ARTICLE

Lunar phases and hawksbill sea turtle nesting

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Abstract

The behavior of sea turtle species can be influenced by the lunar cycle, possibly due to moonlight variability. We analyzed the relationship between nesting behavior and moon phase using nesting hawksbill turtle records for beaches in Northeast Brazil for the 2006–2007 to 2015–2016 seasons. The total number of records was 4807, while the total number with time point registration was 1031. The *Eretmochelys imbricata* inter-nesting period was approximately half the lunar cycle; we therefore expected nesting phase synchronization with lunar phases within each season. We computed the lunar angle for the hawksbill records, and the Kuiper test for uniformity indicated that the species shows some lunar phase preferences. We observed that oviposition at the first and last quarters of the moon is more frequent than at full moon or new moon phases. We also computed the lunar angle throughout several seasons for remigrant turtles and found an absence of preferential lunar phase across different seasons. This indicates that the hawksbill does not choose a lunar phase previously chosen in other nesting seasons. We analyzed the relationship between the presence of the moon in the sky and nesting turtles, and, in sequence, compared the records of false crawls and nest crawls; no relation was found between these variables.

Keywords Behavior · Moon phase · *Eretmochelys imbricata* · Oviposition · Moonlight · Seasonal rhythmicity

Introduction

Physiological events and associated animal behaviors are strongly influenced by variations in circadian systems, the lunar cycle, and seasonal specificities. Circadian (Haus and Smolensky 1999) and seasonal rhythmicity (Nelson and Demas 1996; Plytycz and Seljelid 1997) are widely reported and well described, but there is little in the scientific literature on the influence of the moon cycle on different animal species. Among these few examples, work on honeybees (*Apis mellifera*) found a 29.5-day oscillation in bee weight and steroid variation with a peak rhythm at the new moon phase (Mikulecky and Bounias 1997). Also, several studies

have revealed that hormonal changes in fish (Rahman et al. 2003, 2004; Takemura et al. 2004) can be regulated by lunar periodicity. More specifically, variations in moonlight can regulate melatonin secretion in *Siganus canaliculatus* (Rahman et al. 2004), which reached a plasmatic peak at the new moon.

Several authors have related sea turtle nesting patterns to lunar phases, e.g., a positive relationship was found for loggerhead turtle (*Caretta caretta*) (Baldwin and Lofton 1959; Davis and Whiting 1977). However, a similar analysis by Talbert (Talbert et al. 1980) showed that the tendency for high nesting densities during the new and full moon was valid for a given year but not the following one. The leatherback turtle shows a statistically significant signal for nesting at full moon and new moon (Girondot and Fretey 1996). The Ridley turtle (*Lepidochelis olivacea*) also presents a nesting pattern that is influenced by the moon (Hughes and Richard 1974). However, no correlation was found for green turtle (*Chelonya midas*) nesting in Sri Lanka (Ekanayake et al. 2002), or for leatherback turtle (*Dermochelys choriacea*) nesting in Tobago (Law et al. 2010).

The influence of moonlight or lunar cycle on sea turtles might be interpreted as a consequence of hormonal changes induced by light or radiation variation, and/or as a learned

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behavioral strategy linked to optimal reproductive fitness. Light variation, for instance, which occurs throughout the lunar cycle, can influence light-sensible pacemaker brain structures in reptiles, such as the pineal gland and the suprachiasmatic nucleus; complementary to this, the learning hypothesis predicting the synchronization of behavioral ultradian patterns is supported by the existence of brain anatomical structures specialized in long-term memory formation (López et al. 2003). Regarding the influence of environmental light on melatonin, in a turtle, *Testudo hermanni*, during the active season, levels of this hormone peak at night and are low during the day (Vivien-Roels et al. 1979). Variations in reptilian blood melatonin levels are also documented in a snake, *Nerodia rhombifera* (Tilden and Hutchison 1993), a tuatara *Sphenodon punctatus* (Firth et al. 1989), and in a lizard, *Anolis carolinensis* (Underwood 1985).

The hawksbill sea turtle, *E. imbricata,* is listed as Critically Endangered in both the *IUCN Red List of Threatened Species* ("IUCN Red List for Threatened Species version 2017.1 <www.iucnredlist.org> Accessed on 13 Sep 2017," n.d.) and the *Brazilian Red List of Threatened Species* (Marcovaldi et al. 2011). The reason for the critical state of this species is related to hundreds of years of intense exploitation for meat, eggs and tortoise shell (Meylan and Donnelly 1999). The present study on hawksbill nesting behavior is opportune as it can be applied to improve conservation strategies for this species, specifically for the planning of patrolling effort and nest management.

Important issues for *E. imbricata* conservation concern false crawls and incomplete nesting attempts. In both cases, in contrast with the complete nesting performance, individuals arrive at a beach, crawl in the sand but do not complete their nest successfully. In this work, we test if the presence of the moon in the sky at turtle arrival on a beach has any relation with complete nesting.

