Do Local Environmental Factors and Lunar Cycle Influence Timing and Synchrony of Oviposition of a Turtle with Strict Nocturnal Nesting?

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Abstract: Timing of nesting affects fitness of oviparous animals living in seasonal environments, and females may cue on environmental factors for their nesting behavior, but these relationships are understudied in tropical turtles. Here, the timing and synchrony of egg-laying relative to environmental factors were examined in the South American freshwater turtle *Podocnemis unifilis* on 11 nesting beaches during three nesting seasons. Daily measurements included number of nests laid, rainfall, river level, air temperature, and the phase of the lunar cycle (full moon, last quarter, new moon and first quarter). Results confirmed that *P. unifilis* nested at night and revealed that females in our population nest in groups from 2 to 17 females at a time. Nesting was not correlated with rainfall, but a significant relationship was found with river level, such that nesting started at the onset of the dry season when river levels dropped and nesting grounds emerged. Importantly, we found that (1) nesting events concentrated on days with intermediate daily maximum air temperature (although maxima changed annually), and that (2) larger groups of females nested around full moon, suggesting the reliance on visual cues to initiate nesting activities (consistent with social facilitation behavior). Altogether, the timing of nesting in *P. unifilis* may be shaped by a combination of environmental factors, moon phase and social facilitation, where visual cues play an important role.

Keywords: *Podocnemis unifilis*; weather conditions; moon phase; reproductive timing; social facilitation

1. Introduction

Understanding the mechanisms underlying reproductive patterns may provide important insights into life history evolution and it is a central question in evolutionary ecology [1,2]. For oviparous animals living in seasonal environments, producing progeny is usually restricted to a brief period during the year; thus, the timing of oviposition is a life-history strategy that plays a critical role for reproductive success and individual fitness [3]. Indeed, early oviposition is often characterized by having greater offspring survival than later oviposition [4,5]. Usually, egg-laying coincides with the peak of food availability both in terms of quantity and quality (e.g., snakes [4] and birds [5]) and this timing ensures adequate developmental time for eggs to hatch synchronously and reduce predation risk (e.g., lizards [6] and turtles [7]). But what factors are used by females to time their nesting and are those decisions shaped by natural selection? Local environmental factors have been reported to mediate the fitness effects of the timing of nesting and these factors are thought to influence maternal

decisions, given that they may provide cues that mothers can use to calibrate their oviposition to when conditions are the most favorable in order to maximize their lifetime reproductive success [4,8]. For instance, ambient (or water) temperatures correlate with the start of the nesting season in some birds [9], sea turtles [10] and amphibians [11]. Similarly, rainfall stimulates oviposition in many amphibians [12] and lizards [13], whereas water level influences spawning events in some fishes [14].

For several freshwater turtles, field studies indicate that environmental conditions and the onset of egg-laying are linked, but the variables predicting such relationship vary across species. Namely, temperature (air, water or both) seems to be an important factor in nesting for several species, such as in *Chrysemys picta* [15–17], *Emydoidea blandingii* [18], and *Chelydra serpentina* [19]. For other species rainfall predicts nesting, including *Emydura signata*, *Chelodina expansa* [20] and *Elusor macrurus* [21], whereas both air temperature and rainfall are good predictors for *Trachemys scripta elegans* [22]. And in yet other taxa, river flood level has been documented as influencing oviposition, such as for *Podocnemis expansa* [23], *P. unifilis* [24] and *Dermatemys mawii* [25].

Importantly, quantitative data are very limited for most turtles, are often available from a single reproductive season, and are particularly lacking for tropical freshwater turtles. This scarcity of information precludes rigorous assessments of nesting patterns. These data are essential, not only to understand the reproductive ecology of turtles or the anthropogenic impacts in their nesting behavior [26,27], but also to assess the potential effects of climate change, which are predicted to alter ambient temperatures, hydrological and fluvial cycles, which may negatively shift nesting strategies and survival of turtles [28–30].

The lunar cycle and moonlight intensity are potentially important but neglected factors that might influence turtle nesting behavior as they do in other organisms. For instance, in some marine organisms, oviposition changes synchronously with the lunar cycle and moonlight intensity [31–33]. In the order Anura, egg-laying is linked to the lunar cycle, with some species being more active in nights of full moon and others in dark nights [34]. Similarly, for nocturnal snakes, dark nights increase activity levels in some species [35], whereas in other species this is linked to moonlight [36]. In rodents, nocturnal illumination negatively affects species activity patterns [37], and moonlight avoidance likely occurs as a response to predation risks [38]. Some species of turtles are strictly nocturnal nesters, yet their general nesting behavior remains understudied compared to diurnal nesters, including the effect of the lunar cycle on oviposition, with the exception of some sea turtles (e.g., [10,39]). Furthermore, the scant existing data are contradictory, some supporting an increase of nesting at full moon (e.g., [40]), other providing no evidence for such a pattern (e.g., [10,39,41]). To help fill this gap, here, we examine the effect of multiple environmental conditions (rainfall, river levels and air temperature) and moon phase on the timing and frequency of nesting of the South American freshwater turtle (*Podocnemis unifilis*) across multiple years, and from a single population whose nesting behavior and reproductive traits were previously reported [42,43].

