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Mass-nesting events in olive ridley sea turtles: environmental predictors of timing and size

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During the mass nesting of olive ridley sea turtles, *Lepidochelys olivacea*, thousands of adult females aggregate offshore, then emerge from the ocean together to lay their eggs along small, specific stretches of coastline. Little is known about the mechanisms that underlie synchronization of mass nesting. As a first step towards identifying environmental variables that control or affect the timing of mass-nesting events, we analysed 10 years of nesting data from Ostional, Costa Rica, a Pacific beach where mass-nesting events occur throughout the year. The onset of mass nesting was not uniformly distributed across lunar phase, with mass nesting occurring predominantly near last-quarter moon. Statistical models were developed to investigate whether environmental variables could be used to predict the timing and size of mass-nesting events. Predictions of the onset of nesting were improved by considering lunar phase and the time since the previous mass-nesting event as well as several oceanographic variables. Predictions of the number of turtles participating in nesting events were improved by considering salinity, relative humidity and nearshore current velocity, three parameters related to weather patterns and rainfall. Overall, the results imply that mass-nesting events at Ostional tend to occur near last-quarter moon but do not follow an invariant lunar or seasonal pattern. Instead, the results suggest that physiological and environmental factors interact to influence mass-nesting events, with no single environmental variable serving as an infallible predictor of either timing or size.
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Synchronized reproduction, in which numerous members of a species spawn, mate, lay eggs or give birth simultaneously, is common among diverse animals (Henson, Hayward, Cushing, & Galusha, 2010; Martin, Bailey, Moravek, & Carlson, 2011; Skov et al., 2005). One of the most spectacular examples is the mass-nesting behaviour of olive ridley sea turtles, *Lepidochelys olivacea* E., in which thousands of adult females migrate to specific coastal areas, aggregate offshore, and then emerge from the ocean simultaneously to lay eggs. Mass-nesting events, also known as 'arribadas' (the Spanish word for arrivals), typically last several days and, in some geographical areas, occur intermittently throughout the year (Bernardo & Plotkin, 2007; Coria-Monter; Durán-Campos, 2017; Shanker, Pandav, & Choudhury, 2003; Valverde, Cornelius, & Mo, 1998; Valverde et al., 2012). The brief time during which each nesting event occurs, along with the small geographical scale and extraordinary number of turtles involved, make this behaviour both remarkable and enigmatic.

The simultaneous emergence of numerous turtles from the ocean implies the existence of mechanisms that synchronize the timing of nesting or otherwise enable turtles to coordinate their

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behaviour (Bernardo & Plotkin, 2007). Little is known, however, about how such synchronization occurs. In principle, precisely timed reproduction can occur in several different ways. In some organisms, the timing of reproduction is mediated by lunar phase or tidal cycles (Fukushiro et al., 2011; Skov et al., 2005; Takemura, Sri Susilo, & SaydurMorita, 2004). In others, timing is strongly influenced by factors such as season, temperature and rainfall, which can result in a physiological state conducive for reproduction (Hirschfeld & Rödel, 2011; Salminen & Hoikkala, 2013; Sen Majumder & Bhadra, 2015; Wikelski, Hau, & Wingfield, 2000). Biological rhythms, pheromones, visual cues and social facilitation can also play a role in coordinating behaviour (Gerlach, 2006; Kumar et al., 2010; Koizumi & Shimatani, 2016; Schiml, Mendoza, Saltzman, Lyons, & Mason, 1996). These various mechanisms are not mutually exclusive, inasmuch as reproductive synchrony often involves multiple environmental and physiological factors (English, Chauvenet, Safi, & Pettorelli, 2012; Mduma, Sinclair, & Turkington, 2007; Mohring, Wernberg, Kendrick, & Rule, 2013). Indeed, mass nesting in olive ridleys is likely an adaptive phenotype expressed conditionally under specific environmental circumstances (Bernardo & Plotkin, 2007), inasmuch as olive ridleys engage in both solitary and mass-nesting strategies (Eckrich & Owens, 1995; Hirth, 1980; Kalb, 1999; Pritchard, 1969).

Because of the abrupt timing and large number of turtles participating in mass-nesting events, the management of conservation efforts during these events is particularly complicated. As a first step towards investigating the mechanisms that underlie synchronized nesting behaviour in sea turtles, we analysed 10 years of available data on the timing and size of olive ridley turtle mass-nesting events at Ostional, Costa Rica, a Pacific beach where mass-nesting events occur throughout the year. A statistical model-averaging approach was used to determine whether environmental variables, including lunar phase, improved predictions of the timing of arribadas and the number of turtles that participate. Contrary to anecdotal reports in some previous studies (e.g. Carr, 1967; Pritchard, 1969), our findings suggest that the onset of synchronized nesting in olive ridleys is not invariably triggered by a single, specific environmental cue. Instead, the timing and size of mass-nesting events are likely affected by a complex interplay of multiple physiological and environmental variables.

METHODS

Study Site

The Ostional National Wildlife Refuge is located on the northern Pacific peninsula of Costa Rica (Fig. 1). Within the Refuge, Ostional Beach comprises approximately 4 km of coastline. For research and monitoring purposes, the beach is divided into 50 m sectors numbered from north to south. The data used in this study were collected as part of a long-term monitoring project authorized under Costa Rica permits (MINAE-SINAC-ACT, ACT-OR-DR-033-17).

Mass-nesting Census Data

We analysed approximately 10 years (July 2006–January 2017) of olive ridley turtle mass-nesting census data collected at Ostional Beach. During this period, censuses were conducted for 109 of the 116 mass-nesting events that occurred. Data from the first several years (2006–2010) have previously been published and analysed in a different context (Valverde et al., 2012).