Methods

Study area

The study area is located in northeastern Brazil, in the southern section of the state of Rio Grande do Norte (Fig. 1). Two coastal localities were monitored there. The first area is approximately 4.2 km in length, within the municipality of Tibau do Sul (06.190121°S, 35.084720°W), in a district named Pipa, which consists of Chapadão, Minas and Sibauma beaches. The second monitored area is a stretch of land 4 km long in the municipality of Parnamirim (05.924182°S, 35. 157463°W) close to the city of Natal (a military area called Barreira do Inferno, which is formed by three distinct beaches, Alagamar, Prainha and Morro Branco) (Fig. 1).

The landscape is composed of cliffs, interspersed with dunes and a generally narrow band of sandy beach. The sand is fine grained with a pale yellow color. This region experiences a mesotidal, semidiurnal regime, where normal tides attain a maximum of 2.0 m and spring tides have a range of ± 3.2 m (Hayes 1979). There are no visible obstacles to oviposition in the general sand profile at the studied beaches.

Data collection

We performed morning patrols during the nesting seasons from 2006–2007 to 2015–2016, from 1 November to 30 May to record nest occurrences by observing turtle tracks. In addition, intensive night-long patrols, for each nesting season, were carried out from 10 December to 15 April, from 1900 to 0430 hours to intercept and mark nesting females with Inconel metal tags (no 681; National Band and Tag), on both front flippers. Each nest was marked with numbered stake. More details about monitoring and conservation strategies are found in a previous field study (Marcovaldi and Dei Marcovaldi 1999). Occurrences were classified as nest (confirmed successful oviposition), false crawl (emergence without digging a nest chamber), incomplete oviposition (unsuccessful attempt: emergence where the turtle dug a body pit, but did not complete the nest chamber) and undetermined (emergence where it was not clear if the turtle had dug a nest chamber or not).

Glossary of physical terms

Aiming to characterize lunar phases and the moon dynamics, we describe here a short glossary of mathematical and astronomical terms used in this work.

Lunar period

The lunar period is the time in days between two consecutive new moons, i.e., 29.53 days on average. The lunar period, also called the synodic period, is the basic duration of the lunar period used in behavioral studies concerning the moon cycle. The lunar period should not be confused with the sidereal lunar period, which is the period with respect to the fixed stars. These two periods do not coincide because of the relative motion of the earth around the sun.

Lunar phases

The usual notation for the positions of the moon with respect to the earth and sun is: new moon (NM), waxing crescent (WxC), first quarter (FQ), waxing gibbous (WxG), full moon (FM), waning gibbous (WnG), last quarter (LQ), waning crescent (WnC) and, once again, new moon again.
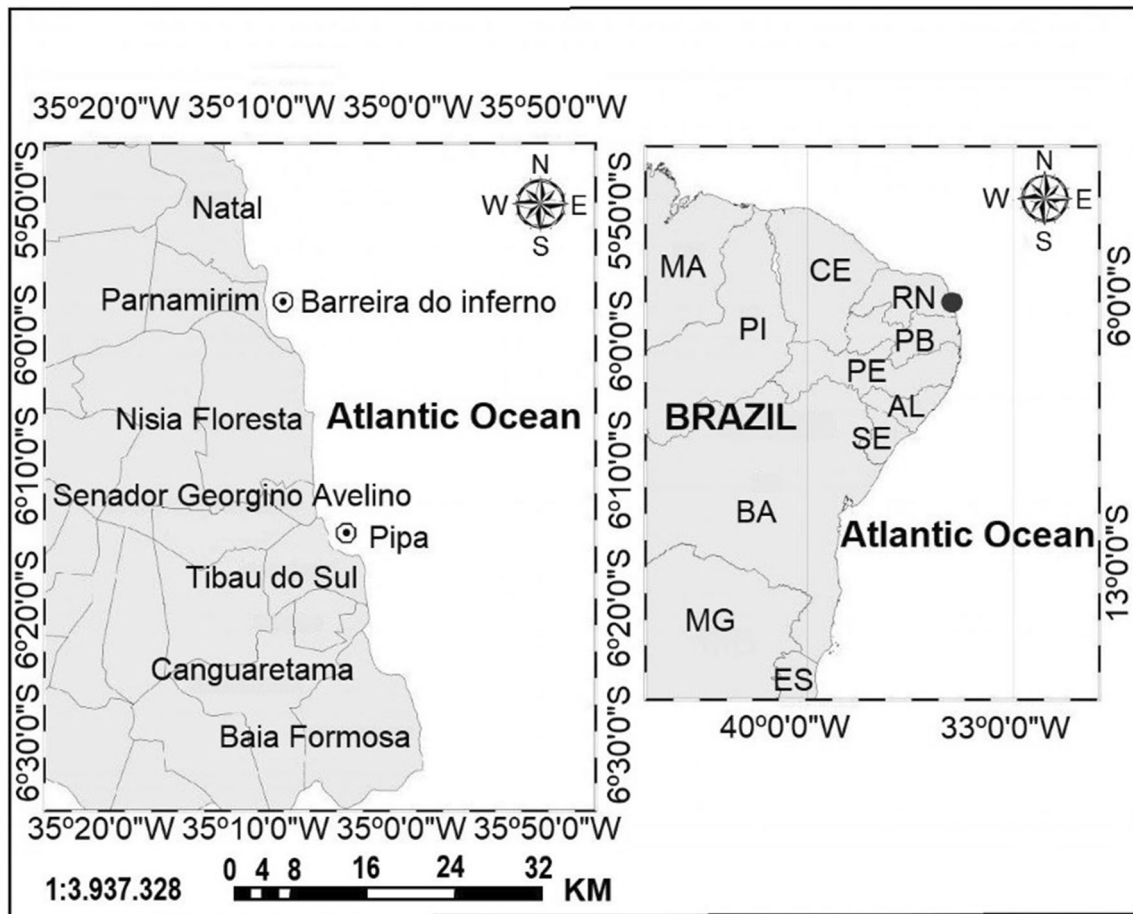
Fig. 1 Map of the monitored beach areas: Barreira do Inferno, and an area located in the municipality of Tibau do Sul, near the tourist beach of Pipa

