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Neglecting cooler low-season nest protection could deprive sea turtle populations of valuable hatchlings

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ABSTRACT

Reproductive seasonality is present across species and phyla. Many species retain seasonal patterns even in tropical regions where climatic variations may be less apparent. Environmental features and large-scale environmental cues play a role in species seasonality and can have major effects on reproductive success. In organisms that present environmental sex determination, the season in which individuals reproduce has consequences for their primary sex ratio. Here we looked at the possible effects on fitness and primary sex ratio for the olive ridley sea turtle (*Lepidochelys olivacea*) when nesting during peak and low nesting seasons. In the eastern Pacific, peak olive ridley sea turtle nesting occurs during the warmest months, which coincide with the rainy season. Yet, as nesting takes place year-round, a small proportion of the nests laid during the dry part of the season are exposed to contrasting environmental conditions. Most of the studies on Pacific coast sea turtles have estimated sex ratios produced during the rainy, high abundance period when most conservation activities are focused. Thus, dry-low season nests have on the whole, been overlooked. Here we compared sex ratios and hatchling fitness for offspring produced during the dry and rainy seasons in 2015. We found that olive ridley clutches incubated during the dry-low season were exposed to lower temperatures, yielded higher hatchling success, mainly produced male offspring and larger, heavier hatchlings with better locomotor abilities. This highlights that, for sea turtles, protecting nests outside of the peak nesting season may help future population viability by yielding higher proportions of males with greater locomotor capacities and, thus, survival. Our results highlight the critical value of monitoring and protecting species during their entire reproductive period and not concentrating all resources on the peak season to collect more data and protect a greater number of organisms. Our results suggest that monitoring low-season reproductive effort (nests in this case), albeit at much lower densities, would be critical for understanding and possibly ensuring population viability and adaptation to contemporary climate change and anthropogenic threats.

1. Introduction

Reproductive seasonality is present across species and phyla. Even in tropical regions where climatic variations may be less apparent, many species maintain some level of seasonal pattern. In marine species, reproductive seasonality may be linked to marine productivity (Afán et al., 2015), local environmental features, and large-scale environmental cues.

In the eastern Pacific, peak olive ridley sea turtle (*Lepidochelys olivacea*) nesting occurs during the warmest months, coinciding with the rainy season from July to October (Hart et al., 2018; Morales-Mérida et al., 2022). However, this species nests year-round, exposing the comparatively small number of nests laid in the dry and cooler months to environmental conditions that contrast with those of the majority of

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nests that incubate during the summer. For example, incubation temperature and humidity are markedly different between the peak and low abundance portions of the season. Temperature is one of the critical factors for the successful embryonic development of sea turtles (Miller, 1985). However, turtle embryos have a narrow thermal tolerance range between 25 °C and 35 °C (Howard et al., 2014), wherein the actual temperature and the duration of exposure impact survival. Olive ridley clutches can survive higher temperatures (>37.9 °C) but only over short durations, with detrimental effects on hatchling emergence success and locomotion performance (Maulany et al., 2012a). Olive ridley turtles, which exhibit temperature-dependent sex determination (Mrosovsky and Pieau, 1991; Broderick et al., 2000; Charruau and Hénaut, 2012), present latitudinal variation in the reported pivotal temperatures, i.e., at which we can expect 50 % of each sex within a clutch (e.g. Costa Rica: 30.5 °C ± 0.13 °C; Mexico: 30.16 °C ± 1.9 °C; Wibbels et al., 1998; Abreu-Grobois et al., 2020). As the incubation temperature rises above the pivotal within a sea turtle clutch, the proportion of females increases to the point of producing all females. The opposite is true as the temperature falls below the pivotal, and all-male production can occur in the lower viable temperature scale. Additionally, rainfall is a factor that varies significantly between seasons, especially in the tropics. Humidity within the nest environment influences moisture uptake by embryos, resulting in longer incubation durations and larger hatchlings (Delmas et al., 2007) and may also affect the sex ratio through temperature changes as a result of evaporation (Godfrey et al., 1996; Wyneken and Lolavar, 2015; Sifuentes-Romero et al., 2018).

Recent studies have attempted to understand the role of humidity during embryo development and how moisture affects phenotype and sex determination. However, moisture and temperature are interconnected, and it can be difficult to isolate the individual effects that these abiotic parameters have during embryogenesis. For example, male hatchlings can be produced above pivotal temperature if there is sufficient moisture (Wyneken and Lolavar, 2015) and temperature appears to have a greater effect during the earlier stages of embryo development and therefore sex determination (Sifuentes-Romero et al., 2018). Once sex is determined and embryo growth becomes the dominant process, moisture instead of temperature helps sustain higher rates of metabolism and yolk utilization. Nevertheless, Gatto et al. (2021) found that moisture had minimal effects on hatchling traits when they compared hatchlings incubated under dry and wet conditions and thus temperature likely has a greater role in determining hatchling traits than moisture.

These factors make sea turtles particularly vulnerable to climate change (Fuller et al., 2013; Refsnider and Janzen, 2016) which is predicted to cause increased not only incubation temperatures but also sea level (IPCC Intergovernmental Panel on Climate Change, 2007). Additionally, storms that are expected to become stronger and more frequent will further impact and modify turtle nesting habitat (Hawkes et al., 2009; Hawkes et al., 2013; Fuentes et al., 2010; Fuentes et al., 2011). Nonetheless, a female turtle can influence reproductive success through the choice of nesting location, nesting timing during the year, and depth at which she lays her eggs (Booth and Freeman, 2006; Santidrián Tomillo et al., 2017). However, even with plasticity of the nesting seasonality (Patrício et al., 2019), sea turtles may have difficulty adapting to rapid climate change (Hawkes et al., 2009; Tilley et al., 2019). Olive ridleys may be the most adept of sea turtles to cope with environmental change as a consequence of their multiple reproductive strategies and flexibility in their nesting site fidelity (Tripathy and Pandav, 2007) and, therefore, may be able to utilize sites that are less impacted by environmental change, and which result in healthy offspring.

Phenotypical variation has been used to study how abiotic changes affect hatchling fitness (Fisher et al., 2014; Liles et al., 2019; Ríos-Huerta et al., 2021). In warmer nests, hatchlings hatch sooner and are smaller as less yolk is converted into tissue (Booth et al., 2004). Smaller hatchlings are slower during the crawl towards the ocean and during initial displacement from coastal zones (Booth and Evans, 2011) when compared with their larger counterparts. Furthermore, hatchlings must be able to maintain a 24–72 h frenzied swimming period upon entering the ocean. Larger hatchlings, which are stronger swimmers than smaller individuals, could be more capable of avoiding the large aggregations of predators offshore of the nesting beach Gatto et al., 2022. Turtles in poor condition upon hatching have a reduced probability of avoiding predation (Wyneken and Salmon, 1992; Booth et al., 2004; Booth, 2009).