Mass-nesting events typically begin at night. The first morning after a mass-nesting event began, transects were set up perpendicular to the coastline. Transects ran from established sector

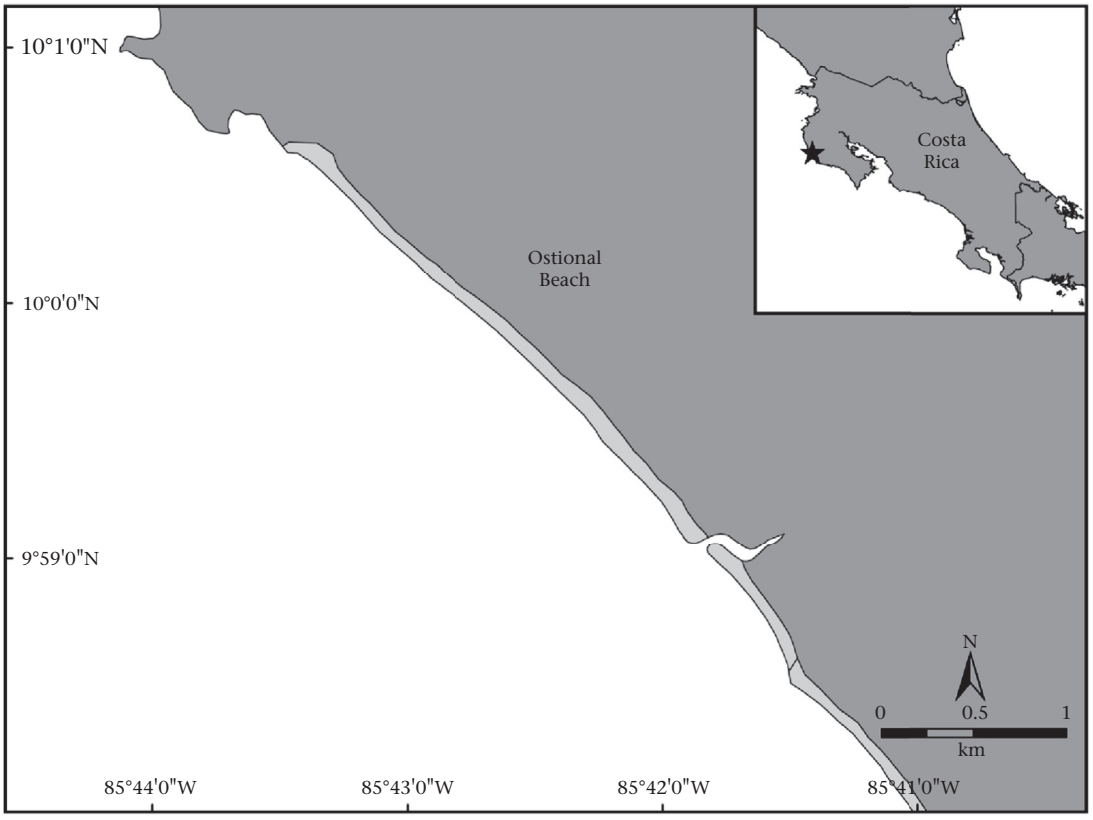

Figure 1. Map of Ostional Beach in Costa Rica. The star in the inset map (upper right) indicates the location of the study site on the Nicoya Peninsula of Costa Rica. The light grey area indicates the terrestrial limits of the Ostional National Wildlife Refuge.

markers (located every 50 m along the vegetation line) to markers placed at the high-tide line; each transect thus spanned the beach zone where turtles nest. Because the start of an arribada was not predictable, data were not acquired on the first night of nesting.

Census data were obtained using a strip-transect-in-time methodology that has been described in detail previously (Gates et al., 1996; Valverde & Gates, 1999). Briefly, observers walked along transect lines every 2 h during mass-nesting events to count the number of egg-laying turtles within each 2 m wide transect. Censuses continued throughout each mass-nesting event until zero turtles were counted across all transects. The data were then entered into the Arribada Portal software, a web-based application designed to estimate the total number of turtles for each mass-nesting event (Valverde, 2013). For purposes of this study, we defined the number of turtles participating in a mass-nesting event as the estimated number of egg-laying females.

Celestial, Meteorological and Oceanographic Data

Diverse environmental factors might influence the reproductive and migratory behaviour of sea turtles, thus affecting both the timing of arribadas and the number of turtles participating. Among cues proposed to function in synchronization of nesting are lunar phase and meteorological conditions such as wind and precipitation (Carr, 1967; Hughes & Richard, 1974; Jiménez-Quiroz, Filonov, Tereshchenko, & Márquez, 2005; Plotkin, Rostal, Byles, & Owens, 1997; Pritchard, 1969; Richard & Hughes, 1972). Similarly, environmental factors that might affect the number of turtles that arrive to nest at a given time include season, sea surface temperature, oceanic currents, oceanic conditions (e.g. upwelling zones, frontal conditions or storms) and changes due to the El Niño Southern Oscillation (ENSO), which affect food availability and thus influence reproduction and migration on a broad scale (Beavers & Cassano, 1996; Luschi, Hays, & Papi, 2003; Plotkin, 2010; Polovina et al., 2004; Swimmer et al., 2006).