Lunar angle

The lunar angle is a continuous angular variable (Φ) from 0, defined here as at the time of the new moon, to 360; the angle returns to that of the starting point. The full moon corresponds to $\Phi = 180$, the first quarter to $\Phi = 90$ and the last quarter to $\Phi = 270$. We calculate Φ using the day (d) of the nesting event, together with the day of the previous new moon (d_P) and the day of the subsequent new moon (d_S), as follows:

$$\Phi = 360(d - d_P)/(d_S - d_P).$$

The phase Φ is multiplied by 360 to convert it to the conventional graduation. Note that $d_p < d < d_S$ implies that $0 < \Phi < 360$. The phases corresponding to the lunar phases are: NM ($337.5 < \Phi < 22.5$), WxC ($22.5 < \Phi < 67.5$), FQ ($67.5 < \Phi < 112.5$), WxG ($112.5 < \Phi < 157.5$), FM ($157.5 < \Phi < 202.5$), WnG ($202.5 < \Phi < 247.5$), LQ ($247.5 < \Phi < 292.5$) and WnC ($292.5 < \Phi < 337.5$).

Hour of the day

Hour of the day is local time. The equatorial zone, where the study took place, shows a great astronomical regularity. In this region, daytime is roughly 12 h duration throughout the entire year. In the study area, the sun rises around 0530 hours in the morning and sets at 1730 hours in the afternoon. The same regularity can be seen in the lunar orbit, which makes interpretation of the data easier than in temperate zones where the duration of day and night varies considerably with season.

Presence of the moon in the sky

At the equator, the moon in visible in the sky for half of the 24 h of the day. The moon is visible during the entire night during the full moon, while at new moon the night is

completely dark. At first quarter the moon rises roughly at midday and sets at midnight. In contrast, at the last quarter, the moon rises at midnight and sets at midday. Using standard interpolation we can compute the hour of day that the moon rises for any lunar angle (Fig. 5a).

Hawksbill inter-nesting period

The hawksbill inter-nesting period, 15 ± 1.5 days (Santos et al. 2013), is the number of days between two consecutive ovipositions of the same individual, and defines the oviposition cycle. The number of days roughly corresponds to half the lunar period.

Frequency synchronization

Frequency synchronization is characterized by a frequency match between two coupled cyclic systems. In general, we consider that two systems show frequency synchronization if the frequencies are multiples of each other (Alligood et al. 1997). As the period is the inverse of the frequency, the same reasoning is extended to the period, but the term "period synchronization" is not employed. In our study, lunar cycle and oviposition cycle show frequency synchronization because one is twice the other.

Phase synchronization

Phase synchronization is a phenomenon characterized by coupling of the phases of two cyclic movements. Two systems that have frequency synchronization will have, in general, phase synchronization. In the case of *E. imbricata* and the moon cycle, phase synchronization can be selected, for instance, using the axis of the new moon and full moon. For a given season, once an individual turtle starts nesting at new moon, nesting phase is synchronized with the new moon and full moon axis.

Ocean tide

Ocean tide is a geophysical phenomenon that provokes a variation in the sea level. Tides are caused by the combined gravitational effect of the moon and sun on the earth. Tidal effects are more accentuated during the new moon and full moon, whereas tides are weak during the moon quarters.

Statistical analysis

The number of episodes of the presence of turtles on the beach was categorized according to two criteria: the presence or absence of the moon in the sky, and occurrence types, i.e., successful nesting, false crawls and unsuccessful nesting attempts. The statistical treatment of categorical data was performed using a χ^2-test. We explored the lunar angle as a continuous variable to test for uniformity using the Kuiper test. The test was executed using the circular statistic package of the R program. All statistical analysis were performed inside the R Program Environment (R Development Core Team R 2011).

The matching between the inter-nesting period and half lunar period points to an agreement in frequency between hawksbill nesting and the lunar phase. In addition, the synchronization in frequency implies, at least for the same reproductive season, phase synchronization. Supposing that an individual arrives at the beach at time t where the corresponding angular phase is Φ_t. This same individual will arrive again at the beach again after one inter-nesting period, which roughly corresponds to 15 days or a lunar angle of approximately half the moon cycle, $\Phi \approx 180$. Thus, we expect that the lunar angle of the subsequent oviposition, Φ_{t+1}, should satisfy the approximate relation $\Phi_{t+1} \approx \Phi_t +180$. In this way we can mathematically express phase synchronization between two subsequent ovipositions separated by one inter-nesting period. In addition, if an individual is not observed on the beach during one oviposition because it has chosen another beach or the monitoring patrol has failed to see it, the lunar angle between the observations will be $\Phi_{t+2} \approx \Phi_t$. In this case, the number of days between the two records is roughly 30 ($\Phi \approx 360$), and the individual will thus reproduce at the same lunar angle.