Since Mexico's 1990 ban on sea turtle use and consumption, multiple nesting beach conservation programs have been created to protect clutches from illegal take and predation. However, with limited resources, many cannot monitor nesting beaches year-round. For species such as the olive ridley that nest along the Mexican Pacific, limits in resources force conservation programs to focus on the rainy season months when nesting is significantly higher (García et al., 2003), leaving nests laid during the latter part of the nesting season without protection. Dry season nests are often not protected or counted, leading to an impression from regional reports that nesting does not occur or is insignificant during this period. Registering dry season nesting could be extremely important as their different abiotic conditions may affect hatchling sex ratio, phenotype, and fitness. Also, as sea turtle nesting seasons have been shown to shift in response to changes in ambient temperatures (Weishampel et al., 2004; Pike et al., 2006; Witt et al., 2010; Morales-Mérida et al., 2022), these behavioral changes may be an adaptive strategy of the nesting turtles in response to climate warming. Nevertheless, recent studies on Loggerhead turtles suggest contrasted responses depending on the population (Almpanidou et al., 2018; Monsinjon et al., 2019a). The drivers of sea turtles' nesting phenology are yet to be fully understood (Mazaris et al., 2013; Monsinjon et al., 2019b), especially in the context of climate change (Patrício et al., 2021).

Majahuas beach is part of the Playón de Mismaloya rookery, where olive ridley turtles would nest in *arribadas* before the population collapsed in the late 1970s due to the unsustainable commercial harvests of nesting females. The rookery's collapse resulted from a 99 % reduction in nesting females (Abreu-Grobois and Plotkin, 2008), and a concomitant reduction in genetic diversity (Rodríguez-Zárate et al., 2013). Despite conservation efforts starting in 1985 at Majahuas beach, no arribada has taken place since the collapse. That said, the area's solitary olive ridley nesting density is high when compared with the regional average (García et al., 2003). The local fishing cooperative Roca Negra runs conservation activities in collaboration with other community members to help protect nesting turtles. Members take turns from June to November to conduct nightly beach patrols and relocate sea turtle clutches to a protected beach hatchery. Once the eggs hatch, they release the hatchlings into the ocean. Beach patrols are sporadic from December to May and focus on locating leatherback (*Dermochelys coriacea*) and green turtle (*Chelonia mydas*) nests that are occasionally laid during the cooler months. Despite the long history of conservation activities, no studies have occurred at the site, and information on the number of adult females, and success of conservation activities have not been assessed.

This study, which will be helpful to improve future conservation strategies, aims at acquiring a better understanding of nest characteristics and hatchling phenotypes outside of the peak season when nests are not effectively protected from illegal take. Our goals were to 1) monitor the number of nesting turtles during 12 months; 2) compare incubation temperatures for nests incubated during the dry and rainy seasons; 3) determine if hatching success varied between these two parts of the season; 4) estimate sex ratios produced in monitored nests; 5) determine if incubation season influenced hatchling fitness and phenotypes; and, 6) discuss the conservation implications of the results.

2. Materials and methods

2.1. Study site

Majahuas beach is located in Jalisco state between 19°50′41″N 105°22′40″W and 19°46′14″N 105°19′38″W on the Pacific coast of Mexico. Majahuas is the southernmost 11 km of the Playón de Mismaloya sea turtle sanctuary. A RAMSAR mangrove wetland backs the beach.

The nesting season begins in June and extends into the following year. Rains occur between June and November, with 80 % occurring between July and October, while the dry period lasts up to 6 months, from December to May. Mean annual rainfall is 748 mm ± 119 (585-961 mm) varies between with a mean annual temperature of 24.9 °C (12–35 °C). Mean monthly temperatures vary with a minimum from 14.8 °C to 22.9 °C and a maximum from 29.1 °C to 32.0 °C (Bullock, 1986).

2.2. Nest collection and incubation

Nightly nest monitoring by the fishing cooperative Roca Negra recorded 1954 nests in 2015, from which data were collected. Nests were protected via relocation to a hatchery (see below and Sosa-Cornejo et al., 2022) to avoid illegal take of eggs, predation, and erosion. We selected 86 nests at random (dry season: N = 40; rainy season: N = 46) to monitor incubation temperature and hatching success. Of these nests, 51 hatched and the sex ratio was estimated for these clutches. Phenotype and fitness tests were conducted on the hatchlings from 38 nests (dry season: N = 28 nests; rainy season: N = 10 nests).

Nests were collected during nightly beach patrols by either locating the recently laid nest via tracks or by encountering the nesting turtle and retrieving her nest. On encountering a female, we waited until she entered a trance-like state before taking morphometric measurements. Curved carapace length (CCL) and curved carapace width (CCW) were taken using a metric tape marked in 0.1 cm intervals. CCL was measured from the nuchal scute to the posterior tip of the supracaudal scute, and CCW from the widest part of the carapace with the tape following the curvature.

On locating a nest, the top egg was checked to make sure that the characteristic white spot on the surface of the eggshell, indicating that the embryo had begun development, was absent before proceeding. The eggs were carefully removed from the egg chamber and counted. Nest depth was measured by placing a pole across the top of the mouth of the nest, and the distance was taken from the pole to the bottom of the nest chamber. For each nest, we recorded the beach section and zone where it was laid (Intertidal (beach face to the berm) = A, Open beach (the berm to the vegetation line) = B, and Beach (vegetation line to the dune) = C). Eggs were transferred to a plastic bag and transported to the hatchery, 2 km from the southern end of Majahuas beach using a quad bike. Only newly laid clutches were used for temperature, phenotype and fitness tests and were identified by the female turtle being observed on the beach or her tracks being fresh in the receding tideline. Care was taken to limit vibrations during transport, and transport from the nest chamber to the hatchery in less than an hour.

Between February and May 2015 patrols were carried out on foot due to mechanical problems with the quad bike. This resulted in shorter patrols during the dry season. Each nest was reconstructed using a manual tree planter to achieve a standardized depth of 45 cm, and then the nest chamber was formed by hand to imitate the shape of a natural nest made by a female turtle. Eggs were transferred into the artificially dug chamber, and a temperature logger (HOBO UA-001-08, Onset USA) was placed in the center of each clutch before the eggs were covered with sand. Temperature loggers measured 5.8 × 3.3 × 2.3 cm and were programmed to register the hourly temperature (accuracy of ±0.5 °C).