Although *P. unifilis* is diurnal, nesting events are strictly nocturnal, highly seasonal and closely synchronized with the river flood regime/low flow [24,42]. Previous studies in this species reported qualitative patterns between nesting and environmental conditions (e.g., [24,40,44]), but quantitative tests are limited (i.e., related to river level [45]), precluding conclusive inferences. Here, we take a quantitative approach to explicitly address whether lunar conditions and other environmental factors affect the timing and frequency of nesting in this species.

2. Materials and Methods

2.1. Study Area

Data on the extent of the egg-laying season and nest counts for the South American freshwater turtle *Podocnemis unifilis* were collected over three years (1999–2001) from late January through mid-March when nesting is known to occur [27]. The study was conducted on 11 nesting beaches distributed along a 13.1 km stretch of the Tawadu-Nichare Rivers, a pristine area of the Caura-Orinoco

Basin, Southern Venezuela (Figure 1a,b), characterized by two distinct climatic seasons: a rainy season spanning May through September and a dry season spanning January through March. All beaches were monitored daily, starting soon after becoming exposed at the end of January, and inspected twice a day during early morning (6–12 am) and late afternoon (4–7 pm) hours until the end of March. This was achieved with two teams of three people each, who were assigned different beaches. Beaches were reached by boat (one per team) and nests were identified through direct observation while walking along transects as described below.
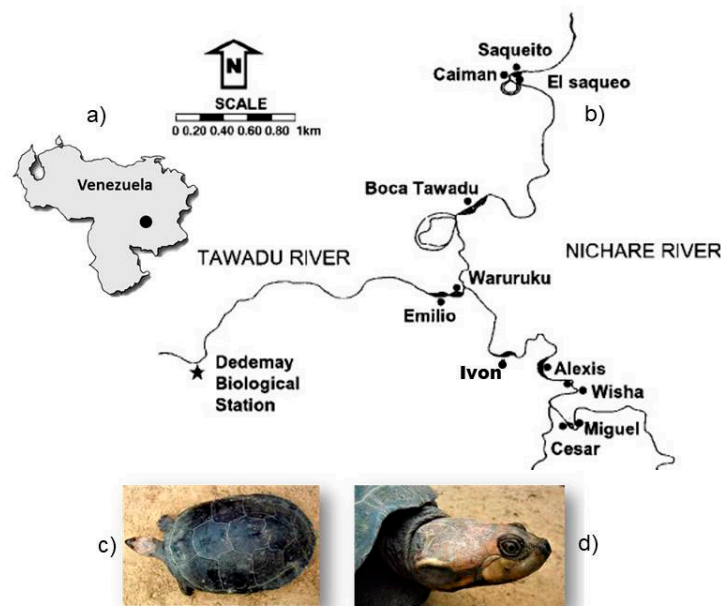

Figure 1. Map of Venezuela (study area in black dot, subpanel **a**) and map of the study area showing the 11 beaches that were monitored during nesting season 1999, 2000 and 2001 (El Saqueo = 6°23′39′′ N, 64°57′31′′ W; Caiman = 6°23′38′′ N, 64°57′36′′ W; Saqueito = 6°23′42′′ N, 64°57′19′′ W; Boca Tawadu = 6°22′01′′ N, 64°58′16′′ W; Waruruku = 6°21′02′′ N, 64°58′18′′ W; Emilio = 6°20′59′′ N, 64°58′29′′ W; Ivon = 6°20′12′′ N, 64°57′51′′ W; Alexis = 6°20′07′′ N, 64°57′27′′ W; Wisha = 6°19′47′′ N, 64°57′13′′ W; Cesar = 6°19′19′′ N, 64°57′14′′ W; Miguel = 6°19′24′′ N, 64°57′17′′ W) (subpanel **b**). Additional beaches existed within the study area that were used negligibly or not at all by *Podocnemis unifilis* females during the study period. Mature adult female of *P. unifilis* (dorsal—subpanel **c**; head view—subpanel **d**; photographs by Andrés Felipe Aponte). Mean size (linear length of carapace) of mature adult females in the study area was 37.4 ± 2.92 cm (*n* = 901).

