be related to the size of the nesting population (Robinson et al. 2014). To test whether the onset and duration of nesting seasons were dependent on the number of individuals nesting each year (i.e. DH), we built a generalized linear model with a Gaussian link function with the number of nests season^{-1} (used as a

proxy for nesting population size) as a predictive variable. We first compared the model built according to the DH to the null model and kept the one with the lowest AIC_c as the model of reference (which is then incorporated into further models). Thereafter, we compared all models based on their AIC_c values, and considered models with $\Delta AIC_c < 2$ as competing models. As a measure of the goodness-of-fit of selected models, we calculated the R^2 coefficient of determination, which gives a measure of the fraction of variance explained by the model.

2.6. Detecting false positives

The detection method may lead to erroneous interpretations if selected variables are false positives. We conducted the same procedure as described above but using random numbers from a standard normal distribution set in place of all SSTs to test whether we might have detected false positives and, if so, whether they would compete with models selected based on actual data. We ran this procedure 20 times to obtain the distribution of AIC_c values for selected models from virtual data. We considered a model selected based on actual data as being a false positive if its AIC_c was higher than the 5% quantile of the AIC_c distribution of models selected from virtual data. All statistical tests and models were performed using R v.3.5.3 (R Core Team 2019).

3. RESULTS

3.1. Long-term phenological changes

An overview model for the dynamics of loggerhead turtle nesting seasons is shown for the 2008–2015 period (Fig. 2). Nesting season onset occurred slightly earlier over 26 yr (between 1989 and 2015) at a rate of 0.22 d yr^{-1} on average, albeit not significantly ($F_{1,24} = 0.67$, p = 0.42, n = 26 seasons; Fig. 3a). The duration of the nesting season was significantly extended at a rate of 3.11 d yr^{-1} ($F_{1,24} = 44.88$, p < 0.001, n = 26 seasons; Fig. 3b). The duration of the nesting sea-

son was negatively correlated with the onset of the nesting season (Pearson's coefficient of correlation = −0.39, $t = -2.09$, df = 24, p = 0.047) and positively correlated with the peak of nesting (Pearson's coefficient of correlation = 0.49, $t = 2.74$, df = 24, p = 0.011) and the end of the nesting season (Pearson's coefficient of correlation = 0.94, $t = 13.18$, df = 24, p < 0.001). The number of nests season^{-1}, previously log-transformed to stabilize the variance of residuals, increased between 1989 and 2015 ($F_{1,24} = 382.4$, p < 0.001, n = 26 seasons; Fig. 4).
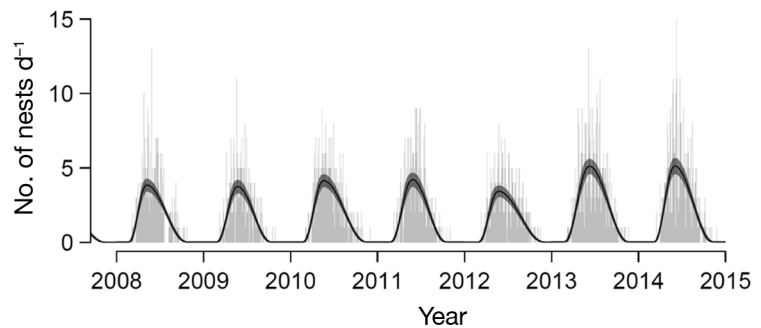