It should be noted that, we need only the record of the nesting day to compute lunar statistics. However, to perform the analysis of the presence of moon in the sky, the time of the nesting record is necessary. Thus, there is a larger sample size for the statistical analysis of the moon phase, and this is more robust than the statistics on moon presence in the sky.

Results

There was a total of 4807 nesting attempts of *E. imbricata* on the beach in the 2005–2006 to 2015–2016 seasons. A total of 3695 successful attempts (nests) were observed, 699 false crawls, 384 unsuccessful nesting attempts, and 29 occurrences without identification. For all data, the day of the year was available; however, the nesting moment (local time) was only available for cases where the female was intercepted ($n = 1301$).

We analysed nesting behavior as a function of the presence or absence of moon in the sky. Figure 2a illustrates the presence of the moon in the sky according to the lunar phase and hour of the night; Fig. 2b shows the same plot, with the addition of all registered nesting records, for which we had the exact hour of the night. The descriptive statistics show that nesting decreased after midnight (Fig. 4). There was
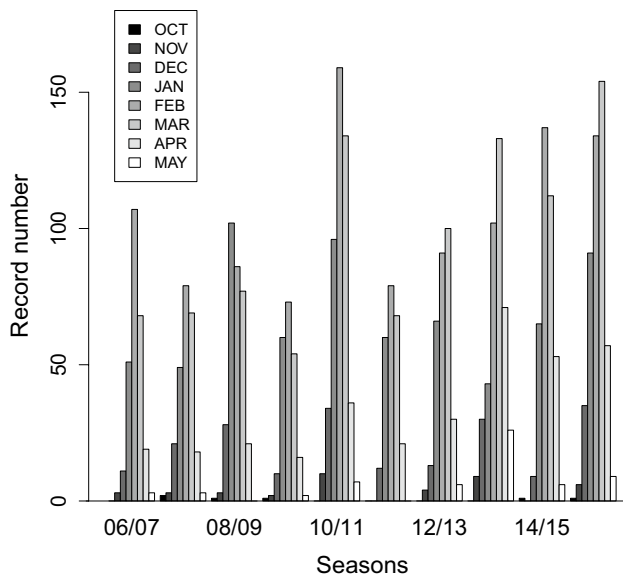
Fig. 2 Seasonal distribution of *Eretmochelys imbricata* nesting attempts on the beach. Histogram of seasonal distribution (per each season, from 2006–2007 to 2015–2016). Note that oviposition most frequently occurred in January, February and March ($n = 4807$)
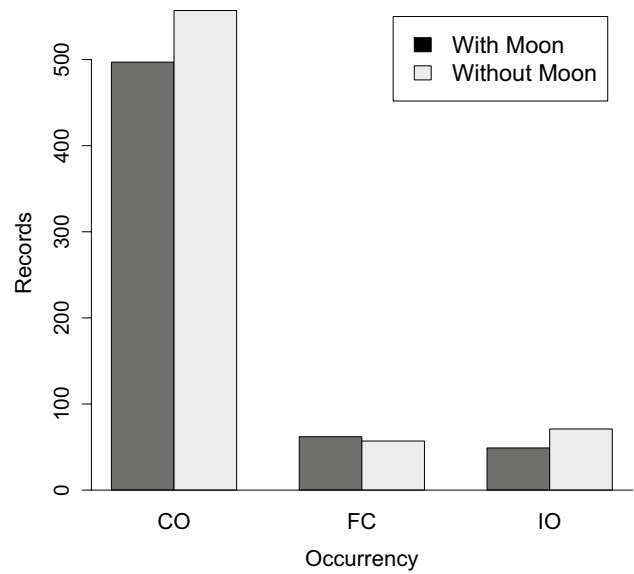

Fig. 4 Plot of turtle emergence on the beach in relation to the moon's presence in the sky. We distinguish between the events of complete (complete oviposition; *CO*) and unsuccessful recordings [false crawls (*FC*), incomplete oviposition (*IO*)]. There was a weak turtle preference for the absence of moonlight, but no influence of moon presence on either *FC* or *IO* ($n = 1293$)
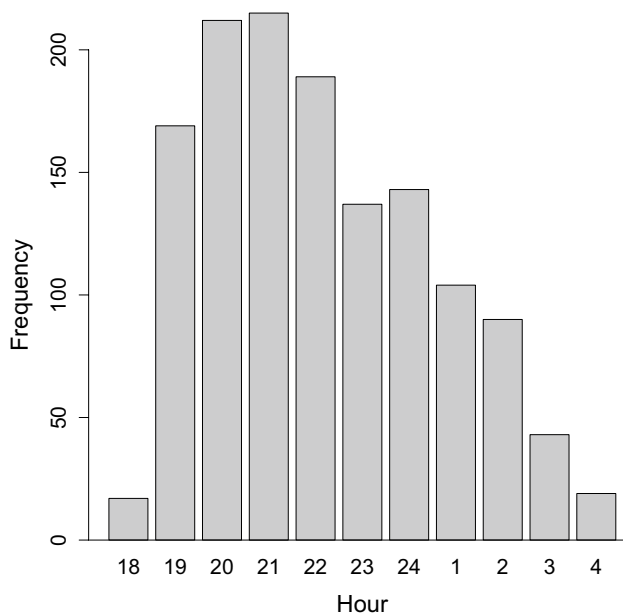