Meteorological observations (daily maximum, minimum, and mean air temperature and precipitation) were obtained from the Universidad Autonoma de Mexico's Biological Research Center in Cuixmala, Jalisco from 1 January 2015 to 31 December 2015 (located 55 km from Majahuas beach).

2.3. Hatchling phenotype and fitness

Phenotype and fitness tests were carried out on hatchlings from 38 clutches. We selected 20 hatchlings at random upon emergence to partake in fitness tests and for morphological measurements. When hatching success was too low to provide a total of 20 hatchlings, we used those that were available. Supplementary Table 2 states the number of hatchlings studied from each nest. Hatchlings were weighed using an electronic balance (±0.1 g), and their straight carapace length (SCL), straight carapace width (SCW), and carapace depth were measured using an electronic caliper (±0.1 mm). Tests to measure crawling speed (cm s^{-1}) were carried out at night and recorded by measuring the time each hatchling took to crawl along a raceway of 3 m, 100 mm wide, dug into the hatchery's sand. We assigned hatchlings that failed to move within 300 s of being placed on the raceway to a failed to crawl category. We installed a LED light at one end of the raceway, and care was taken to ensure that the track was flat. The time taken for hatchlings to self-right themselves was measured by placing the turtle upside down on its carapace and taking the time it took to right itself. This was repeated six times for each hatchling, with a 5 s rest period between attempts. If an individual did not self-right themselves in 60 s, the failure was recorded, and they were given a 5 s rest period on their plastron before the next attempt (maximum of 6 attempts). After the tests, hatchlings were returned to the container with their siblings and released into the ocean.

2.4. Sex ratio estimation

Of a total of 86 nests with temperature data, 35 failed to hatch. Therefore, we estimated sex ratio for the remaining 51 clutches (Table 1). We used the R package ***embryogrowth*** v.8.4 (Girondot, 2022) to account for the effects of varying field temperatures on the dynamics of embryonic development. The thermal reaction norm of embryo growth was estimated according to the method of Girondot and Kaska (2014). Then the thermosensitive period (TSP) dates when gonad differentiation occurred were identified for each nest (Girondot et al., 2018). To do so, we estimated the thermal reaction norm for growth rate from our nest temperature time series (n = 51 nests, Table 1) and SCL measurements (mean = 40.51 mm ± SD = 2.03): we fitted the 4-parameter equation using maximum likelihood and refined the confidence intervals using Bayesian MCMC following the method described in Girondot and Kaska (2014). With this, growth-weighted mean incubation temperatures during the TSP (Fuentes et al., 2017) were estimated for each nest and sex ratios derived using the thermal reaction norm for the species (Abreu-Grobois et al., 2020). We estimated the sex ratio thermal reaction norm with data from the literature at constant incubation temperatures (McCoy et al., 1983; Dimond, 1985; Wibbels et al., 1998; Castheloge et al., 2018), we fitted the logistic equation using maximum likelihood, and refined the confidence intervals using Bayesian MCMC following the method described in (Abreu-Grobois et al., 2020). Sex ratio estimates are presented as mean ± SE.

2.5. Statistical analysis

Reported statistics are arithmetic means ± standard deviation (SD). All statistical tests were conducted using Minitab® 18.1 (Minitab Inc., State College, Pennsylvania, USA). Kolmogorov-Smirnov test was used as a normality test. ANOVA with Tukey's method was conducted to examine mean differences among neonate fitness data obtained. A statistical test based on Pearson's product-moment correlation coefficient was used to evaluate the size of the adult females with number of eggs and hatching size, and the effect of the incubation temperature on hatchling morphology and locomotor performance. Levels of

Table 1
Summary for data from 86 olive ridley clutches with ranges of incubation temperatures (n = 86 clutches) and estimated sex ratios as proportion of males (n = 51 clutches).