To investigate whether these or related environmental variables improve predictions of the timing of mass nesting or the number of turtles participating, we used the geographical coordinates of Ostional Beach (9°59′37″N, 85°42′3″W) to extract meteorological and oceanographic variables corresponding to every day over the 10-year period in our study (July 2006–January 2017). Sea level pressure (atmospheric pressure at sea level), relative humidity and wind velocity were extracted from the National Centers for Environmental Prediction (NCEP) Reanalysis 2 database. Ocean current velocity, sea surface temperature, salinity and sea surface height (the relief of the ocean's surface) were extracted from the Global Hybrid Coordinate Ocean Model (HYCOM, http://hycom.org). Ocean current and wind velocity data each consist of two separate directional values (northward and eastward), with the sign indicating directionality and the absolute value indicating magnitude. The resolution of oceanic and atmospheric data differs; HYCOM provides approximately 9 km resolution while NCEP provides approximately 275 km resolution. However, the NCEP grid point is relatively close to our study site (approximately 76 km away). Additionally, we obtained monthly multivariate ENSO (El Niño Southern Oscillation) index values from the National Oceanic and Atmospheric Administration. Lunar data were derived from the lunar package in R (version 0.1.4; Lazaridis, 2014). Two continuous variables were obtained using cos and sin transformations: 'lunar phase' indicated the illuminated proportion of the moon (e.g. 1 = full, 0 = quarter, -1 = new moon), whereas 'quarter moon' indicated the waxing or waning state of the moon (e.g. 1 = first-quarter, 0 = full/new, -1 = last-quarter moon).

Statistical Analysis

We used JMP Pro 13 (SAS Institute Inc., Cary, NC, U.S.A.) to calculate descriptive statistics and standard statistical tests. R (version 3.2.1, R Core Team, 2014) was used for circular data and statistical modelling analyses. To analyse the timing of arribadas in relation to the lunar cycle, the lunar day corresponding to the start of each mass-nesting event was determined. These data were then transformed into angular data suitable for circular statistics (Batschelet, 1981; Zar, 1999). Rayleigh tests were then conducted using the circular package in R (version 0.4.93; Agostinelli & Lund, 2017) to determine whether the onset of mass-nesting events was uniformly distributed across the lunar cycle. We ran diagnostic pairwise correlations to ensure that no strong correlations existed between environmental variables included in our models ($r \leq 0.50$). We scaled and centred all predictor variables to both facilitate maximizations and allow comparison of relative effect sizes (i.e. standardized to 0.5 SD; Grueber, Nakagawa, Laws, & Jamieson, 2011). Additionally, relative humidity was logit-transformed to normalize the distribution of the data because it is expressed as a percentage. This scaling and transformation permits comparison of variables despite differences in scale and magnitude.

Timing of mass-nesting events

To investigate whether environmental variables improve predictions of the timing of mass-nesting events, we conducted a parametric survival analysis of exponentially distributed events (Jackson, 2016) using environmental data for every day in the 10-year period as predictors for the timing of events. Survival analyses can be used to model the rate of an event happening, with the time until an event occurs serving as the response variable (e.g. time to death observed in patients under different treatment regimes; Kelly & Lim, 2000). For our analysis, we fitted a parametric survival model with exponentially distributed event times using the R package 'flexsurv' (version 1.1; Jackson, 2016). In an exponential distribution, the daily rate of transitioning into a state of mass nesting is:

$$\text{Rate} = \beta_0 + \sum_{i=1}^{p} \beta_i \times x_i \quad (1)$$

In this equation, β_0 is the base rate of transitioning, p is the number of variables and β_i is the effect of variable i (x_i) on the rate of transitioning. Thus, we used input variables to predict the rate of transitioning into a 'state' of mass nesting; in other words, the model predicted the probability of a mass-nesting event beginning on any given day.

In addition to all of the environmental variables, we included the interval or number of days since the previous arribada, as this biological variable might potentially confound our analysis of environmental variables with similar periodicities (Jiménez-Quiroz et al., 2005). Our analysis was therefore limited to events for which there were no missing observations for (1) the end date of the previous nesting event, (2) all days before the event and (3) the start of the event itself. Because the multivariate ENSO index is a monthly value and our model involved daily measurements, we excluded this variable from the analysis.

A set of candidate models was generated by fitting models that included all possible combinations of the predictor variables that matched equation (1). Based on these criteria, we fitted a total of 4096 models for 12 predictor variables for a total of 3101 dates. Model fit was assessed using corrected Akaike information criteria (AICc). As a first step to simplifying the final model set, we removed models that had higher AICc values than those of models nested within them (i.e. models in which adding a new parameter does not improve the likelihood by more than the penalty of adding the parameter; Grueber et al., 2011). We then averaged parameters across models with Δ AICc < 10 from the model of best fit (see Appendix, Table A1; Bolker et al., 2008). We used the unconditional or full average from the resulting averaged parameters to interpret the results (Grueber et al., 2011).

This model-averaging approach accounts for model selection uncertainty and provides robust parameter estimates when several models are ranked highly. Because predictor variables were scaled, the estimate represents the relative effect size for each variable considering the observed variation in that variable. This provides a quantitative measure independent of the units of measure to compare the effect of a variable in a model on the mean response, with a larger absolute value indicating a stronger effect or greater proportion of variance explained by the variable. Additionally, two measures further provide a quantitative comparison of the importance of a variable across all models and in comparison to all other variables. First, to enable comparison of uncertainty in parameter estimates, standard error values and confidence intervals derived from them are reported as the unconditional, adjusted standard error. Second, the relative variable importance is the calculated sum of all model weights for models that included the predictor and therefore represents the strength of support of the particular predictor in the final model set.

To quantitatively compare the predictive ability of our model to that of a null model (i.e. based on random chance), we generated the area under the curve (AUC) of a receiver operating characteristic (ROC) curve (Zou, O'Malley, & Mauri, 2007). This value quantitatively classifies the accuracy of a model using the rate of true positives and true negatives across all potential cutoff values for predicting an event. An AUC value of 0.5 would result from an uninformative model and a value of 1.0 would result from a perfect model (i.e. 100% accurate).