Fig. 3 Nesting attempt records for each night hour considering all analyzed seasons ($n = 1301$). Nesting attempt peak is ca. 2000–2200 hours. Around 81% of all nesting behaviors occurred before midnight

a weak preference or marginal significance ($P = 0.065$) for oviposition related to nesting in the moon's absence.

Comprehensive temporal data are given in Fig. 3, in which the turtle records are shown according to season and month for all the 10 years of patrolling. Figure 3 shows the

complete survey as we recorded season and month for the presence of turtles on the beach, considering all attempt types. The nesting period spanned from November to May, but was concentrated in February and March. We also present an illustrative histogram of nesting attempts distribution across the hours of the night (Fig. 4). Median $\pm$ SD of the time distribution was 22.5 ± 2.5 h. This second data set has a smaller size, $n = 1301$; the number of observed successful nests was 1054, false crawls 119, unsuccessful nesting attempts 120 and occurrences without clear identification eight.

We performed a χ^2-test with two categories to verify the hypothesis that the presence of the moon in the sky at the moment of turtle emergence affects turtle nesting behavior: presence or absence of visible moon in the sky at the time of the nesting event ($\chi^2 = 3.42$; $df = 1$; $P = 0.065$). This result suggests a weak influence of lunar luminosity on nesting behavior. In addition, we tested if the presence of the moon in the sky at nesting is associated with false crawls or unsuccessful nesting attempts; the result was not significant ($\chi^2 = 3.08$; $df = 2$; $P = 0.214$; (Fig. 5).

A Kuiper test was conducted to test the effect of lunar cycle on turtle nesting preferences for the complete records [$t = 2.87$ and $P < 0.01$ ($n = 4087$ visits)]. A circular histogram of oviposition behaviour is presented in Fig. 6, in which eight boxes are used with the first one centered on the new moon, i.e., the same lunar phases as described in
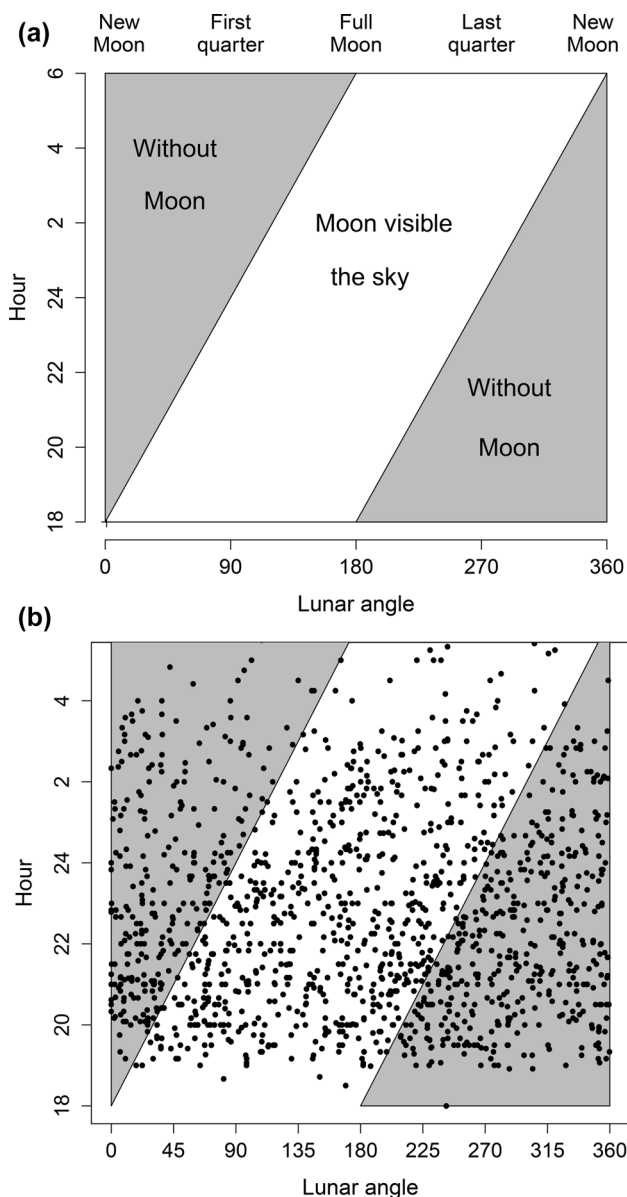
(a)

(b)