Field code	Season	Starting incubation date	Incubation duration (d)	Clutch size	Hatching success	Fitness tests	% > 34 °C	% < 26 °C	Mean °C ± SD (range)	Sex ratio
MJ 1	Dry	18 Feb	61.2	79	21.5	Yes	0.0	4.8	28.2 ± 1.6 (23.2–31.2)	0.99
MJ 2	Dry	18 Feb	60.6	87	100	Yes	0.0	4.6	28.9 ± 2.1 (23.6–32.9)	0.98
MJ 3	Dry	18 Feb	59.8	100	85	Yes	0.0	4.8	28.8 ± 2.1 (23.7–32.9)	0.98
MJ 4	Dry	16 Feb	59.2	104	100	Yes	0.0	5.1	28.7 ± 2.3 (23.2–33.2)	0.98
MJ 5	Dry	16 Feb	59.8	93	90.3	Yes	0.0	6.6	28.2 ± 2.2 (22.9–32.7)	0.99
MJ 6	Dry	16 Feb	58.8	103	100	Yes	0.0	5.0	29.0 ± 2.3 (22.2–33.6)	0.98
MJ 7	Dry	16 Feb	59.8	85	94.1	Yes	0.0	4.8	28.9 ± 2.2 (23.3–33.3)	0.98
MJ 8	Dry	16 Feb	58.0	96	87.5	Yes	0.0	4.9	28.6 ± 2.3 (22.8–33.3)	0.98
MJ 9	Dry	16 Feb	59.8	77	15.6	Yes	0.0	6.6	27.7 ± 1.6 (23.1–30.5)	0.99
MJ 10	Dry	16 Feb	59.0	92	97.8	Yes	0.0	4.9	28.8 ± 2.1 (24.0–32.8)	0.97
MJ 11	Dry	19 Feb	59.3	157	96.2	Yes	1.7	7.0	29.0 ± 2.8 (20.1–34.3)	0.93
MJ 12	Dry	22 Feb	–	101	0	No	0.0	8.2	27.3 ± 1.1 (22.3–29.7)	–
MJ 13	Dry	22 Feb	59.9	87	66.7	Yes	0.0	6.6	28.3 ± 1.9 (20.6–31.5)	0.96
MJ 14	Dry	24 Feb	64.2	74	50.0	Yes	0.0	8.4	28.2 ± 1.9 (20.4–31.1)	0.97
MJ 15	Dry	24 Feb	58.8	123	96.7	No	0.0	6.4	28.8 ± 2.4 (24.0–33.1)	0.95
MJ 16	Dry	25 Feb	57.0	94	83.0	Yes	0.0	5.9	28.8 ± 2.3 (23.1–32.9)	0.93
MJ 17	Dry	25 Feb	58.5	96	89.6	Yes	0.0	5.1	29.2 ± 2.3 (23.9–33.7)	0.88
MJ 18	Dry	25 Feb	57.5	84	98.8	Yes	0.7	4.9	29.2 ± 2.5 (24.2–34.6)	0.89
MJ 19	Dry	25 Feb	60.0	113	88.5	Yes	0.0	4.6	28.8 ± 1.8 (24.4–32.0)	0.94
MJ 20	Dry	25 Feb	59.3	97	96.9	Yes	0.0	5.1	29.2 ± 2.4 (23.9–33.2)	0.89
MJ 21	Dry	03 Mar	62.1	102	71.6	Yes	0.0	6.1	29.3 ± 2.3 (23.6–32.4)	0.77
MJ 22	Dry	02 Mar	58.2	77	53.2	Yes	0.0	8.4	28.6 ± 2.2 (23.4–32.1)	0.91
MJ 23	Dry	03 Mar	–	78	0	No	0.0	12.1	27.6 ± 1.7 (22.4–30.6)	–
MJ 24	Dry	04 Mar	61.0	92	91.3	Yes	0.0	7.9	28.7 ± 2.1 (23.5–32.0)	0.87
MJ 25	Dry	04 Mar	55.0	112	98.2	Yes	0.0	6.7	29.2 ± 2.3 (23.4–32.9)	0.77
MJ 26	Dry	04 Mar	55.1	79	81.0	Yes	0.0	5.5	29.2 ± 2.1 (24.3–32.4)	0.76
MJ 27	Dry	04 Mar	55.2	112	97.3	Yes	0.0	5.3	29.5 ± 2.3 (23.9–33.2)	0.66
MJ 28	Dry	04 Mar	62.0	83	92.8	Yes	0.0	3.2	29.6 ± 1.9 (25.3–32.5)	0.67
MJ 29	Dry	05 Mar	–	111	0	No	0.0	6.8	28.3 ± 1.6 (23.3–30.8)	–
MJ 30	Dry	05 Mar	61.2	78	62.8	Yes	0.0	6.3	28.8 ± 1.7 (23.3–31.3)	0.83
MJ 31	Dry	19 Mar	51.9	89	88.8	Yes	0.0	0.2	30.3 ± 1.6 (25.0–32.9)	0.26
MJ 32	Dry	21 Mar	53.8	106	97.2	No	0.0	0.0	29.8 ± 1.7 (26.3–32.7)	0.62
MJ 33	Dry	21 Mar	53.8	64	60.9	No	0.0	0.2	29.9 ± 1.9 (25.5–33.3)	0.53
MJ 34	Dry	21 Mar	53.8	103	98.1	No	0.0	0.2	29.9 ± 1.9 (25.5–33.3)	0.53
MJ 35	Dry	21 Mar	55.1	85	98.8	No	0.0	0.2	29.4 ± 1.7 (24.5–32.5)	0.73
MJ 36	Dry	21 Mar	56.2	128	99.2	No	0.5	0.3	29.5 ± 2.1 (25.1–34.3)	0.76

(*continued on next page*)

Table 1 (*continued*)

Field code	Season	Starting incubation date	Incubation duration (d)	Clutch size	Hatching success	Fitness tests	% > 34 °C	% < 26 °C	Mean °C ± SD (range)	Sex ratio
MJ 37	Dry	21 Mar	55.3	86	91.9	No	0.0	0.4	28.9 ± 1.8 (25.8–32.4)	0.83
MJ 38	Dry	22 Mar	–	86	0	No	0.0	0.5	28.6 ± 1.1 (25.0–30.1)	–
MJ 39	Dry	22 Mar	52.2	76	89.5	No	0.0	0.2	29.5 ± 1.7 (24.6–32.6)	0.67
MJ 40	Dry	22 Mar	50.3	107	93.5	Yes	0.0	0.2	30.1 ± 1.9 (24.2–33.4)	0.50
MJ 41	Rainy	03 June	–	112	0	No	48.9	0.0	33.8 ± 1.7 (29.4–36.4)	–
MJ 42	Rainy	02 Jun	46.9	92	56.5		41.7	0.1	33.5 ± 1.6 (29.5–36.0)	0.03
MJ 43	Rainy	02 Jun	–	81	0	No	5.5	0.0	32.3 ± 1.1 (30.0–34.2)	–
MJ 44	Rainy	02 Jun	–	98	0	No	0.0	0.0	32.1 ± 1.0 (30.2–33.6)	–
MJ 45	Rainy	03 Jun	47.0	123	62.6	No	0.1	0.0	32.0 ± 1.2 (29.6–34.1)	0.01
MJ 46	Rainy	10 Jun	–	80	0	No	46.7	0.0	33.7 ± 1.7 (28.8–36.5)	–
MJ 47	Rainy	10 Jun	50.5	121	92.6	No	7.6	0.0	32.3 ± 1.3 (29.7–35.2)	0.01
MJ 48	Rainy	20 Jun	–	90	0	No	51.1	0.0	33.6 ± 1.7 (23.6–35.6)	–
MJ 49	Rainy	20 Jun	45.2	109	96.3	Yes	1.6	0.8	31.7 ± 1.4 (23.6–34.1)	0.41
MJ 50	Rainy	21 Jun	46.5	97	88.7		50.9	0.2	33.7 ± 1.6 (23.9–35.9)	0.03
MJ 51	Rainy	26 Jun	–	80	0	No	5.7	0.0	32.0 ± 1.4 (28.4–34.3)	–
MJ 52	Rainy	26 Jun	–	103	0	No	53.9	0.0	33.5 ± 1.7 (27.8–36.6)	–
MJ 53	Rainy	02 Jul	44.9	93	71.0	Yes	38.4	0.0	33.3 ± 1.8 (28.8–37.1)	0.00
MJ 54	Rainy	02 Jul	–	107	0	No	74.7	0.0	34.6 ± 1.5 (29.8–36.6)	–
MJ 55	Rainy	02 Jul	45.3	91	42.9	Yes	16.2	0.0	32.6 ± 1.5 (28.3–34.9)	0.01
MJ 56	Rainy	02 Jul	–	126	0	No	74.3	0.0	34.5 ± 1.5 (29.3–36.6)	–
MJ 57	Rainy	05 Jul	45.2	98	28.6	Yes	37.1	0.0	33.2 ± 1.9 (28.1–36.5)	0.00
MJ 58	Rainy	05 Jul	–	57	0	No	73.4	0.0	34.5 ± 1.6 (28.6–36.6)	–
MJ 59	Rainy	05 Jul	49.1	106	12.3	Yes	11.5	0.0	32.6 ± 1.5 (27.9–35.1)	0.01
MJ 60	Rainy	05 Jul	–	87	0	No	63.6	0.0	34.1 ± 1.6 (28.1–36.2)	–
MJ 62	Rainy	14 Jul	–	54	0	No	75.5	0	34.5 ± 1.7 (28.2–36.4)	–
MJ 64	Rainy	14 Jul	–	80	0	No	79.9	0.0	34.7 ± 1.7 (28.1–36.4)	–
MJ 65	Rainy	14 Jul	46.2	105	13.3	Yes	0.0	0.0	32.1 ± 1.4 (27.9–33.8)	0.02
MJ 66	Rainy	14 Jul	–	77	0	No	80.1	0.0	34.8 ± 1.8 (28.3–36.7)	–
MJ 67	Rainy	14 Jul	48.1	109	24.8	Yes	0.0	0.0	32.1 ± 1.4 (27.4–34.0)	0.02
MJ 68	Rainy	14 Jul	–	108	0	No	81.0	0.0	34.8 ± 1.7 (28.3–36.9)	–
MJ 69	Rainy	14 Jul	–	111	0	No	3.6	0.0	32.5 ± 1.4 (27.9–34.4)	–
MJ 70	Rainy	14 Jul	–	69	0	No	82.5	0.0	34.7 ± 1.8 (26.1–36.9)	–
MJ 71	Rainy	23 Aug	–	100	0	No	29.3	0.0	33.1 ± 1.5 (29.0–35.9)	–
MJ 73	Rainy	24 Aug	–	87	0	No	30.6	0.0	33.2 ± 1.5 (29.0–36.0)	–
MJ 74	Rainy	24 Aug	44.7	86	68.6	Yes	30.1	0.0	33.1 ± 1.6 (28.9–36.2)	0.04
MJ 75	Rainy	24 Aug	45.2	56	92.9	Yes	43.3	0.0	33.8 ± 0.9 (26.2–36.1)	0.00
MJ 76	Rainy	24 Aug	–	92	0	No			33.8 ± 1.5 (29.1–37.1)	–
MJ 77	Rainy	24 Aug	46.0	68	19.1	Yes	28.4	0		0.02