2.2. Nesting Season

Female nesting forays initiated at the onset of the dry season (end of January–early February), when the river levels dropped exposing the open sandy beaches used by *P. unifilis* as nesting grounds (Figure 2a,b). The length of the nesting season was defined as the earliest date to the latest date of oviposition. Within this period, days interrupted by flooding events (years 1999 and 2000) were not included in the data analysis, but were counted to estimate the total length (in days) of the nesting season each year and to calculate the average total rainfall and river level by year.
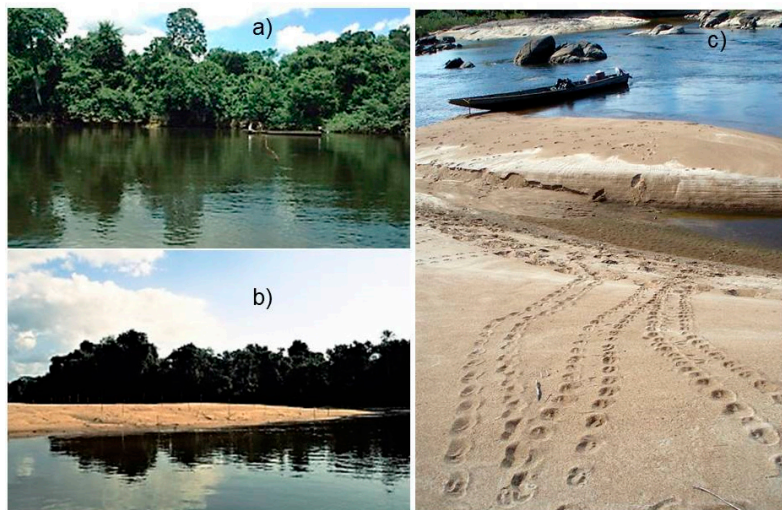
Figure 2. Nichare River, showing high flow (**a**), nesting grounds exposed during low flow (**b**), and tracks left on the beach by female *Podocnemis unifilis* during their nesting forays (**c**).

2.3. Timing of Nesting

When (date) and how many nests were laid by females was recorded for each beach. Nests constructed each night were easily located the following morning by inspecting the beaches systematically along lengthwise transects 2 m apart throughout each beach (15 to 40 transects per beach, depending on beach size), and by following fresh female tracks which are highly visible (Figure 2c). A small stick was placed on each nest site indicating the nest number and nesting date.

2.4. Environmental Variables

Daily measurements were taken for three environmental variables that were suggested as important cues used by other freshwater turtle species to trigger oviposition (e.g., [17,46]): rainfall (mm), river level (m) and air temperature (°C). These variables were measured at the Dedemay Biological Station (6°21′17.9″ N, 64°59′47.9″ W; Figure 1b) during early morning hours, and river levels were registered at least in one other location of the Nichare River. Daily rainfall was registered using a weather rain gauge to the nearest 0.1 mm. River level gauge data was registered using two 5 m long measurement tapes held in a vertical pole placed permanently on the river at two locations separated 10 km from each other. Air temperatures were recorded using a digital maximum-minimum thermohygrometer (accuracy 0.1 °C) placed on a tree 1 m from the ground, protected from sunlight and rain.

2.5. Lunar Cycle

The lunar cycle was registered daily as one of four categories: full moon, last quarter, new moon and first quarter. The exact date of the peak of each phase of the lunar cycle was obtained using data from the U.S. Naval Observatory, Astronomical Applications Division [47]. The 7-day interval (week) around the full moon and the new moon was determined by selecting the three days prior to and following the peak date of each phase. The remaining days were treated as first and last quarter, following [48].

2.6. Data Analysis

Several analyses were performed to test whether patterns of oviposition were associated with local environmental conditions. First, to assess whether various environmental parameters affected nesting, linear regression analyses were performed between the number of nests laid per day (dependent variable) and 1) daily rainfall or 2) river level as independent variables. To test for air temperature effects on nesting behavior, we compared for each year the distribution of nesting events by maximum daily

air temperature to both a normal and a uniform distribution, using the 'fitdist' function in the R-package Fitdistrplus, version 1.0.14 [49] and the Cramér–von Mises criterion (TCvM). This approach tested the null hypothesis that nesting is independent of temperature, in which case a uniform distribution of oviposition events is expected across all temperature values. Additionally, to identify whether there were differences in nesting associated with the lunar cycle, an analysis of variance (one-way ANOVA) was performed to compare the number of nests laid per day among the four phases of the lunar cycle. When statistical differences were detected, Tukey–Kramer post-hoc comparison tests were conducted to determine whether the mean number of nests laid per day during full moon phase (the week around the full moon) was greater than those laid during the new moon phase (the week around the new moon). We focused on differences between these two moon phases to test the hypotheses that nocturnal nesting is part of a camouflage strategy by females to avoid detection, and thus more nesting should occur during the darkest nights, versus the alternative hypothesis that visual cues are a critical component of female nesting, in which case nesting should be concentrated during the lighter nights when such cues are more detectable.

All data and residuals were tested for normality (using Shapiro–Wilk test), and if their distribution was significantly different from normal, variables were natural-log-transformed prior to their analysis, as described previously [50]. Analyses were performed in JMP Pro 13 [51] and R-package version 1.0.14 [49].

3. Results

3.1. Nocturnal Nesting Behavior

In all three years, the nesting behavior of female *P. unifilis* was nocturnal, as all females emerged to nest only during night-time hours (fresh female tracks were found exclusively during the daily early morning inspections and never during the afternoon inspections). Additionally, we found that females laid their eggs either individually, or in groups of 2 to 17 females.