Number of turtles participating in mass-nesting events

To analyse whether environmental variables improve predictions of the number of turtles participating in events, we used a generalized linear mixed model. All of the previously mentioned variables corresponding to the start date of arribadas were used as predictors of the number of nesting turtles (Bartoń, 2016). We included the corresponding monthly multivariate ENSO index values for each mass-nesting event in our analysis. We excluded one event (April 2011) for which a reliable estimate of the number of turtles could not be produced because the confidence intervals for this event encompassed zero. Based on these criteria, we included 108 events in our analysis.

We fitted the model by log likelihood using a negative binomial distribution of the number of turtles with a log link using the R package 'glmmADMB' (version 0.8.3.3; Fournier et al., 2012; Skaug, Fournier, Bolker, Magnusson, & Nielsen, 2016). This distribution proved more appropriate than the Poisson distribution for this model (lower AICc), given the overdispersion of the data. We added season as a potential fixed effect considering the apparent seasonality in the abundance of nesting turtles at this site (i.e. rainy or dry season). We also included specific calendar month (i.e. month and year) as a random intercept to account for potential temporal correlation in events occurring close in time. We selected this random effect structure by comparing AICc values among models including all fixed effects and different random effect structures (i.e. nested effects of year, season and month). We used the same model generating and selection procedure as with the model for the timing of mass-nesting events (Appendix, Table A2). We used the dredge function from the 'MuMIn' package in R (version 1.15.6; Bartoń, 2016) to automate fitting all possible model subsets based on the full model (i.e. including all 12 environmental variables).

To quantitatively compare the fit of our averaged model to that of a null model (i.e. predictions based on seasonality alone), we generated a 'pseudo-R^2' using the squared correlation between the predicted and observed values, where a value of 1.0 would mean all variation in turtle abundance would be explained by the model.

RESULTS

Patterns of Mass-nesting Behaviour

During the 10-year period encompassed by the data set, a mean of 11 ± 0.2 (mean ± SEM) mass-nesting events occurred each year. Arribadas had a mean duration of 3 ± 0.2 days and a mean interval of 34 ± 1.4 days between events. The interval between events was longer in the dry season (37 ± 2.3 days) than in the rainy season (32 ± 1.8 days; *t* test: $t_1 = -1.77$, $N = 103$ intervals, $P = 0.040$). During the rainy season, two events occurred within a single month on nine occasions; this never occurred during the dry season.

The number of turtles participating in events varied throughout the year, with the largest events occurring in the months of September and October (ANOVA: $F_{11,96} = 24.63$, $N = 108$ events, $P < 0.001$). More turtles participated in events during the rainy season (86 953 ± 10 500 turtles per event) than in the dry season (44 298 ± 13 422 turtles per event; *t* test: $t_1 = 6.27$, $N = 108$ events, $P = 0.014$).

A Rayleigh test was used to determine whether the onset of mass-nesting events was nonrandomly distributed across the lunar month. Results indicated a highly nonrandom distribution ($r = 0.56$, $N = 109$ events, $P < 0.001$) with a mean lunar day of 23 (i.e. the overall mean start time of all arribadas was a few days after last-quarter moon; Fig. 2).

Timing of Mass-nesting Events

A null model (AUC = 0.50), which considered the timing of mass-nesting events to be the result of random chance, was used as the point of comparison for evaluating the effectiveness of models constructed to predict the timing of mass nesting. A combination of several environmental variables improved the accuracy of the model (AUC = 0.83). Consistent with previous observations (Fig. 2), the waxing or waning state of the moon was the most important predictor of the timing of events based on relative effect size (Table 1), but the best predictions were obtained from models that also included sea surface height and the number of days since the previous mass-nesting event (Table 1). Specifically, the probability of a mass-nesting event increased (1) near the time of the last-quarter moon, (2) with longer intervals since the previous event and (3) with an increase in sea surface height. The illuminated proportion of the moon was not as important as the waxing or waning state of the moon in predicting the onset of mass nesting (i.e. smaller effect size; Table 1). Additionally, southward ocean current velocity emerged as a predictor, although this variable had a relatively small effect size (Table 1). Sea level pressure, relative humidity, wind velocity, sea surface temperature and salinity did not significantly improve our model predictions of the timing of events (all models that included these variables had ΔAIC > 10). When considered individually, each variable in our model had a

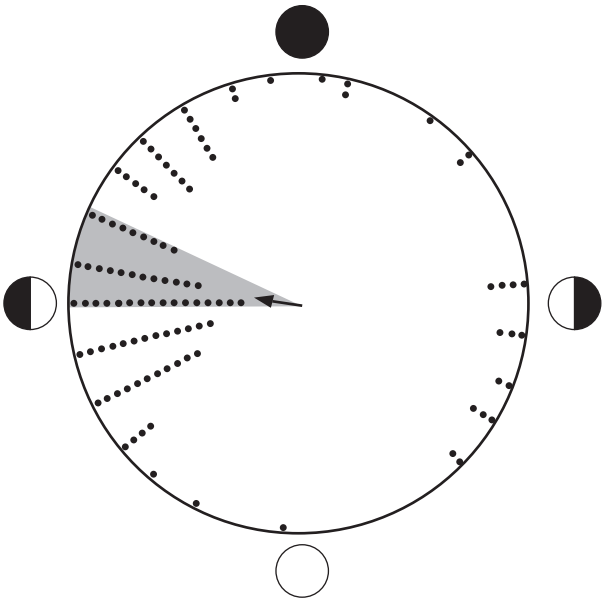

Figure 2. Onset of mass-nesting events at Ostional Beach relative to the lunar cycle. Each dot on the plot represents the start date of mass-nesting events in this study ($N = 109$ events occurring 2006–2016) in relation to the lunar cycle (29.5 days), indicated clockwise from the top: new; first-quarter; full; last-quarter moon. The arrow indicates mean lunar day and the shaded area indicates 95% confidence intervals. The timing of mass-nesting events coincided predominantly with the last-quarter phase of the moon (mean lunar day = 23; Rayleigh test: $r = 0.56$, $P < 0.001$).

relatively small influence on the probability (< 0.10) of a mass-nesting event starting. Overall, the relatively low predicted probabilities (< 0.50) for the start of mass-nesting events generated by the models suggests that the timing of events is probably not induced reliably by any combination of the variables we considered (Fig. 3).