(*continued on next page*)

Table 1 (*continued*)

Field code	Season	Starting incubation date	Incubation duration (d)	Clutch size	Hatching success	Fitness tests	% > 34 °C	% < 26 °C	Mean °C ± SD (range)	Sex ratio
									33.2 ± 1.5 (29.0–36.7)	
MJ 78	Rainy	24 Aug	44.8	117	13.7	Yes	25.7	0	33.1 ± 1.6 (28.8–36.8)	0.03
MJ 79	Rainy	24 Aug	–	120	0	No	29.6	0.0	33.2 ± 1.5 (29.2–36.0)	–
MJ 98	Rainy	25 Sep	–	93	0	No	32.2	0.0	33.2 ± 1.8 (28.8–36.2)	–
MJ 99	Rainy	25 Sep	–	66	0	No	39.4	0.0	33.3 ± 1.8 (28.6–36.3)	–
MJ 100	Rainy	25 Sep	–	113	0	No	40.8	0.0	33.6 ± 2.0 (28.9–38.5)	–
MJ 101	Rainy	25 Sep	–	87	0	No	30.6	0.0	33.1 ± 1.6 (29.1–35.9)	–
MJ 103	Rainy	25 Sep	–	112	0	No	29.4	0.0	33.2 ± 1.5 (28.6–35.6)	–
MJ 105	Rainy	25 Sep	–	92	0	No	24.7	0.0	32.8 ± 1.6 (28.3–35.3)	–
MJ 106	Rainy	25 Sep	–	111	0	No	31.1	0.0	33.1 ± 1.7 (28.6–35.8)	–
MJ 107	Rainy	25 Sep	–	98	0	No	32.6	0.0	33.2 ± 1.6 (28.9–35.8)	–
MJ 108	Rainy	25 Sep	–	85	0	No	40.2	0.0	33.3 ± 1.7 (28.8–35.8)	–
MJ 110	Rainy	25 Sep	–	93	0	No	39.9	0.0	33.5 ± 1.6 (29.5–36.0)	–

significance are stated as *p values*.

2.6. Ethics statement

Sampling and behavior tests were covered by permits granted by Mexico's Dirección General de Vida Silvestre/Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) SGPA/DGVS/05366/15.

3. Results

3.1. Nesting

We recorded a total of 1954 nests over 12 months (1st January 2015–30th December 2015). Nesting occurred year-round, with the highest levels recorded in October when the conservation project relocated 605 nests to the beach hatchery and the lowest levels in May (n = 22 nests) (Fig. 1). The majority of nests (n = 1573, 80.5 %) were laid in the rainy season while 19.5 % of nests (n = 381) occurred during the dry season. Nesting was predominately on beach berm or zone B where 79.3 % of nests were laid (n = 1547 nests) (zone A: 7.3 %, 143 nests; zone C: 13.4 %, 261 nests). Proportionally, a greater number of nests were laid in intertidal zone A during the dry season (9.0 % n = 34 nests) than during the rainy season (6.9 % n = 109). We measured 25 nesting females and found that the mean curved carapace length (CCL) and width (CCW) were 67.6 cm (range: 63–76 cm) and 73.8 cm (range: 68–82 cm), respectively (Supplementary Table 1). There was no significant relationship between the size of the adult females and the number of eggs laid ($r = -0.136$; $p > 0.05$) or hatchling sizes ($r = 0.273$; $p > 0.05$).

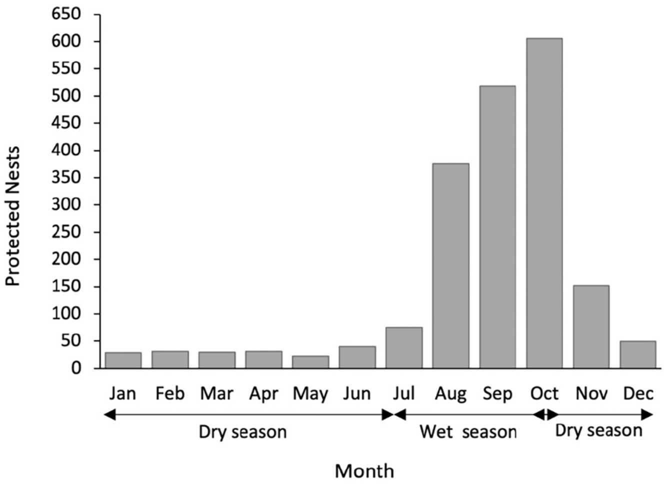

Fig. 1. Temporal distribution during 2015 of *Lepidochelys olivacea* nests monitored at Majahuas beach, Jalisco, Mexico.