Fig. 2. Dynamics of loggerhead turtle nesting seasons. Black curve: modelled number of nests d^{-1}; dark grey band: 95% CI based on nest counts (light grey vertical lines) shown for the 2008–2015 period
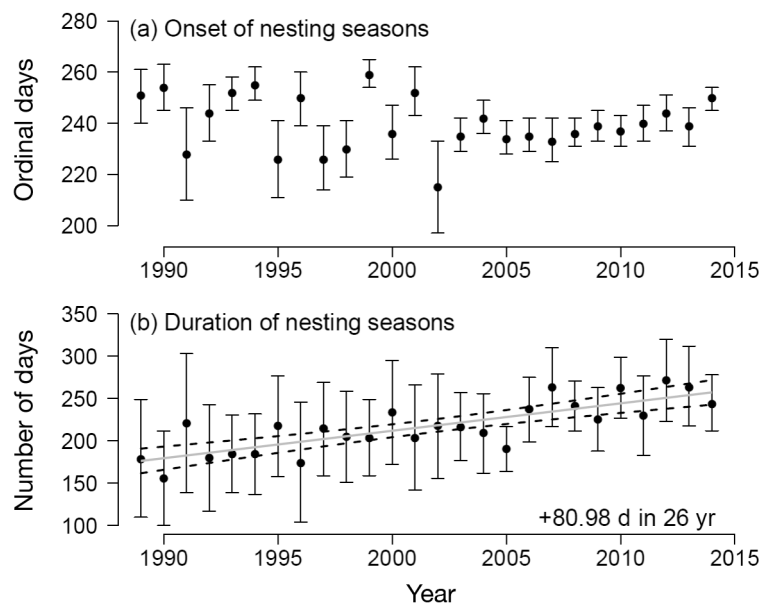

Fig. 3. Mean (±95% CI) (a) onset and (b) duration of loggerhead turtle nesting over time. Grey line in (b): linear regression according to season; black dashed lines: 95% CI. Note that the linear regression for the onset of the nesting season was not significant
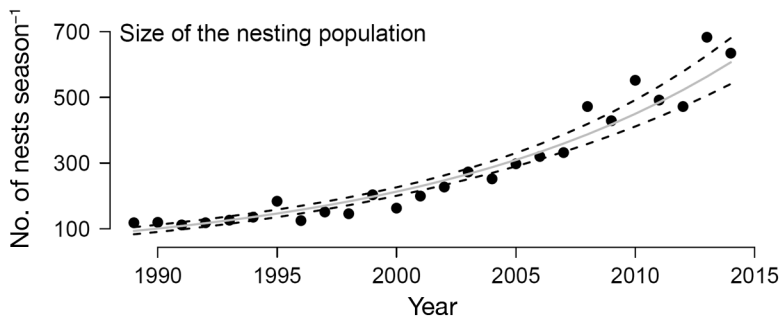
Fig. 4. Long-term trend in the size of the loggerhead turtle nesting population. Black points: number of nests season^{-1}; grey curve: log-transformed linear regression according to season; black dashed lines: 95% CI. Note that the number of nests per season was previously log-transformed before the linear regression

3.2. Onset of the nesting season

The model built according to the DH did not differ from the simplest model (Table 2). SSTs 120–136 d before the onset of the nesting season (approximately in April and May) at potential foraging Site 11 best explained variations in the onset of the nesting season (AIC$_c$ = 176.32; Akaike weight = 0.95; Table 2). According to this model, the onset of the nesting season

shifted 7.1 d in response to a 1°C increase in SSTs (Fig. 5a). The selected model outperformed any other (Table 2) and appropriately predicted the onset of the nesting season (Fig. A1a in the Appendix). This model explained >50% of the variance of observations (R^2 = 0.64).

3.3. Duration of the nesting season

The model built according to the DH outperformed the simplest model (AIC$_c$ = 231.68; Akaike weight = 0.99). According to this model, the duration of the nesting season extended as the number of nests season^{-1} increased (Fig. 5b). SSTs 80–88 d before the onset of the nesting season (approximately in June) at potential foraging Site 1 improved predictions of the duration of the nesting season (AIC$_c$ = 226.49; Akaike weight = 0.56; Table 2). The selected model outperformed any other (Table 2) and appropriately predicted the duration of the nesting season (Fig. A1b). This model explained >50% of the variance of observations (R^2 = 0.73).