3.2. Effect of Environmental Variables on Nesting

We did not find a significant relationship between daily rainfall and the number of nests laid per night (Table 1). Rainfall was much higher in 1999 (Figure 3a) and 2000 (Figure 3b) when nesting beaches flooded and interrupted oviposition, and only for these two years there was a negative linear relationship between river levels and the number of nests laid per night (Table 2). In 2001, however, no flooding occurred during the nesting period but flooding took place after the hatching season ended. In 2001, there was a significant positive relationship between river level and the number of nests laid per night (nesting was more frequent at higher river levels), although river levels were considerably more stable that year compared to the previous two years (Figure 3c). In 1999 and 2000, the total nesting season (including flooding days) lasted 36 (nests = 352) and 40 (nests = 422) days, respectively, whereas it lasted 29 days (nests = 326) in 2001.

Table 1. Results from regression analyses of number of nests oviposited vs. daily rainfall (mm) during three consecutive years. Variables were Log_n-transformed.

Year	Rainfall (mm) Mean ± SD	F-value	df	p-value	R^2	Slope
1999	3.79 ± 8.68	0.70	1,30	>0.05, ns	0.02	−0.20
2000	1.85 ± 3.63	0.80	1,35	>0.05, ns	0.02	0.21
2001	0.26 ± 0.58	0.005	1,27	>0.05, ns	0.0002	0.03

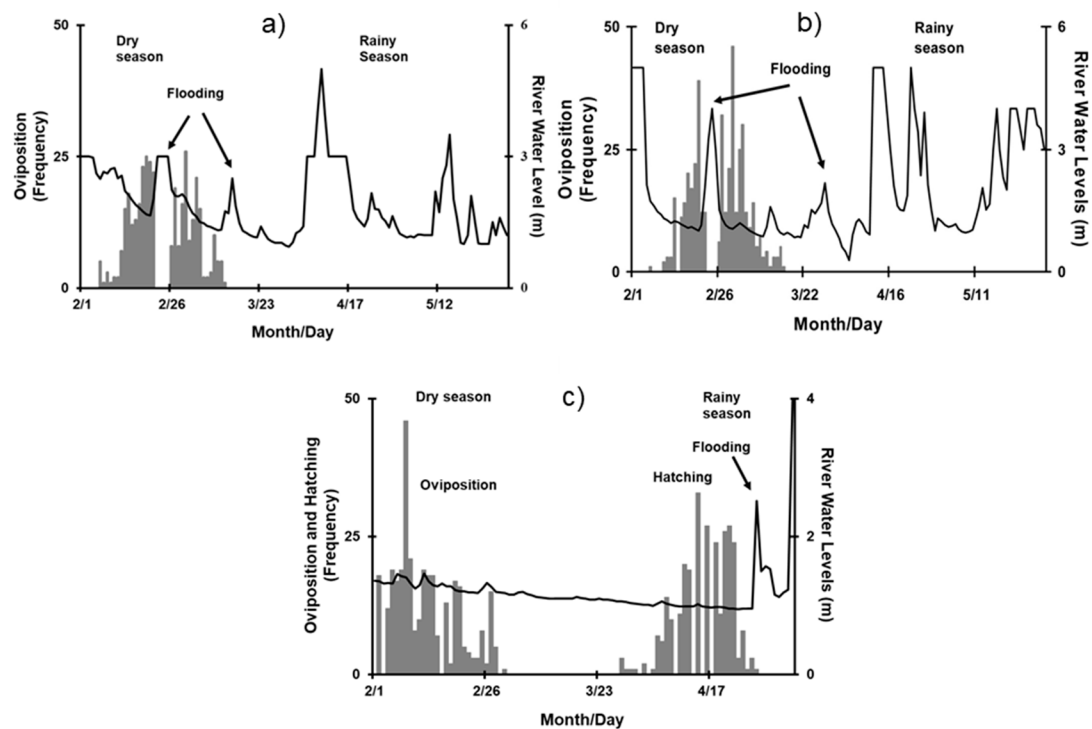Abbreviations: R squared (R^2); degrees of freedom (df); non-significant (ns).

Figure 3. Daily river fluctuations (solid black line) and nest numbers (grey bars) during the dry and rainy season of the Tawadu-Nichare Rivers, Venezuela. Three nesting seasons are (**a**) 1999, (**b**) 2000, and (**c**) 2001. For year 2001 grey bars at the right side represent the hatching portion. The arrows points to when beach flooding occurred.

Table 2. Results from regression analyses of number of nests oviposited vs. daily river level (m) during three consecutive years. Variables were Log_n-transformed (except for year 1999).

Year	River Level (m) Mean ± SD	F-value	df	p-value	R^2	Slope
1999	2.21 ± 0.84	0.81	1,30	>0.05, ns	0.03	−2.71
2000	1.39 ± 0.68	4.06	1,35	>0.05, ns	0.10	−2.38
2001	1.29 ± 0.08	14.15	1,27	<0.001	0.34	8.14

Abbreviations: R squared (R^2); degrees of freedom (df); non-significant (ns).