Fig. 5 **a**, **b** Night hours versus lunar angle showing the moon presence in the sky and turtle emergence onto the beach. **a** Hours of the night versus lunar angle: 0 and 360 correspond to new moon, 90 to first quarter, 180 to full moon, 270 to last quarter. *Gray shaded area* indicates absence of moon in the sky; *white area* indicates the moon's presence at night. During the full moon phase, for instance, the moon is visible in the sky for the entire night. **b** The same graph with multiple dots indicating the actual observations of turtle emergence events onto the beach ($n = 1301$). Note that, after midnight, the oviposition records largely decrease, as also seen in Fig. 4

Fig. 6 Lunar phase and nesting occurrences of hawksbill sea turtle. Circular histogram representing moon phase and turtle emergence episodes on the beach, for seasons 2006–2007 to 2015–2016. Eight typical moon phases are shown: new moon (*NM*), waxing crescent (*WxC*), first quarter (*FQ*), waxing gibbous (*WxG*), full moon (*FM*), waning gibbous (*WnG*), last quarter (*LQ*) and waning crescent (*WnC*). We performed a circular statistics test, which indicated that turtle beach visits are not uniform ($P < 0.01$). Thus, we also show periods of preferential oviposition phases: WnG/LQ and WxG/FQ

arrived at the beach (Φ_A); the vertical axis shows the lunar phase of the subsequent observed arrival (Φ_S). Fig. 7a ($n = 919$) shows Φ_A versus Φ_S for all subsequent records, even if they are occur at the same season or not, i.e., we plotted all subsequent records without checking if they were separated by one inter-nesting period, two inter-nesting periods, or even by remigration intervals (separated by years). This plot is useful for a comparison with differentially filtered data, as discussed in the following paragraph.

To explore turtle lunar phase regularity or the preference of individuals for a given lunar phase, we made additional plots. Fig. 7b ($n = 742$) shows Φ_A versus Φ_S only for the records during a reproductive season; the trends for $\Phi_A \approx \Phi_S + 180$ and $\Phi_A \approx \Phi_S$ show a quite evident synchronization during the seasons. To test phase synchronization along distinct seasons, we plotted ($n = 177$) Φ_A versus Φ_S only for remigrants (Fig. 7c), i.e., we plotted the lunar phase of the last record of one season versus the lunar phase of the observed first record of the next season, which typically occurs 2 years later (Santos et al. 2013). There was no clear trend of phase synchronization for the remigrants.

Discussion

The hawksbill sea turtle revealed a nesting preference for the waxing crescent moon phase (immediately before the first quarter) and the waning gibbous phase (immediately before the third quarter). There was also a tendency, although not

the methodology. The axes new moon and full moon were less populated than the axis respective to the quarters.

To examine phase synchronization of *E. imbricata*, we selected all individuals that nested at least two times. We examined the relationship between the horizontal axis of the lunar phase corresponding to the time at which individuals
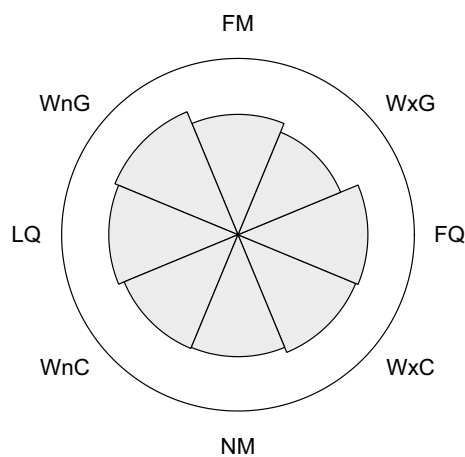
Fig. 7 a, **b**, **c** Successive turtle oviposition records related to lunar phase. *Zero* corresponds to new moon and *180* to full moon. x-axis indicates the first encounter, y-axis indicates the successive one. **a** All successive events, **b** only successive events during a season, **c** successive events of remigrant turtles. Hawksbill sea turtle exhibited phase synchronization within a season, but not between seasons
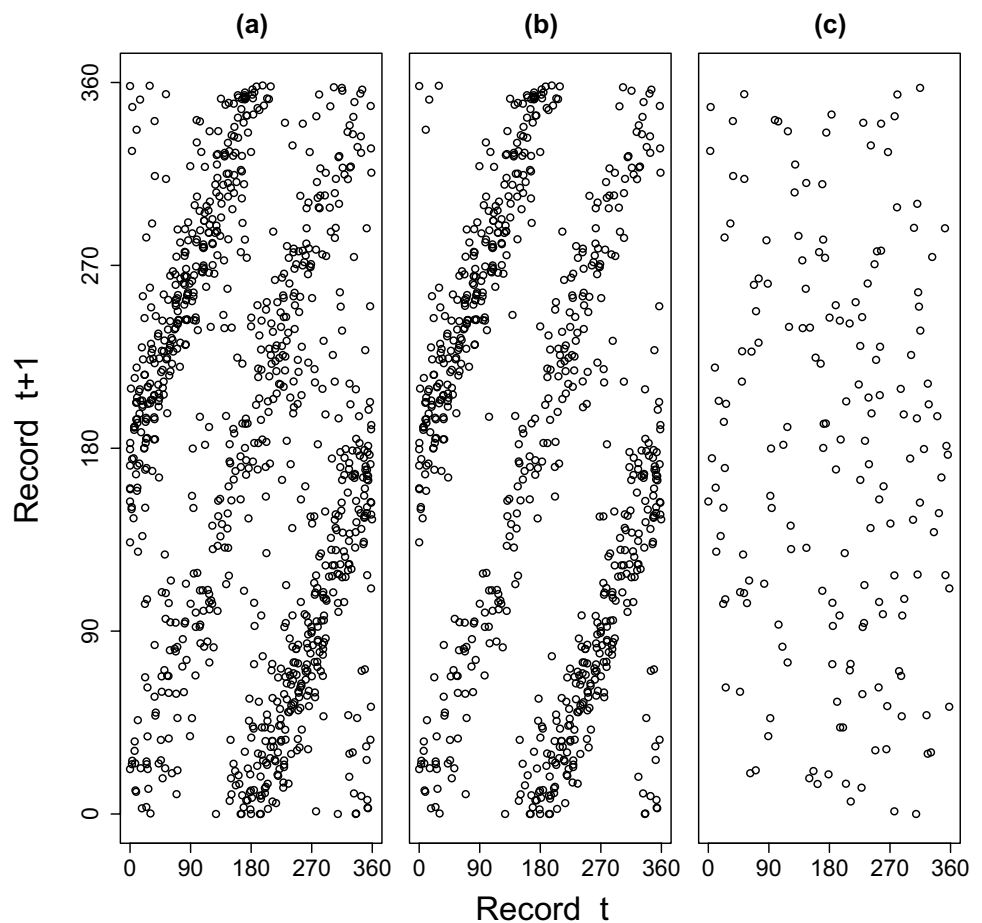
statistically significant ($P = 0.065$), for *E. imbricata* to nest when the moon was absent from the sky. In addition, 81% of nesting records for northeast Brazil for this species were recorded before midnight.