Table 2. Models used to determine the onset and duration of loggerhead turtle nesting seasons using actual sea surface temperature (SST) data and demography (i.e. the size of the nesting population in number of nests). Models were selected based on Akaike's information criterion corrected for finite sample size (AIC$_c$). Numbers next to SST indicate the identity of the foraging site where the cue was detected; the period within which variables were averaged (in number of days before the onset of the nesting season) is indicated in square brackets. Selected models are indicated in **bold**

| Phenological parameter	Hypothesis	Model	AIC$_c$	ΔAIC$_c$	Akaike weight
Onset of the season	**Null**		**200.57**	**0**	**0.740**
	Demography	Log(No. of nests)	202.66	2.095	0.259
	Null			24.25	<0.001
	+ Foraging sites	SST2[80–88]	191.06	14.74	<0.001
		SST4[56–72]	183.94	7.62	0.021
		SST4[64–72]	184.22	7.90	0.018
		SST5[64–72]	186.45	10.13	0.005
		SST8[176–200]	197.91	21.59	<0.001
		SST11[120–136]	**176.32**	**0**	**0.950**
	+ Nesting site	SST[112–120]	187.76	11.44	0.003
		SST[120–128]	197.18	20.86	<0.001
Duration of the season	Null		255.33	23.650	<0.001
	Demography	**Log(No. of nests)**	**231.68**	**0**	**0.999**
	Demography			5.19	0.041
	+ Foraging sites	**SST1[80–88]**	**226.49**	**0**	**0.561**
		SST9[232–240]	230.76	4.27	0.066
		SST9[232–264]	232.26	5.77	0.031
		SST11[24–32]	229.63	3.14	0.116
		SST11[24–40]	231.18	4.68	0.053
	+ Nesting site	SST[104–120]	231.89	5.40	0.037
		SST[112–120]	230.54	4.05	0.074
		SST[Within the season]	233.62	7.12	0.015
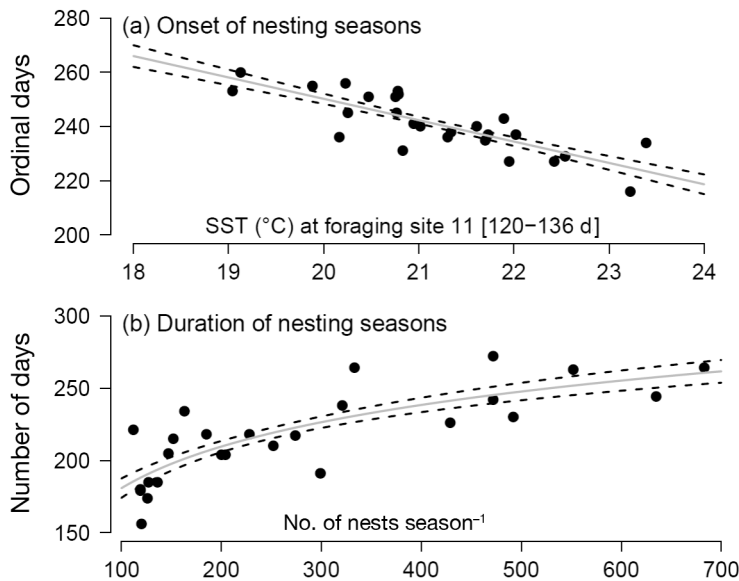
Fig. 5. Phenological responses of loggerhead turtles to sea surface temperature (SST) and demography. (a) The onset of the nesting season is linked to average SSTs at foraging Site 11 120–136 d before the onset of the nesting season; (b) the duration of the nesting season is linked to the number of nests season^{-1}. Note that the number of nests season^{-1} was previously log-transformed before the linear regression. Grey lines: fit of respective models; black dashed lines: 95% CI

3.4. Detection of false positives

The AIC$_c$ values of models selected based on actual data were lower than the 5% quantiles of the AIC$_c$ values of the models selected based on virtual data (Fig. A2). This allowed us to dismiss potential false positives in the models that were selected based on actual data.