3.2. Nest temperatures

We monitored temperature in 86 nests but could only estimate sex ratios in 51 nests because the 35 others did not hatch (Table 1). Nest temperatures presented significant seasonal differences ($F_{(1,69)} = 143.26$; $p < 0.001$), with those incubated during the dry season (29.09 °C ± 0.52) being a mean of 3.89 °C cooler than those incubated in the rainy season (32.98 °C ± 0.58). The temperature within the 86 nests ranged between 20.1 °C and 38.5 °C. The most frequent temperature interval for dry season nests was 27–28 °C with 24 % of recorded values, while in the rainy season, the most frequent temperature interval was 33–34 °C with 28 % of records (Fig. 2).

Within the hatchery, mid-nest depth temperatures were regularly lower than atmospheric temperature, and tropical storms and hurricanes caused occasional and drastic drops in nest temperatures (Supplemental Fig. 1).

3.3. Hatchling morphology and locomotor performance

Mean incubation temperature within nests was found to be significantly correlated with some of the hatchling morphological traits: weight ($r = -0.36$; $p < 0.05$), SCW ($r = -0.35$; $p < 0.05$), carapace depth ($r = -0.34$; $p < 0.05$), and locomotor ability (run speed ($r = 0.46$; $p < 0.01$)) (Supplementary Fig. 1).

Hatchling morphology was significantly affected by season, with dry-season hatchlings presenting both larger SCL, (Dry: 40.62 mm ± 1.82; Rainy: 40.15 mm ± 2.53; $F_{(1,758)} = 7.16$; $p = 0.008$), SCW (Dry: 32.84 mm ± 1.714; Rainy: 32.12 mm ± 2.104; $F_{(1,758)} = 20.71$; $p < 0.001$),

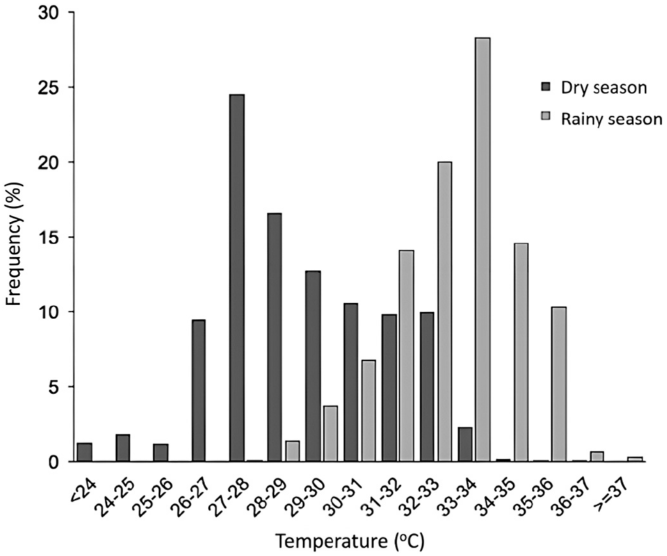

Fig. 2. Temperature frequency registered in the center of hatched *Lepidochelys olivacea* clutches during incubation in the hatchery at Majahuas beach.

and weight (Dry: 16.23 g ± 1.686; Rainy: 14.93 g ± 2.317; $F_{(1,758)} = 64.55; p < 0.001$) compared to those hatched in the rainy season. Significant differences in terrestrial locomotor performance were observed between seasons ($F_{(1,758)} = 60.17; p < 0.001$), with dry-season hatchlings having a faster mean crawl speed (0.97 cm s^{-1} ± 0.594) compared to those hatched in the rainy season (0.55 cm s^{-1} ± 0.359). In addition, rainy season hatchlings also presented a slower mean righting response (3.33 s ± 2.11) than those hatched in the dry season (3.87 s ± 2.41; $F_{(1,758)} = 04.641; p = 0.032$) (Table 2). Overall hatching success was 52.7 % and presented a significant difference between dry season hatchling success 74.3 % and rainy season hatchling success 24.2 % ($F_{(1,1952)} = 38.08; p < 0.001$). Data for each nest studied can be found in Supplementary table 2.

3.4. Estimates of hatchling sex ratios

The nests incubated during the February–March dry season that successfully hatched (n = 36) produced between 26 % to 99 % male hatchlings, whereas those incubated during June–September rainy season (hatched nests: n = 15) produced between 0 and 41 % males (Fig. 3), but 14 of 15 nests were extremely female-biased (Table 1).

4. Discussion

4.1. Hatchling phenotype and fitness

Seasonal effects were present in our study with dry-season hatchlings having superior locomotor abilities, larger body size, and weight than their rainy-season counterparts. This is similar to other studies which have looked at the effect of nest temperature and found that cooler nests produce larger hatchlings (Booth et al., 2013; Maulany et al., 2012b; Wood et al., 2014) that may be better equipped (larger carapaces and flippers) to crawl and swim faster than their smaller counterparts from warmer nests (Ischer et al., 2009; Rivas et al., 2019). The phenotype and fitness advantages received from cooler incubation temperatures highlight the importance of protecting dry season nests which occur when nesting levels are low because these nests produce higher hatching success. The resulting hatchlings may have an increased chance of survival because they may be quicker to exit predator-rich coastal waters due to their larger size and better fitness characteristics. However, the lower number of nests laid during the dry season increases the likelihood of eggs and hatchlings being predated as there are fewer available to satiate predators (Ims, 1990). However, hatchlings from nests with high emergence success also have a higher chance of avoiding predators on their natal beach during their crawl to the sea, as predators rarely consume large numbers of hatchlings from an individual nest (Erb and Wyneken, 2019).

Table 2
Mean temperature for 86 nests (40 in Dry season and 46 in Rainy season) and mean phenotype measurements (straight carapace length (SCL: mm), straight carapace width (SCW: mm), and weight (g)) and crawl speed and righting response for olive ridley sea turtle hatchlings from 38 nests at Majahuas beach by season (Dry: n = 28; Rainy: n = 10) in 2015.