Every year, a normal distribution provided a better fit to the oviposition data than a uniform distribution (1999: TNormal = 4.77; TUnif = 10.73; 2000: TNormal = 3.27; TUnif = 10.46; 2001: TNormal = 3.15; TUnif = 7.59). This indicated that nesting events were concentrated at intermediate temperature values (Figure 4a–c), yet that value changed annually (28 °C in 1999, 34 °C in 2000, and 33 °C in 2001). We also observed a seasonality in daily maximum air temperature with increasing temperature over the reproductive season that was more marked in some years than others (Figure 5a–c).
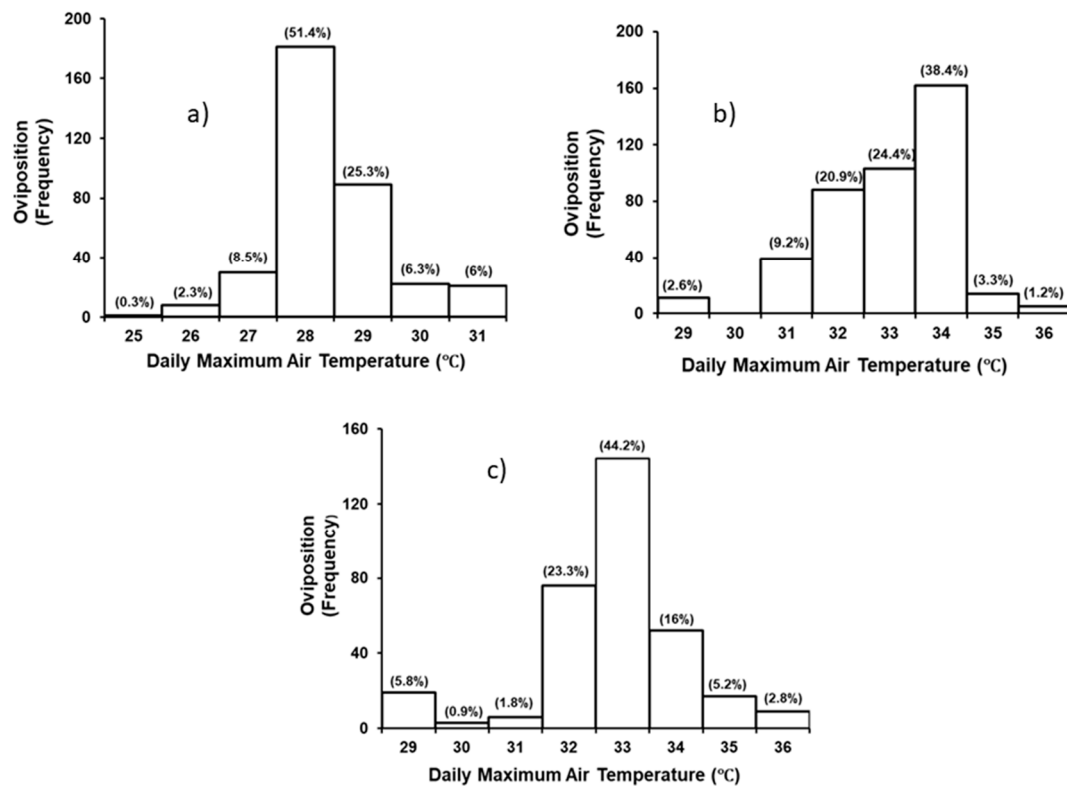
Figure 4. Number of *Podocnemis unifilis* turtles nesting in relation to the maximum daily air temperature in the Tawadu-Nichare Rivers, Venezuela. Three nesting seasons are (**a**) 1999, (**b**) 2000, and (**c**) 2001. Numbers in brackets indicate the total percent of nests laid at each temperature interval.
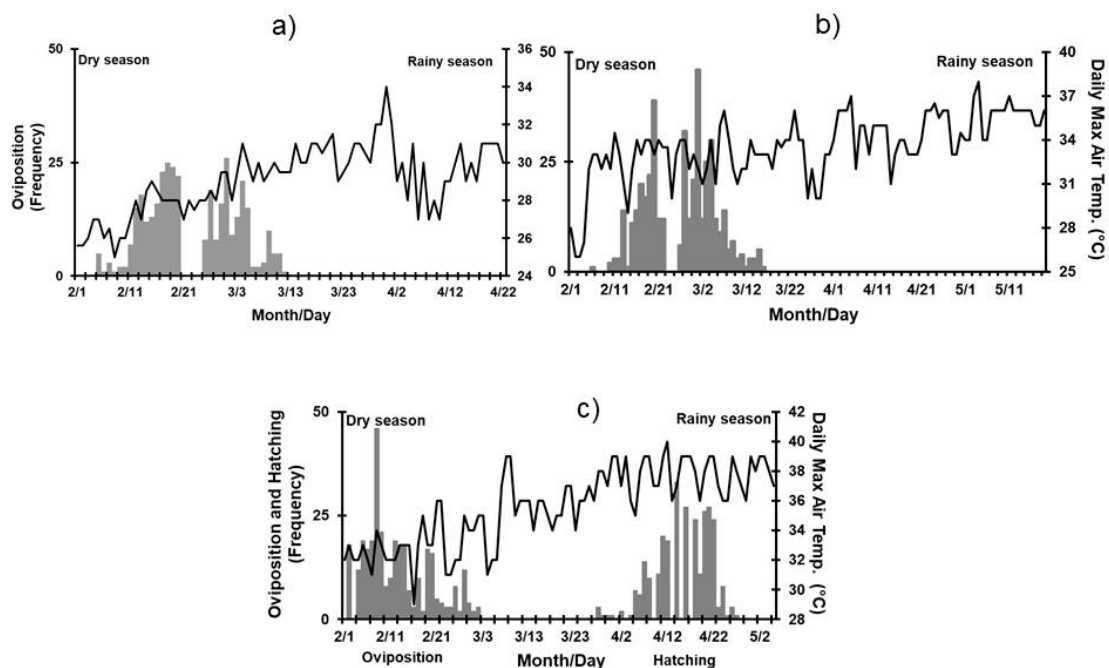