4. DISCUSSION

The FSH best described the onset of the nesting season for loggerhead turtles *Caretta caretta* nesting at Praia do Forte, Brazil—whereby females start migrating to nesting areas in response to temperature (either directly or mediated by food availability) at foraging sites and begin to nest soon after arriving at the nesting site (Mazaris et al. 2009). It is thought that sea turtles will start migrating towards their nesting site as soon as they have accumulated enough body fat and resources for reproduction (Kwan 1994). Therefore, nesting earlier because of warmer temperatures at foraging sites could be explained by an acceleration of the loggerheads' metabolism that could speed up prey capture, hence advancing the timing of when females have stored

sufficient reserves for departure to their nesting site. Alternatively, prey abundance at foraging sites may be linked to climatic conditions (Broderick et al. 2001); warmer years could be associated with either better foraging conditions or an earlier occurrence of prey, which would also advance females' departure to nesting areas. Our finding contrasts with the NSH—where sea turtles arrive early at the nesting site and wait for optimal conditions to nest (e.g. suitable temperature and moisture conditions for incubation of eggs; Pike 2009). To confirm this finding, additional research is required in which turtles should be equipped with satellite tags that would continue transmitting for at least 2 nesting seasons, which is still challenging because loggerheads' remigration intervals range from 1–16 yr (Phillips et al. 2014).

Our model enabled us to detect a temperature signal at a potentially important foraging area for loggerheads in Brazil, as suspected by Monteiro et al. (2016), and which warrants further attention for conservation purposes. This suggests that turtles from this particular foraging area drive variations in the onset of the nesting season, and thus should be the first females arriving at the nesting site. However, we do not know the relative contribution (in terms of number of turtles) of this foraging aggregation (or of the others) to the number of nesting females coming to Praia do Forte each year. This information can be obtained by increasing the number of turtles equipped with satellite tags, and by combining satellite telemetry with stable isotope analysis to identify the contribution of turtles from other foraging areas to the nesting population (Ceriani et al. 2017).

Sea turtles' ability to shift their nesting phenology, and nest earlier, could be an effective strategy as a response to changes in temperature (Almpanidou et al. 2018). Indeed, earlier nesting may allow turtles to stay synchronized with cooler temperatures at nesting grounds, which could be more suitable for embryonic development and hatchling production than extremely warm temperatures (Doody et al. 2006, Almpanidou et al. 2018). Here, we found that the onset of the nesting season shifted 7.1 d earlier in response to a 1°C increase in SST. Given that near-surface temperatures in northeastern Brazil may reach +4°C in 2100 compared to present-day temperatures according to an extreme climate change scenario (IPCC 2014), the onset of the nesting season

would be shifted 28.4 d earlier for the population nesting at Praia do Forte. Further research is needed to determine whether such phenological adjustment will allow this nesting population to track suitable thermal conditions for egg incubation. This can be achieved by predicting current and future hatching success and hatchling sex ratios under different climatic scenarios, and considering temperature-induced phenological changes.

Earlier nesting as a response to warmer temperatures at foraging areas has been observed across several populations of loggerhead turtles nesting in Florida (Weishampel et al. 2004, 2010, Pike et al. 2006, Pike 2009), North Carolina (Hawkes et al. 2007), the Gulf of Mexico (Lamont & Fujisaki 2014) and the Mediterranean (Mazaris et al. 2008, 2009, Patel et al. 2016). This suggests that loggerhead populations in different areas respond similarly to temperature changes. However, the situation appears to be more complex for other sea turtle species, as previous studies have reported contrasting phenological responses between 2 populations. For example, green turtles *Chelonia mydas* were found to nest earlier in response to warmer temperatures along Florida's east coast (Weishampel et al. 2010) whereas the opposite response was reported in the southwestern Indian Ocean (Dalleau et al. 2012). However, no relationship between green turtle nesting phenology and environmental temperatures was found at Canaveral National Seashore in central Florida (Pike 2009). Leatherback sea turtles tend to nest later in response to warmer temperatures, but the strength of this response has been found to differ among populations (Robinson et al. 2014, Neeman et al. 2015). Our results for loggerheads are in line with previous studies, but it remains unclear whether the within-species differences of other sea turtles are due to site-specific environmental conditions, population-specific breeding behaviours, differences in study methodologies or false positives. We urge further studies to follow the standardized approach developed in the present study to allow proper comparisons among other sea turtle populations.