The tendency for nesting in the absence of the visible moon may be related to predation. Several species have been found to show a the preference for foraging on dark nights to avoid predators, and predatory behavior may change across the lunar cycle (Horning and Trillmich 1999; Dowding et al. 2010). We visually confirmed the presence of the following potential predators in the study area: foxes, armadillos, domestic dogs and crabs. Among these predators, canids can potentially exert more influence on turtle arrival because they use combined visual and olfactory signals to locate prey (Österholm 1964; Wells and Lehner 1978; Jacobs et al. 1993). We also observed nest predation on a regular basis throughout the years of beach monitoring. For leatherbacks in Tobago, West Indies, no difference in the frequency of nesting events between the full and new moon was observed, suggesting that lunar illumination does not have a discernible effect in this region (Law et al. 2010).

Sea turtle nesting behavior is strongly impacted by marine coastal features. In particular, tide amplitude, that had a

maximum of 3.2 m in the study area, which is high (Hayes 1979). The preference of *E. imbricata* to nest around the quarter phases instead of at the new moon or full moon may be related to the amplitude of the tide.

The tide cycle closely follows the lunar cycle. In this study, the hawksbill turtle inter-nesting interval is roughly half the lunar cycle, but it should be noted that this is also the tide cycle. Moreover, the movement of the tide behavior is characterized by a strong tide amplitude at full and new moon, and lesser amplitude during the moon quarters. In particular, and increased number of oviposition observations during the moon quarters reveals a preference for lower tides. We hypothesize that the sea turtle preference for smaller tide amplitudes facilitates swimming and orientation during access to the beach for nesting, which could be confirmed by future research.

We believe that beach topography and the tide effect play roles in our studied site. Indeed, reefs near the beach would prevent the sea turtle from accessing the beach during low tide but at larger tides would have facilitated access to land. However, reefs are not prevalent in these specific nesting areas. Most of the nesting beaches are composed of open sandy spaces, although in some cases there are cliffs by the

sandy beach (Santos et al. 2013). In addition, the sand slope varies according to the beach, and also with season following the marine currents that carry sediments along the coast. Future studies focusing on the tide would clarify this and help us to elucidate if the tides facilitate sea turtle arrivals on a beach according to the distinct topography of coastal northeast Brazil."

In Loggerhead turtles (Pike 2008), a preference for nesting during moderate tides was also observed. Pike (2008) studied the impact of 15 environmental factors including temperature, rainfall, wind, tides and moon luminosity, and found no correlation of moon luminosity with nesting behavior.

In our study, we showed that the hawksbill turtle does not exhibit an oviposition pattern associated with lunar cycle that is compatible with a long-term memory over several seasons. However, we note that this species has a behavioral repertoire compatible with long-term memory, or repeatability behavior, for some behavioral parameters. Santos et al. (2016) showed that the hawksbill turtle shows repeatability for choice of nesting distance from the tide line and also for microhabitat site within a season. Individuals that prefer to nest in vegetation, or on open sand, repeat this behavior in subsequent seasons (Kamel and Mrosovsky 2005). However, this observed repeatability is stronger during a season and decreases along several reproductive seasons, revealing behavioral plasticity (Santos et al. 2016).