Number of Turtles Participating in Mass-nesting Events

Several environmental variables also improved our ability to predict the number of turtles participating in mass-nesting events (pseudo-$R^2 = 0.28$) relative to a null model (pseudo-$R^2 = 0.03$), which considered seasonality alone. The most important parameters for predicting the number of turtles participating were salinity, relative humidity and ocean current velocity (Table 2). Specifically, a decrease in salinity and an increase in relative humidity and southward ocean current velocity were all associated with higher numbers of turtles nesting (Fig. 4). Relative humidity is likely to mirror rainfall, and indeed was well correlated with rain gauge data acquired from a nearby weather station in Nosara (approximately 10 km away; Spearman's rank correlation: $r_S = 0.4590$, $N = 100$, $P < 0.0001$). Wind speed and direction were also considered relevant in model predictions of the number of turtles participating in mass-nesting events, although these variables had a relatively small effect size (Table 2). Interestingly, our analysis indicates that time of year alone is not a good predictor of the abundance of nesting turtles (i.e. rainy season of May through November versus dry season of December through April, $\Delta AIC > 10$); likewise, sea level pressure, sea surface temperature, sea surface height, monthly multivariate ENSO index, the waxing or waning state of the moon and the illuminated proportion of the moon were not good predictors.

DISCUSSION

Several authors have speculated that environmental cues such as onshore winds, precipitation, lunar phase and/or tidal cycle either trigger or strongly influence the timing of mass-nesting events in ridley turtles (Carr, 1967; Hughes & Richard, 1974; Jiménez-Quiroz et al., 2005; Plotkin et al., 1997; Pritchard, 1969). These suggestions have arisen largely from anecdotal observations and short-term studies spanning periods of a few months. By contrast, our study of mass-nesting events over a 10-year period at Ostional, Costa Rica, represents the most extensive effort to date to identify environmental variables that can be used to predict arribada timing and size.

Our analyses revealed a significant association between the onset of mass-nesting events and lunar phase. The majority of arribadas began near the time of last-quarter moon (Fig. 2), although mass-nesting events at other times in the lunar month were not uncommon. These results are consistent with earlier observations suggesting a possible association between mass-nesting events and last-quarter moon at another Costa Rican beach (Nancite) located approximately 100 km away (Plotkin et al., 1997). Interestingly, however, arribadas at the two locations rarely start on the same night (Bernardo & Plotkin, 2007; Hughes & Richard, 1974), suggesting that local cues or other unidentified factors play a role in determining when mass nesting begins.

Models for Predicting Timing of Mass-nesting Events

In agreement with our observations, the occurrence of the last-quarter moon was the best predictor of the onset of mass-nesting events in our models (Table 1). In addition, the models indicated that the interval since the previous mass-nesting event, sea surface height (the topography of the ocean's surface) and ocean current velocity were also predictors of the timing of mass nesting (Table 1, Fig. 3).

Table 1
Model averaging results from the survival analysis of environmental variables as predictors of the timing of mass-nesting events

Predictor variable	Estimate	SE	*z*	*P*	*r*[d]	*N*[e]
Quarter moon[a]	-0.4686	0.0705	-6.6456	<0.0001	1.00	3
Interval[b]	0.2542	0.0435	5.8397	<0.0001	1.00	3
Sea surface height	0.2203	0.0545	4.0389	<0.0001	1.00	3
Lunar phase[c]	-0.1728	0.0617	-2.7995	0.0051	0.99	2
Southward ocean current velocity	0.0657	0.0539	-1.2195	0.2265	0.98	1

Predictors are listed in decreasing order of estimate or effect size. Because predictor variables were scaled, the estimate represents the relative effect size for each variable with a larger absolute value indicating a stronger effect or greater proportion of variance explained by the variable.
[a] Waxing or waning state of the moon.
[b] Number of days since the previous nesting event.
[c] Illuminated proportion of the moon.
[d] Relative importance or the weighted proportion of predictor importance based on the AIC value and the number of models that included the predictor.
[e] Number of averaged models that included the predictor variable.