Changes in nesting phenology may affect the duration of the nesting season across species and populations. For loggerheads, earlier onset of the nesting season has been associated with a shortened nesting duration on Florida's east coast (Pike et al. 2006, Weishampel et al. 2010), whereas the opposite pattern was found in North Carolina (Hawkes et al. 2007) and the Gulf of Mexico (Lamont & Fujisaki 2014). For loggerheads nesting at Praia do Forte, we found a different pattern — an extension of the length of the nesting season associated with earlier onset and a delay in the peak and end of the nesting season. The variations in nesting season duration were explained by both the DH and FSH, which suggests a more complex interplay between the size of the nesting population and temperatures experienced by some females before they start migrating. This could be explained by 3 factors: (1) the loggerhead nesting population at Praia do Forte is currently recovering as a result of conservation efforts (Casale & Marcovaldi 2015); indeed, the number of nests per season in Praia do Forte has increased from 100 to roughly 700 nests in the last 26 yr (Fig. 4). Given the rate of increase in nest numbers, an extension of the nesting season is more likely due to an increase in the number of nesting females rather than an increase in the number of nests female[−1] (Esteban et al. 2017); (2) higher variability in females' arrival at the nesting site and (3) the co-occurrence of experienced breeders (that would arrive earlier) and neophyte breeders (that would arrive later) (Lamont & Fujisaki 2014, Robinson et al. 2014).

In most studies, the first nest observed is typically used as an indication of the onset of the nesting season; the duration of the nesting season is calculated as the period between the first and last nests (Pike et al. 2006, Hawkes et al. 2007, Mazaris et al. 2008, 2009, Pike 2009, Lamont & Fujisaki 2014, Patel et al. 2016). However, these metrics are not robust statistics because the first and last nests may be outliers and may not reflect the actual initiation of nesting or the duration of the overall season. Here, we used a model of the dynamics of the nesting season, which allows consideration of a biologically relevant description of sea turtles' nesting activity. We also tested if the results we found were false positives. This allowed us to avoid erroneous interpretations, and we urge other researchers to use the same methods — especially when using a large data set of meteorological data to detect a response of phenological changes.

Females' migration can also be constrained by other factors (e.g. salinity, bathymetry, precipitation, currents or resource availability) (Neeman et al. 2015). Further studies are needed to broaden our understanding of what triggers the females' departure from foraging sites and how climate influences their migration and breeding behaviour. The phenology of some migratory birds seems to be driven by photoperiodicity, and may provide an adaptive response to climatic changes (Coppack et al. 2003, Bradshaw & Holzapfel 2008, Visser et al. 2010). To our knowledge, this type of response has never been

investigated in sea turtles, and thus provides an interesting avenue for future research. For instance, can sea turtles genetically adapt to respond to shorter or longer day-length cues? Do temperatures in combination with changes in photoperiod influence the nesting phenology of sea turtles? Either way, phenological changes will most likely influence hatchling output, by modifying hatching success and sex ratio (Santidrian Tomillo et al. 2012, 2015) as well as hatchling dispersal in different ocean currents (Mansfield et al. 2017), which may either enhance or jeopardize the resilience of sea turtle populations. Our results emphasize the need to use a standardized approach to detect and disentangle the effects of biological and environmental parameters on sea turtle nesting phenology so we can properly understand and anticipate their capacity to adapt to the current rate of climatic changes.