Figure 5. Seasonality in daily maximum air temperature (solid black line) and nest numbers (grey bars at the left side) with increasing temperatures over the three reproductive seasons: (**a**) 1999, (**b**) 2000, and (**c**) 2001. Fluctuations are more marked in some years than others. For year 2001, grey bars at the right side represent the hatching portion.

3.3. Effect of the Lunar Cycle on Nesting

Across all years, there were significant differences in the average number of nests laid per night among the phases of the lunar cycle (Figure 6a–c). Pairwise comparisons revealed that significantly more nests were laid per night during the week around the full moon than around the new moon in 2000 and 2001, but not in 1999 (Table 3). However, in 1999, the single night on which the most females oviposited was during the full moon phase (Figure 7a). Thus, all data combined indicate that females increased nesting during the full moon phase, a trend made evident when oviposition was visualized as a function of the lunar cycle (Figure 7a–c).
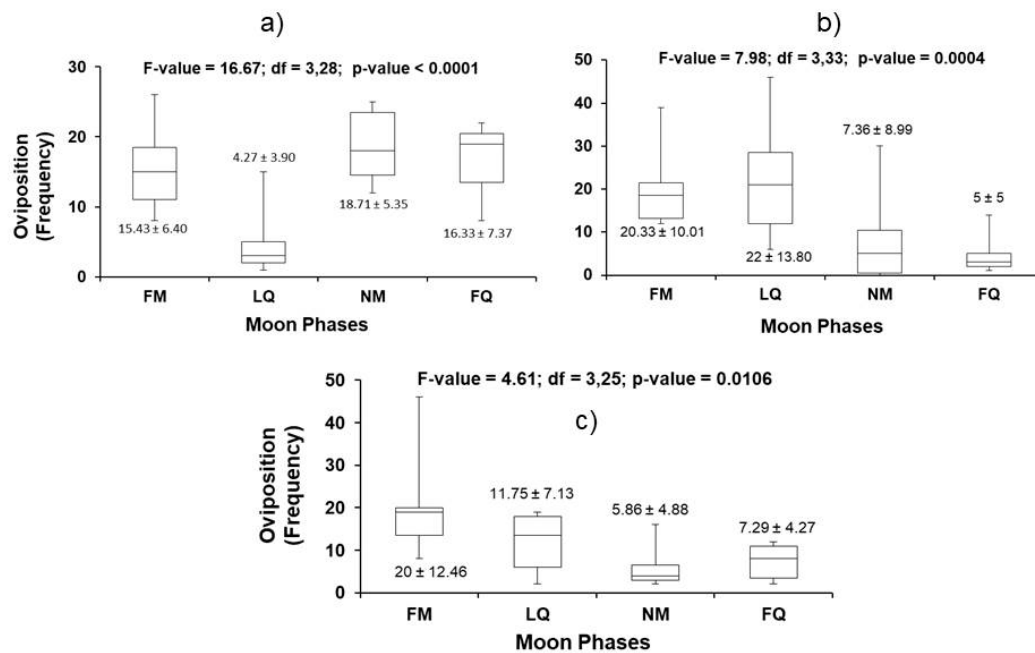

Figure 6. Box-plot with error bars of the analysis of variance (one-way ANOVA) results comparing the average number of nests oviposited per day for the four phases of the lunar cycle (full moon—FM, last quarter—LQ, new moon—NM, first quarter—FQ) over the three reproductive seasons: (**a**) 1999, (**b**) 2000, and (**c**) 2001. Numbers below or above the error bars represent the average and standard deviation (average ± SD).

Table 3. Results from the Tukey–Kramer test (T-K) between full moon and new moon phases, using a Qcritical (Qc) of k = 4 and alfa = 0.05. Variables were Log_n-transformed.