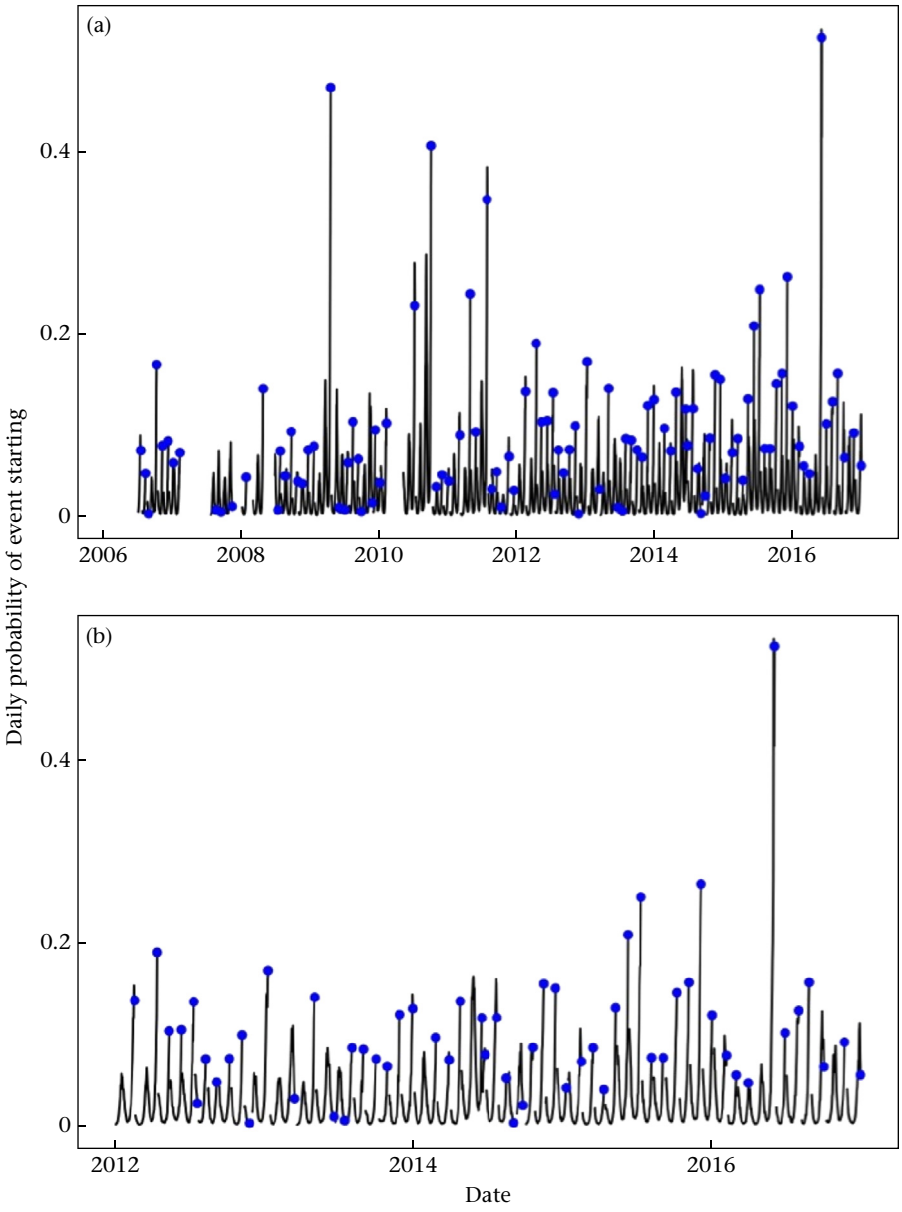

Figure 3. Model-predicted daily probability (black line) of a mass-nesting event starting and the start date of observed mass-nesting events (blue points) for (a) the entire duration of the study and (b) a subset of 4 years, to show detail. A combination of several environmental variables improved our ability to predict the timing of mass-nesting events (AUC = 0.83) relative to a null model (AUC = 0.50), which considered timing as a result of random chance (i.e. higher rate of true positives). Relatively low predicted probabilities (< 0.50) for the start of mass-nesting events indicate that the timing of events is not likely induced by any combination of the variables we considered.

Table 2
Model averaging results from the generalized linear mixed model of the environmental variables as predictors of the number of turtles participating in mass-nesting events

Predictor variable	Estimate	SE	*z*	*P*	*r*[a]	*N*[b]
Salinity	-0.3031	0.0609	4.973	<0.0001	1.00	5
Relative humidity	0.1749	0.0880	1.987	0.0470	0.88	2
Southward ocean current velocity	0.1548	0.0745	2.078	0.0377	0.93	4
Southward wind velocity	0.0083	0.0349	0.237	0.8124	0.07	1
Westward wind velocity	0.0032	0.0209	0.153	0.8783	0.03	1

Predictors are listed in decreasing order of estimate or effect size. Because predictor variables were scaled, the estimate represents the relative effect size for each variable with a larger absolute value indicating a stronger effect or greater proportion of variance explained by the variable.

[a] Relative importance or the weighted proportion of predictor importance based on the AIC value and the number of models that included the predictor.

[b] Number of averaged models that included the predictor variable.