Parameter	Season				Statistical test
	Dry		Rainy		
	Mean ± SD	Min–max	Mean ± SD	Min–max	
Temperature (°C)	29.09 ± 0.52 (a)	27.3–30.1	32.98 ± 0.58 (b)	31.7–34.8	$F_{(1,84)} = 723.92; p < 0.001$
Hatching Success (%)	74.2 ± 2.97 (a)	0.000–100.0	24.1 ± 3.56 (b)	0.00–92.70	$F_{(1,1952)} = 38.08; p < 0.001$
SCL (mm)	40.62 ± 1.823 (a)	34.00–47.50	40.15 ± 2.535 (b)	30.00–49.00	$F_{(1,758)} = 7.16; p = 0.008$
SCW (mm)	32.84 ± 1.714 (a)	26.40–38.00	32.12 ± 2.104 (b)	26.00–29.50	$F_{(1,758)} = 20.71; p < 0.001$
Weight (g)	16.23 ± 1.686 (a)	12.00–24.00	14.93 ± 2.317 (b)	8.020–19.88	$F_{(1,758)} = 64.55; p < 0.001$
Crawl Speed (cm s^{-1})	0.977 ± 0.594 (a)	0.132–3.600	0.550 ± 0.359 (b)	0.086–1.597	$F_{(1,758)} = 60.17; p < 0.001$
Righting Response (s)	3.870 ± 2.412 (a)	0.980–19.00	3.336 ± 2.110 (b)	0.830–18.00	$F_{(1,758)} = 04.641; p = 0.032$

N.B.: The statistical test used is the analysis of variance (ANOVA); statistical test data as mean ± SD followed by Tukey's test in parentheses if significant differences were found. Hatching success data in percentage.

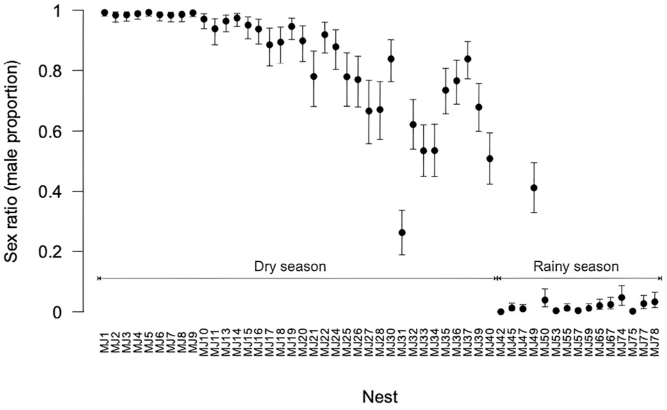

Fig. 3. Sex ratio (male proportion) of the 51 *Lepidochelys olivacea* nests on Majahuas Beach that hatched.

Our study tested hatchlings that emerged from nests relocated to a beach hatchery. However, the relocation of clutches to artificially excavated nest chambers can affect hatchling fitness and phenotype through modification of the nest microenvironment. Tanabe et al. (2021) found that green turtle hatchlings from relocated nests were smaller, and less fit than those from in situ nests. However, as all the nests compared in our study were relocated to the hatchery all hatchlings would have experienced the effects of relocation and therefore this would not influence the observed difference between seasons.

Temperature is not the only factor that presents seasonal changes. Hatchlings entering the sea at different times of the year can encounter seasonal changes in oceanic circulation (Scott et al., 2017). Ocean currents can change in both intensity and direction (Portela et al., 2016). Therefore, neonates hatching at different times can end up in vastly different locations and be exposed to different conditions (Mansfield et al., 2017). In Spring, along the Mexican Central Pacific, sea turtles have been observed to aggregate in coastal upwelling areas and near cyclonic gyres. Whereas in winter, colder water flowing from the northwest into the oceanic zone causes thermal fronts where turtles forage (Zepeda-Borja et al., 2017). These currents may move hatchlings from coastal waters into oceanic waters and away from predators.

4.2. *Rainfall and hurricane season*

Moisture is vital in determining temperature regimes (Gatto et al., 2021) and has been associated with an increase in male hatchling production (Godfrey et al., 1996). However, rainwater filtering through sand has been found to quickly match the ambient sand temperature even at the top of loggerhead turtles (*Caretta caretta*) egg chambers (Lolavar and Wyneken, 2017). Olive ridley turtles lay relatively shallow nests exposed to greater daily fluctuations in temperatures but may also increase the possibility of rainfall reaching and cooling the eggs through evaporation. However, rainfall occurred during only 61 days (16.7 %) in 2015, and only 33.3 % (n = 41 d) of rainy season days and 12.1 % of dry season days (n = 20 d). Therefore, the temperature is likely the principal factor driving the differences in the sex ratios between rainy and dry seasons. Rainfall was related to the number of storms with hurricane season occurring from May 15th to November 30th in the Eastern North Pacific (NHC), which coincides with peak olive ridley sea turtle nesting activity. The 2015 storm season was particularly active, with 18 cyclones registered for the northern East Pacific, of which 13 were hurricanes, nine were major hurricanes, and three were tropical depressions (Avila, 2016; Collins et al., 2016). Seven storms (Supplementary Fig. 2) affected Majahuas nesting beach during this study. This resulted in the loss of hundreds of nests due to beach erosion and wash-out of hatcheries. However, these storms also lower incubation temperatures, which help lower sand temperature in some cases below pivotal temperature. During August and much of September, the sand temperature remained above 34 °C, which has been identified as the lethal superior incubation temperature for some olive ridley populations (Maulany et al., 2012a). For example, when the effects of Hurricane Kevin and Linda occurred within the same week, a drop in mid-nest depth temperature of 3 °C (35 °C to 32 °C) occurred, taking incubation temperatures out of lethal limits.

4.3. *Sex ratio*

Dry season nests were estimated to produce mainly male clutches, and males' increased hatch rate and survival may help balance out female-biased sex ratios at Majahuas beach. Sandoval Espinoza (2012) estimated sex ratios for olive ridleys along the Mexican Pacific coast and found that ratios varied greatly, with beaches in Jalisco (Chalacatepec and Playon de Mismaloya) producing 23 % male sex ratios. For the Mexican Pacific, they estimated that temperatures would have resulted in male hatchlings throughout the study period (July-Dec 2010), with 31 % of males in September, 11 % in August, 17 % in October, 20 % in November, and 19 % in December. They did not monitor temperatures during the dry season. This is contrary to our results, where the 2015 high rainy season temperatures resulted in very low levels of male hatchling production.