Year	Full Moon Mean ± SD	New Moon Mean ± SD	Q_s	Q_c	T-K p-value
1999	15.43 ± 6.40	18.71 ± 5.35	1.69	3.86	>0.05, ns
2000	20.33 ± 10.01	7.36 ± 8.99	3.98	3.82	0.039
2001	20 ± 12.46	5.86 ± 4.88	4.77	3.89	0.012

Abbreviations: degrees of freedom (df); non-significant (ns), Tukey-Kramer test (T-K), Qstatistics (Qs).
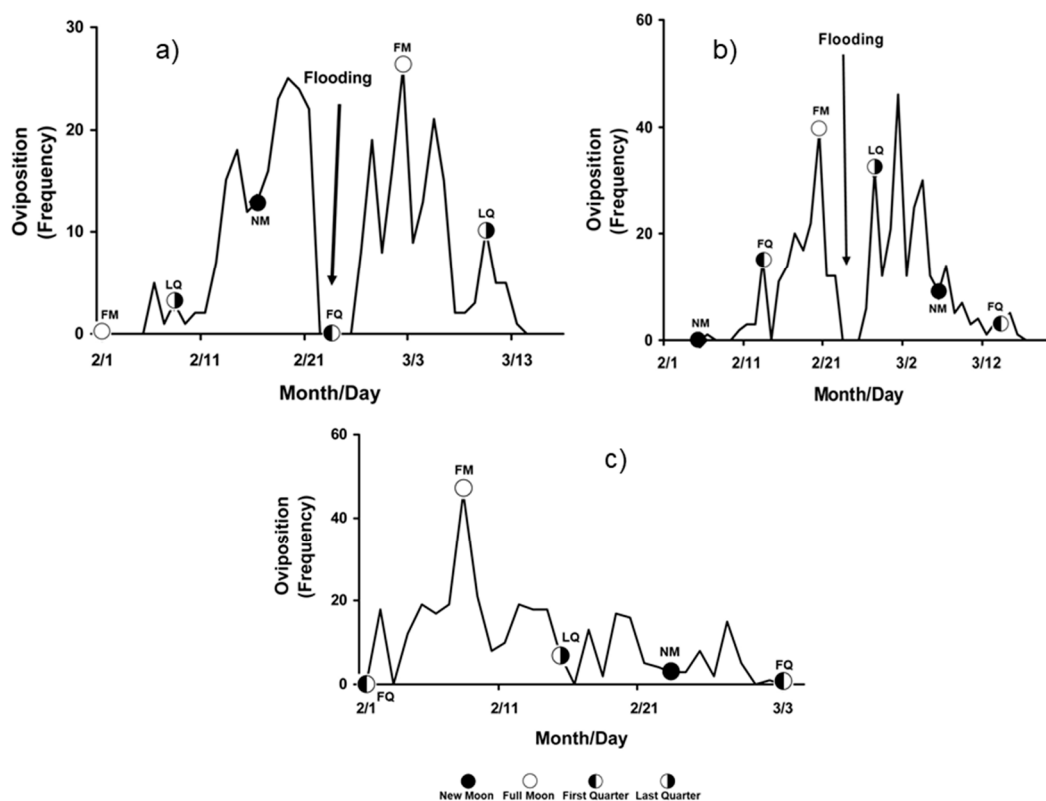
Figure 7. Daily oviposition frequency and lunar cycle in the Tawadu-Nichare Rivers, Venezuela. The three nesting seasons are (**a**) 1999, (**b**) 2000, and (**c**) 2001. Lunar cycle is denoted as: NM = new moon, FQ = first quarter, FM = full moon, LQ = last quarter.

4. Discussion

Egg-laying organisms have limited options for ensuring reproductive success, and adjusting their nesting activities based on local environmental conditions may be one mechanism to improve the survival and fitness of their offspring. Previous studies of the freshwater turtle *Podocnemis unifilis* reported anecdotal accounts of the relationship between nesting and various environmental conditions, but a quantitative analysis was never performed. In this study, the relationship between nesting behavior and various environmental variables was examined to explicitly address whether these factors affect the timing and frequency of nesting in this species, and the strongest effects were detected for air temperature and the lunar phases, such that turtles tended to nest more frequently at intermediate values of maximum daily air temperature, and during the full moon phase rather than the new moon phase, as described below.

During the study period, all nesting activity was nocturnal, consistent with previous observations of this species in other locations (e.g., Perú [44], Ecuador [45], Brazil [52] and Colombia [53]). Females tended to nest in groups of 2 to 17 individuals at a time, suggesting that *P. unifilis* may nest synchronously. This observation agrees with recent evidence of communal nesting in this species [42,44], which indicated that nesting behavior in *P. unifilis* may be in part the result of communal social behavior (social facilitation) rather than a female's exclusive response to environmental cues [42]. Further, though *P. unifilis* females were generally thought to nest individually [54], small aggregations of up to five to nine females were previously observed [53,55], and in one location (Pacaya River, Perú), between 20 and 46 females were observed nesting simultaneously [44]. Our results provide further support for the hypothesis that nesting behavior in *P. unifilis* can be synchronous, at least occasionally (see also Escalona et al. [42]).