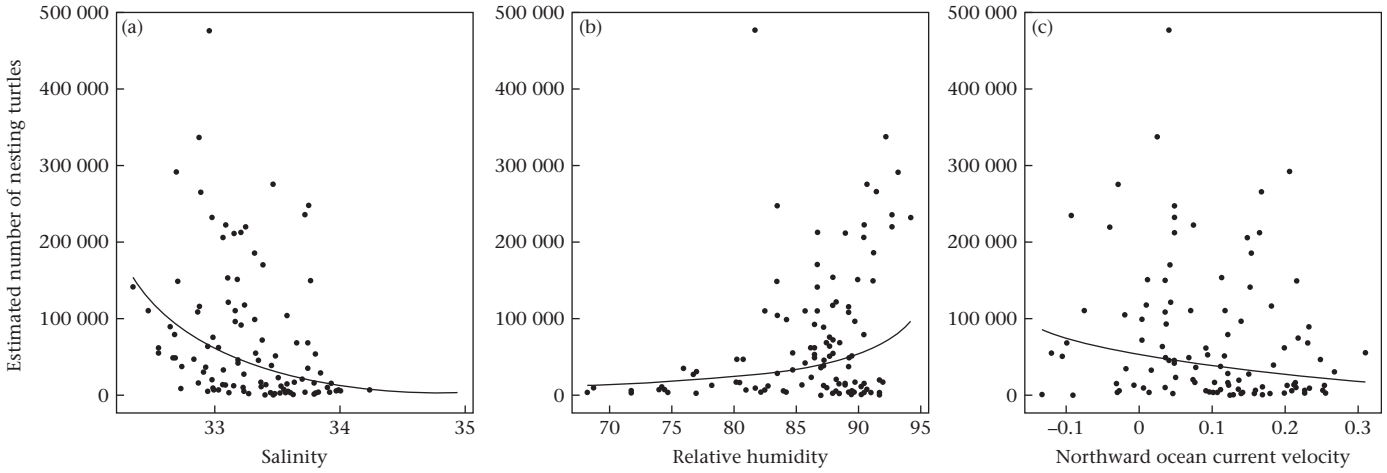

Figure 4. Marginal plots of model fits (lines) and observed data (points) for the number of nesting turtles participating in mass-nesting events for the most important variables in our model: (a) salinity; (b) relative humidity; and (c) ocean current velocity. Model predictions assume all other variables are at their means and therefore isolate the effect of each individual variable. A decrease in salinity and an increase in relative humidity and southward ocean current velocity were all associated with higher numbers of turtles participating in mass-nesting events. Ocean current velocity data consists of two separate directional values (northward and eastward), with the sign indicating directionality and the absolute value indicating magnitude. The inclusion of these variables in addition to wind velocity in our model improved our ability to accurately predict the number of turtles participating in mass-nesting events (pseudo-$R^2 = 0.28$) relative to a null model (pseudo-$R^2 = 0.03$), which considered seasonality alone (i.e. stronger correlation between observed and predicted values). Because each individual curve does not incorporate all predictor variables, deviation of observation from predictions includes both variation due to other predictors and observation-level variation. Regardless, negative binomial-distributed observations should show an increase in variation with increasing predicted counts.

Although the model reveals an association between the onset of mass nesting and lunar phase, it cannot explain the nature of the relationship or whether it is causal. One of several possibilities is that the timing of mass nesting is influenced by a lunar rhythm. Such rhythms exist in a variety of marine species and are especially common among organisms that exhibit mass synchronous spawning (Naylor, 2001; Tessmar-Raible, Raible, & Arboleda, 2011). For such animals, the timing of synchronized reproduction typically provides advantages for offspring or adult survival. In corals, for example, the synchronization of larval release with the full moon and tidal maxima ensures the effective dispersal of larvae (Jokiel, Ito, & Liu, 1985). For mass-nesting turtles, the advantage of nesting near last-quarter moon is less clear. Interestingly, however, the incubation period at Ostional is such that subsequent mass-hatching events occur around the time of the full moon, when lunar illumination might assist hatchlings in reaching the ocean and/or the tidal maxima may increase hatchling dispersal at sea (Hamann, Grech, Wolanski, & Lambrechts, 2011; Salmon & Witherington, 1995). Nevertheless, whether lunar phase functions as a zeitgeber for the entrainment of a biological rhythm, or instead covaries with another environmental cue that influences mass nesting in an unknown way, remains to be determined.

In addition to lunar phase, the interval since the previous arribada was a strong predictor of the timing of mass nesting (Table 1, Fig. 3). This finding is consistent with studies of reproductive physiology in sea turtles, which have revealed that females typically lay several clutches of eggs over the course of each season that they nest, and that considerable time is required for the production of eggs for each clutch (Aitken, Solomon, & Amoroso, 1976; Licht, Wood, Owens, & Wood, 1979; Owens, 1980). Thus, after nesting, turtles cannot immediately nest again.

The reason why the relief of the ocean's surface and ocean current velocity are associated with the timing of mass-nesting events is less clear. Sea surface height reflects a variety of physical and biological factors in the ocean including temperature, productivity, upwelling and convergent fronts (Pennington et al., 2006; Willett, Leben, & Lavín, 2006; Wilson & Adamec, 2001). In our study, sea surface height was most closely correlated with temperature, humidity and precipitation, elements of weather that all affect the success of egg incubation (Güçlü et al., 2010; Valverde, Wingard, Gómez, Tordoir, & Orrego, 2010). Variations in sea surface height and ocean current velocity can also be indicative of eddies, which might in turn facilitate the movements of turtles or concentrate chemical cues useful in locating the nesting area (Coria-Monter & Durán-Campos, 2017). Turtles tracked by satellite telemetry sometimes have movement patterns that appear to be linked with sea surface height, suggesting that this variable (or variables correlated with it) might attract turtles or influence their movements under some conditions (Eguchi, Gerrodette, Pitman, Seminoff, & Dutton, 2007; Luschi et al., 2003; Plotkin, 2010; Polovina, Kobayashi, Parker, Seki, & Balazs, 2000). In summary, sea surface height might reflect conditions favourable for reproduction, conditions that facilitate migration, currents that transport chemical cues to arriving turtles, or other unknown processes.

Models for Predicting Number of Turtles in Mass-nesting Events

Analyses revealed that the three most relevant predictors of the number of turtles participating in mass-nesting events were salinity, ocean current velocity and relative humidity (Fig. 4, Table 2). All three of these variables are associated with weather patterns. In particular, decreases in ocean salinity and increases in relative humidity are associated with rainfall. Thus, a reasonable interpretation is that turtles nest in larger numbers during times of considerable rainfall, while nesting less frequently during periods of limited precipitation. Although turtles are known to nest in higher numbers during the rainy season when precipitation is more abundant (Valverde et al., 2012), models incorporating salinity, current velocity and relative humidity had better predictive performance than a null model based strictly on a division between 'rainy season' months (May through November) and 'dry season' months (December through April). This result might reflect the

influence of year-to-year differences in the onset of seasonal rains or the pattern of rain within a season, or other factors that generally follow a seasonal pattern but do not necessarily occur on the same calendar days each year.