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Appendix. Additional figures showing the goodness-of-fit and detection of false positives
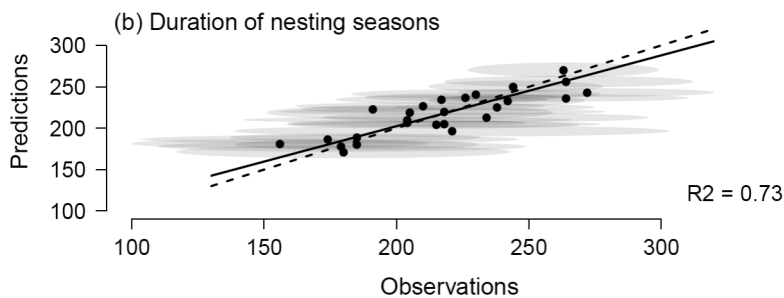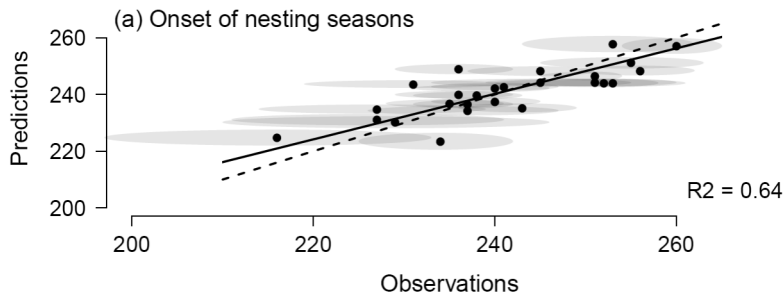

Fig. A1. Goodness-of-fit of predictions for loggerhead turtle nesting phenology. Black points: predicted and observed (a) onset and (b) duration of the nesting seasons. Black dashed lines: lines of equality; black solid lines: orthogonal regression lines. Grey shaded ellipses: 95% confidence intervals for both observations and predictions. R^2 coefficients of determination are shown
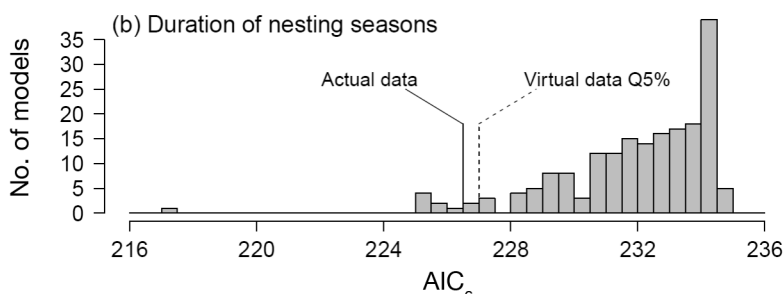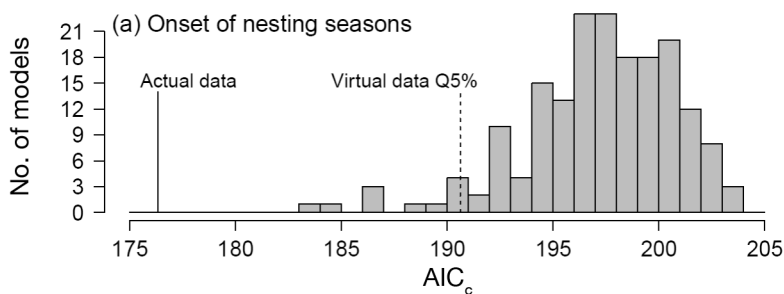

Fig. A2. Detection of false positives: distribution of Akaike's information criterion corrected for finite sample size (AIC_c) values of models selected based on virtual data for both the (a) onset and (b) duration of loggerhead turtle nesting seasons. Black segments: AIC_c of models selected based on actual data (see Table 2); black dashed segments: 5% quantiles (Q5%) of the distribution of AIC_c values of models selected based on virtual data