No significant relationship was found between daily nesting activity and rainfall, similar to other river turtles (e.g., *Chrysemys picta*, [56]). However, nesting in our study was concentrated at the time of

the year when water levels are decreasing and nesting grounds emerge, as observed in other localities (i.e., Capanaparo River, Venezuela, [24]; Aguarico River, Ecuador, [45]; Solimões River, Brazil, [57]), in other Podocnemididae species (e.g., *P. expansa* [23] and *P. sextuberculata* [58]), and other river turtles (e.g., *Tryonix muticus* [59], *Apalone mutica* and *Glyptemys insculpta* [60]). Yet, it was surprising to find little relationship within the nesting period between river water levels and nesting activity in our study, and to detect a positive correlation between the number of nests laid and river level. Indeed, there was no significant relationship between nesting activity and river levels for 1999 and 2000, but in 2001 (a year with no flooding until after hatching; Figure 3c) the number of nests laid was positively associated with river levels. A closer inspection of Figure 3c resolves this apparent paradox. Figure 3c reveals that nesting activity in 2001 took place during a time of the year when the general trend of the water level was decreasing. These lower levels are part of the yearly cycle that exposes nesting grounds during the dry season. Early in the season, nesting intensity increased and reached a peak as the river level was dropping, but later in the season when fewer females were left to nest, the number of nesting events decreased as the river continued to fall.

An important finding in our study is that daily maximum air temperature was associated with the abundance of nesting events. Indeed, daily temperature was normally distributed, such that most females nested on days that were intermediate in temperature when compared to the entire nesting season, although this value differed somewhat among years. To the best of our knowledge, this result is the first such report for this species, and perhaps for any tropical river turtle. Furthermore, although effects of air temperature on nesting behavior are known in temperate freshwater turtles, such that thermal effects on nesting appear to be a trait shared between temperate and tropical lineages, it is uncertain if nesting in temperate turtles also conform to a normal distributed pattern as observed in our study perhaps because the effect of temperature on nesting date is often inspected using correlation analysis (e.g., [15,16,18]). Here, we found no linear relationship between temperature and nesting frequency (results not shown). Nonetheless, similar to *P. unifilis*, temperate turtles display temperature preferences for egg-laying and have thermal limits. In temperate turtle lineages the timing of nesting is synchronized with the warmest time of the year, but the onset of the nesting season varies year to year, such that females may start earlier in one season and later in another season if air temperatures are warmer or colder, respectively [15,56]. Moreover, nesting activities within a species may increase or decrease with warmer temperatures depending on geographic location [17,61]. This reproductive variability in oviposition year to year among and within species has been interpreted as a result of individual plasticity in nesting phenology [62], as may also be the case for *P. unifilis*, given the changes in the intermediate temperature values preferred by females among years. In this sense, nesting females have the potential to shift their nesting behavior rapidly and reversibly based on the ambient temperature regime of a given nesting season, and such responses may be synchronized with thermoregulatory strategies (basking) prior to oviposition that are stimulated when suitable thermal conditions are available to optimize egg-shell maturation and ensure their successful nesting [63].

Finally, the strongest temporal nesting pattern observed in this study was related to the lunar cycle. Significant differences in the number of nests laid were detected between the four phases of the lunar cycle, and more nests were laid per day during the week of the full moon than during the week of the new moon. This suggests that *P. unifilis* relies on visual cues for nesting. Perhaps females nest on bright nights to minimize predation of themselves and their nests, as the majority of nocturnal species show an inverse relationship between activity and lunar light [64]. Another potential explanation is that more visibility is a requirement for social nesting. Turtles of the genus *Podocnemis*, particularly *P. expansa* and *P. unifilis*, are well known colonial nesters, and this behavior was more prominent prior to human colonization of their habitat and its subsequent exploitation [26,65]. This implies that some form of social behavior, such as social facilitation (i.e., influence of one animal's behavior on that of its associates [66]), combined with visual cues, may trigger the initiation of oviposition and synchronous nesting in this species [42].

In summary, we found that females of *Podocnemis unifilis* emerge to nest in the Tawadu-Nichare Rivers at the beginning of the dry season as the river levels drop, exposing the nesting grounds. Nesting events were concentrated at intermediate daily maximum air temperature relative to the entire nesting season, but preferred values changed annually. However, nesting events within this reproductive season appeared independent of rainfall trends. Our finding that females tended to nest in groups and these were largest during nights of full moon compared to darker nights, also suggests that females rely on visual cues to initiate nesting, which could be associated with social behaviors typical of colonial nesters (e.g., social facilitation [42]), or perhaps to minimize predation. If visual cues are important for nest placement and reproductive success, this implies that areas affected by humans (i.e., heavily harvested) are likely to alter female behavior (e.g., nest individually and on dark nights more frequently) and potentially nest selection and survival. Long-term studies are needed to test these hypotheses and to help predict female reproductive response and survival in the face of climate change. For instance, climate change may disrupt the natural pattern of the river flooding cycles and could magnify the effect of the El Niño and La Niña weather episodes. Interestingly, the years 1999 and 2000 were characterized by extreme flooding events that resulted in zero hatching, and both years were under the effect of La Niña, an event that is related to above-normal precipitation levels, especially in northern South America [67,68]. This suggests that extreme changes in the seasonal river flow cycles in the Nichare, as a consequence of climate change, may negatively impact nesting activities and the reproductive success of *P. unifilis*.

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