Indeed, the observed seasonality in nesting at Ostional is likely a reflection of numerous factors that affect reproductive success. For example, peak nesting probably occurs near the time when conditions such as temperature and humidity are optimal for nest incubation (Valverde et al., 2010). Similarly, seasonal changes in the proximity of ocean currents to the coastline may facilitate the migration of adult sea turtles towards the nesting beach or the migration of hatchlings out to sea (Beavers & Cassano, 1996; Luschi et al., 2003; Putman, Bane, & Lohmann, 2010). Time-lagged environmental variables not considered in our analysis and at locations distant to the nesting beach might also influence the long-distance migration of sea turtles towards nesting grounds or their nesting behaviour (Beavers & Cassano, 1996; Luschi et al., 2003; Plotkin, 2010; Polovina et al., 2004) and provide further explanatory power for the number of nesting turtles. Further research is needed to explore how spatiotemporal variation in nesting patterns are adaptive or constrained by the requirements of different life-history stages.

What Triggers Mass Nesting?

The near-simultaneous emergence of thousands of turtles in an arribada implies the existence of mechanisms for synchronizing or coordinating group behaviour, yet the way in which this synchrony is achieved remains enigmatic. Although our findings reveal a relationship between lunar phase and the timing of mass-nesting events, both the results of models (Fig. 3, Table 1) and the fact that some arribadas start at times that are not close to last-quarter moon (Fig. 2) indicate that lunar phase alone is not an infallible predictor of timing. Indeed, the relatively low predicted probabilities (< 0.50) for the start of mass-nesting events generated by the models imply that the onset of an arribada is probably not induced reliably by any combination of the variables we considered (Fig. 3). Our results instead suggest that a number of physiological processes and environmental factors interact to influence the timing and abundance of mass-nesting events, and that no single environmental variable is a reliable predictor or trigger.

A limitation of the analysis is that it cannot exclude the possibility that an environmental cue not considered in the models does effectively predict mass nesting. Similarly, it cannot address the possibility that a signal originating from the turtles themselves serves to coordinate emergence. The nature of such a signal, if it exists, remains unknown, but candidates include a pheromone (Owens, Grassman, & Hendrickson, 1982), vocalizations (Ferrara, Vogt, Sousa-Lima, Tardio, & Bernardes, 2014) or visual cues (Bernardo & Plotkin, 2007; Mora & Robinson, 1982; Owens et al., 1982). Social facilitation might also play a role in synchronizing emergence on the beach; for example, a turtle swimming towards the beach to nest might do so more vigorously in the presence of other turtles behaving similarly.

An interesting speculation is that the absence of a rigid linkage between arribada timing and an environmental cue is adaptive for olive ridleys, inasmuch as it allows turtles to avoid nesting when short-term weather conditions makes the survival of eggs unlikely. It is noteworthy in this context that heavy rainfall, which can lead to high mortality of eggs due to immersion and drowning, reduction of gas exchange or fungal growth on egg shells (McGehee, 1990; Packard, Tracy, & Roth, 1977), is thought to suppress mass-nesting events (Cornelius & Robinson, 1986; Plotkin et al., 1997). Indeed, turtles in such circumstances are capable of retaining eggs and ovipositing later when conditions improve (Plotkin et al., 1997). An additional advantage of irregular timing of mass-nesting events is that predators cannot reliably anticipate when each arribada will occur.

In summary, although our analyses have identified several environmental cues that are useful in predicting the timing and size of arribadas, the models do not provide much predictive power for individual events. Nevertheless, this study exemplifies the use of model-averaging approaches and the importance of long-term data to answer questions in a complex system. The results of this study can inform the coordination and management of research, nearshore fishing and boating activity and tourism at Ostional and possibly other mass-nesting beaches. For future analyses, local measurements of the variables we considered (as opposed to measurements extracted from global databases) might improve the accuracy of model predictions. Similarly, inclusion of additional variables not considered in our initial analyses (e.g. tidal fluctuations at the nesting beach or changes in magnetic parameters that might affect navigation to the area; Lohmann & Lohmann, 2019) might improve predictions of timing, size of events, or both. These possibilities notwithstanding, the lack of an obvious environmental trigger for mass nesting suggests that future research may benefit from an integrative approach that considers not only environmental variables, but also factors related to reproductive state and possible social interactions.

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Declaration of Competing Interest

We declare no financial or competing interests.

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Appendix

Table A1
Component models used for model averaging in the survival analysis of the association of environmental variables with the timing of mass-nesting events

Model	Variables	AICc	ΔAICc	Weight
1	12345	769.3125	0	0.9776
2	2345	773.4824	4.1698	0.0151
3	235	774.2080	4.8955	0.0073

1 = Northward ocean current velocity; 2 = sea surface height; 3 = quarter moon; 4 = lunar phase; 5 = interval.

Table A2
Component models used for model averaging in the generalized linear mixed model of the relationship of environmental variables with the number of turtles participating in mass-nesting events

Model	Variables	*df*	Log likelihood	AICc	ΔAICc	Weight
1	1235	7	-1282.63	2580.38	0	0.81
2	12	5	-1286.57	2583.73	3.35	0.15
3	23456	8	-1285.04	2587.53	7.15	0.02
4	235	6	-1287.72	2588.27	7.89	0.02

1 = Relative humidity; 2 = salinity; 3 = eastward ocean current velocity; 4 = eastward wind velocity; 5 = northward ocean current velocity; 6 = northward wind velocity.