Our main findings are that: (1) there is a preference for nesting during days with low moonlight and around the moon quarters (which are temporally related to mild tides), and (2) oviposition occurs during seasons on a half-moon cycle. We postulate that neural and behavioral mechanisms may be related to the moon cycle, which influences oviposition patterns. With the advent of satellite tracking, we have been able to divide the inter-nesting interval into different phases, which includes movement among the nesting beach, pre-emergence area, and quiescence area, and places where female turtles remain to rest between nesting events (Walcott et al. 2012). The distance between the resting area and the nesting beach will influence how much time is required for displacements. In addition, the quiescence period is likely to be influenced by temperature in other chelonids (Sato et al. 1998; Hays et al. 2002); consequently, the quiescence period may change due to small variations in water temperature in the study area (Clayson and Weitlich 2007). So, even in the case of a subtle change in water temperature, the inter-nesting duration of the studied specimens may also change. In summary, in parallel to the moon and tide synchronization hypothesis emphasized here, two alternative explanations also have to be considered as possible causes for the half-moon interval (around 14–15 days) observed in this population of *E. imbricata*. One is that there is a hot climate throughout the whole year at the study area (at a

latitude near the equator), and cycle length may be reduced by an average high temperature when compared to other populations. Other possible causes of this specific interval might be related to physical features of the sea near the observed beaches, which in this case could be relatively near the beaches, which may reduce less time for turtle displacement from quiescence to oviposition sites.

The studied population nests near the equator, where the seasons do not have a huge variation in terms of temperature or humidity. In the sea around the equator, the main infradian environmental variation cycle may be related to the moon and, by consequence, there is an infradian variation in tide mean level. Along the evolutionary trajectory of this species, lunar cycle variations probably contributed to the synchronization of specific infradian behavior, such as oviposition. This is supported both by neural and behavioral mechanisms, one related to neuroendocrinal regulation by environmental light variations in reptiles (Tosini et al. 2001), and the other by learning mechanisms (López et al. 2003). These mechanisms could help to adjust behavioral phases in agreement with the influence of the moon on the environment.

Reptiles are influenced by environmental light, which modulates their secretion of hormones such as melatonin. In reptiles, environmental light stimulates retinal cells, the pineal gland (the melatonin source in animal brain), and the suprachiasmatic nucleus (SCN), which is the main pacemaker regulator of circadian body rhythms (Tosini et al. 2001). In rodents, the SCN has been shown to comprise a circadian multioscillator system that acts as the primary pacemaker for orchestrating physiological and behavioral patterns (Evans et al. 2011). In addition, recently it was described that SCN plays a similar role in circadian systems of reptiles (Minutini et al. 1995; Miranda-Anaya et al. 2000). Reptiles exhibit neural plasticity and learning skills. The presence of a medial cortex, an analog structure of the mammalian hippocampus (López et al. 2003), can account for the storage of new information that results in environmental adaptation, such as synchronizing infradian cycles according to the lunar cycle within an oviposition season.

Inter-nesting period synchronization in marine turtles is not peculiar to this population of *E. imbricata;* other species such as *Caretta caretta* and *Natator depressus* also have an inter-nesting period of around half the moon cycle. The following inter-nesting periods are given in the literature: *Caretta caretta* (10–14 days), *Dermochelys coriacea* (9–10 days), *Lepidochelys olivacea* (21 days), *Chelonia mydas* (11 or 12 days), *Natator depressus* (12–14 days), *Lepidochelys kempii (25 days)* (Hirth 1980; Gomes et al. 2007; Pendoley et al. 2014). In *E. imbricata* populations across tropical waters of the globe, some populations, in Australia and Barbados, present an inter-nesting interval compatible to our observations (on average 14–15 days)

(Dobbs et al. 1999; Walcott et al. 2012); other populations in Cuba, Solomon islands and Costa Rica have a higher inter-nesting interval (average 16–18 days) (Moncada et al. 2010; Hirth 1980; Bjorndal et al. 1985). These differences, as explained above, may be related to tide profile, temperature and distance from quiescence sites to the beach. Future work on this subject, taking into consideration the many reproductive sites of *E. imbricata*, could confirm if high tide variation is really related to inter-nesting intervals in agreement with the half-moon cycle as observed here.

Behavioral studies that can help to improve our understanding of the reproductive success of *E. imbricata*, an endangered species, may have an impact on its conservation. There is currently a great deal of effort for the conservation of marine turtles globally (Marcovaldi and Dei Marcovaldi 1999). We call attention to the fact that *E. imbricata* has an important nesting site in the northeast of Brazil (Santos et al. 2013). In this area, several non-governmental organizations patrol and monitor beaches to improve protection to the nesting of marine turtles. In order to optimize the patrolling of beaches, stakeholders will be interested to know this species' nesting preferences, as this knowledge could save time and effort. For example, in the case of material or human resource limitations to patrolling beaches, this study indicates that patrolling should be conducted according to three nesting behavior preferences: from 1900 hours to midnight, at hours or days at which the moon is absent from the sky, and in the WnG, LQ, FQ, WxC lunar phases. Moreover, we also suggest that environments with less light and tides of lower amplitude should have special consideration when creating a conservation plan for this species in South America.

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