When we compare our results with those of a study in 1993 (Valadez González et al., 2000) at a beach 5 km north of Majahuas we find similar variations in sex ratio, with 100 % females produced in October and 100 % males in December. However, the overall sex ratio of 7:3 in the 1993 study is not the same as that found in Majahuas during our research. The incubation period in 1993 (Valadez González et al., 2000) was 44 to 65 days, which is similar to our results where we recorded the most prolonged incubation duration in February (64.2 d) and the shortest in August (44.7 d). However, the temperature registered in the La Gloria beach hatchery ranged from 27 °C ± 0.10 (December) to 34 °C ± 0.36 (August), even when considering a higher temperature within nests due to metabolic heat (Sandoval et al., 2011) the 1993 study nests would not have experienced the extreme upper temperatures (max 38.5 °C) that we registered within clutches. As expected from our 12-month study period, we registered lower temperatures than in the La Gloria study, which did not monitor temperature during the dry winter season. Although Valadez González et al. (2000) only recorded the hatchery sand temperature at 12-hour intervals at nest depth but not from within clutches, the study allows us to compare our results with data taken two decades ago.

All nests protected during the study were relocated to a beach hatchery. Beach hatcheries are commonly located at the point furthest away from the tide line to protect clutches from erosion. Yet for species such as olive ridley turtle that prefer to nest on the beach berm (Hart et al., 2014), this upper dune environment presents significantly higher temperatures and lower humidity than those closer to the ocean (Spotila et al., 1987; Martins et al., 2022) this could have contributed to the high female-biased sex ratios during the hotter rainy season. If a proportion of nests could be left in situ during the rainy season, this would expose them to a variety of microenvironments. That said, they would still be exposed to the high levels of predation, illegal take and erosion that threaten clutches on this beach.

In the context of contemporary climate change, female-biased sex ratios could provide an advantage (Santidrián Tomillo and Spotila, 2020). However, if these primary sex ratios persist into adulthood, it is possible that genetic erosion would occur as a result of decreased effective population size, and this could become detrimental. Our results suggest that low-season nests, which produce individuals of the rarer sex, are critical for the long-term persistence of this population. That said, male sea turtles have been found to reproduce more frequently than females, and this may help balance the operational sex ratio on breeding grounds (Hays et al., 2014). This, coupled with the olive ridleys' behavioral plasticity in nesting (Bernardo and Plotkin, 2007), migration, and foraging (Santos et al., 2019; Figgener et al., 2022) will likely help olive ridleys adapt to environmental change.

4.4. *Benefits of low-season nesting for females*

Olive ridleys present high levels of multiple paternity (MP), and this is especially prominent in *arribada* breeding populations, with 92 % of clutches having two or more fathers (Jensen et al., 2006) and clutches sampled at the arribada in Escobilla, Mexico having between two and seven fathers (González-Cortés et al., 2021). Similar results at other large sea turtle nesting sites led to the hypothesis that population size has a dominant effect on MP (Jensen et al., 2006; Lee et al., 2018). In contrast, at solitary nesting beaches, clutches shared 2 to 3 fathers (Duran et al., 2015). High MP was observed at the beginning of the arribada season, with each subsequent mass nesting event presenting fewer sires per clutch (González-Cortés et al., 2021). As for solitary nesting sites, in-water observations of mating near beaches are highest between July and September (Plotkin et al., 1996), whereas Zepeda-Borja et al. (2017) observed mating only during October.

Despite the high frequency of MP in sea turtles, polyandry appears to be without fitness benefits for female turtles, and clutches with multiple fathers may contain fewer eggs overall (Wright et al., 2013). In addition, avoiding males has energy requirements that may exceed that of mating (Lee et al., 2018). Therefore, females that nest in times of low abundance are likely to encounter fewer males and benefit from a lower chance of multiple encounters with aggressive males (Jensen et al., 2006). However, Duran et al. (2015) reported that some solitary breeding populations also present high levels of MP, which could result from the low breeding and feeding site fidelity (Plotkin, 2010) and sea turtle females' ability to store sperm over multiple years.

4.5. Implications for current conservation efforts

Concentrating effort and resources on peak nesting season conservation and research may seem the best use of limited funds. However, in our region, nests laid during peak nesting season have lower possibilities of hatching than those in the low season due to lethally high temperatures and beach erosion resulting from storms. When protected from predation in hatcheries, the comparatively small number of nests laid in the low season has higher hatch rates and produce a higher proportion of male hatchlings, which are a rare occurrence during the high rainy season. Although in 2015, the number of nests laid during the low season represented just 19.5 % of overall nesting, they are of high conservation value because they produce the rarer sex and could help population viability. It is important to note that patrols between February and May 2015 were limited due to mechanical problems with the projects quad bike on which patrols are made of the 11 km beach. This resulted in reduced monitoring capacity during the dry season; therefore, nesting levels may have been higher than those reported here. Despite this, our study highlights the fact that viable nests are laid year-round and that these nests produce valuable male hatchlings. Of relevance is that under current practices, most of these nests are left on the beach without protection. Most of them (>65 %) are predated by raccoons, coatis, or humans during the first night after laying (LATS, personal observation). Methods exist to limit predation and include the use of mesh (O'Connor et al., 2017; Nordberg et al., 2019) which could be implemented to allow at least some nests to be protected in situ each season and therefore experience distinct microenvironments that could produce hatchlings of distinct sex ratio, phenotype, and fitness to the hatchery. However, further work would be needed in the local community to avoid these nests being taken for illegal consumption.

5. Conclusion

Understanding how seasonality affects reproductive success and influences sex ratios and phenotype in species is vital to conservation, especially for species identified as at particular risk of environmental change. In recent years, attention has been placed on the effects of climate change on primary sex ratios, offspring phenotype, and fitness in reptiles due in part to environmental sex determination. For vulnerable species, conservation projects may concentrate solely on the peak reproductive season. However, for species such as sea turtles, this may inadvertently favor the production of female hatchlings while leaving the cooler male-producing nests without protection from illegal take by humans and animal predation. Indeed, we found that clutches incubated during the dry-low season also yielded higher hatchling success and produced larger, heavier hatchlings with better locomotor abilities.

Although it may be tempting to concentrate limited funds on peak season, winter nests are of high value in areas such as Majahuas beach, where summer nests do not produce male offspring and are subject to erosion due to tropical storms and hurricanes. Future research into other environmental differences between seasons for species that reproduce year-round or over many months with differing environmental conditions, such as humidity and how this interacts with temperature in natural nests, will be important for understanding how species may be able to adapt to climate change through possible shifts in their principal reproductive season.

CRediT authorship contribution statement

CEH and LATS conceived the study, participated in data collection and analysis, and drafted the manuscript; CPLQ, AAZN, JM and FAAG carried out the statistical analyses and wrote the manuscript; JM and MG analyzed the sex ratio data. All authors gave final approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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