


## ORIGINAL RESEARCH

# Assessing the phenology and reproductive output of loggerhead turtles in relation to climatic variables at Patara Beach, Türkiye

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## Keywords

loggerhead turtle; climatic variables; global warming; phenology; nesting success; sex ratio; hatching success; *Caretta caretta*.

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## Abstract

Loggerhead turtles (*Caretta caretta*), being ectothermic organisms, could be especially susceptible to climate change effects, and may exhibit climate-related variation in their reproductive behaviours such as phenology, annual nest numbers, clutch size, hatching success, incubation period and sex ratio. This study investigated the reproductive phenology and outputs of loggerhead turtles and their relationships with climatic variables over a 5-year period (2019–2023) at Patara Beach, Türkiye. We found significant fluctuations in atmospheric temperature, sea surface temperature and relative humidity, and that female turtle emergences on Patara Beach could temporarily adjust their phenology in response to these minor environmental changes. We highlight the importance of understanding the impacts of phenological shifts on the ability to satisfy the conditions over the nesting season that determine reproductive output. Our statistical analyses also showed that increasing sea water temperatures and atmospheric temperatures, as well as decreasing precipitation and relative humidity, had direct and/or indirect effects on the nesting phenology and reproductive output of loggerhead turtles. The findings from this study indicate that atmospheric temperature significantly affected incubation period, hatching success rate, the number of dead embryos and the number of empty eggshells. Additionally, relative humidity had a significant impact on the incubation period and the number of empty eggshells. In this context, rising temperatures led to drier nest conditions, decreased incubation periods and increased nest temperatures, resulting in higher proportions of female offspring. In conclusion, there are still gaps in our understanding of the effects of climate change on the reproductive biology of loggerhead turtles, and more studies are needed at both the Mediterranean and global scales to better understand these effects.

## Introduction

All species of sea turtles are included in the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species, and the loggerhead turtle is globally listed as 'Vulnerable' (Casale & Tucker, 2017). However, the Mediterranean subpopulation of loggerhead turtles is currently classified as 'Least Concern' (Casale & Tucker, 2015) due to conservation and monitoring efforts that began in Greece, Cyprus and Türkiye in the 1970s and 1980s (Casale et al., 2020; Casale & Margaritoulis, 2010). Despite this, numerous factors, such as coastal erosion and wave action, tourism, fishing, the use of shorelines, coastal and marine pollution and climate change, pose a threat to the Mediterranean subpopulation (Báez et al., 2013; Caut et al., 2010; Katselidis et al., 2014; Lucchetti et al., 2017; Mazaris, Matsinos, & Pantis, 2009a; Rizkalla & Savage, 2011;

Ware & Fuentes, 2018; Witt et al., 2010). Global warming is now a known fact, and 300 years of sclerosponge thermometry show global warming has exceeded 1.5°C (McCulloch et al., 2024). Simantiris (2024) evaluated the current knowledge and research outcomes on the impact of climate change on sea turtles, and presented several potentially negative impacts on life history of sea turtles. The previous studies have also shown that climate change has many potential impacts on sea turtles, such as loss of nesting habitat, increase in inundation risk, decline in hatching success and egg survival rates, increased feminization rate and shifts in nesting phenology (Chaloupka et al., 2008; Hawkes et al., 2007, 2009; Hays et al., 2002; Katselidis et al., 2014; Lolavar & Wyneken, 2015; Mazaris, Kallimanis, et al., 2009b; Patel et al., 2016; Pike et al., 2006; Saba et al., 2007, 2012; Santidrián Tomillo et al., 2012, 2014; Sönmez, Elginöz, et al., 2021a; Weishampel et al., 2004).

In Türkiye, there are 21 key nesting beaches for loggerhead turtles and green turtles (*Chelonia mydas*), as well as essential feeding and wintering areas for both species (Baran & Kasperek, 1989; Türkozan et al., 2020). Although Türkiye contains 29.9% of loggerhead turtle nests and 78.3% of green turtle nests in the Mediterranean (Casale et al., 2018), the potential impact of climatic variables (CVs) on the reproductive output (RO) and phenology of loggerhead turtles at nesting beaches in Türkiye has received almost no attention, with only a few studies conducted (Sarı & Kaska, 2015; Sönmez, Karaman, & Turkozan, 2021b). Sarı and Kaska (2015) evaluated the effects of air, sand and sea surface temperatures on loggerhead sea turtle hatchling sex ratio. Sönmez, Karaman, and Turkozan (2021b) found that climate change causes habitat loss and nest destruction due to inundation or density-dependent factors, potentially causing one third of Samandağ Beach's coastal habitat loss. Therefore, we first gathered detailed reproductive data on loggerhead turtles on Patara Beach during the 2019–2023 nesting seasons. Then, we examined the effects of CVs on nesting phenology and RO parameters of loggerhead turtles. Finally, we aimed to evaluate all these results by comparing them with those of previous studies conducted on Patara Beach. We investigated the reproductive behaviours of loggerhead turtles, focusing on their

timing and reproductive outcomes in relation to the climatic conditions at Patara Beach over a 5-year period (2019–2023).

## Materials and methods

### Study area

Patara Specially Protected Area (SPA), which covers *c.* 190 km<sup>2</sup>, is located within the borders of Antalya and Muğla provinces, Türkiye (Fig. 1). Patara SPA contains residential areas, greenhouse areas, shrubland maquis areas, pastures, forests, wetlands, agricultural areas and sand dunes. In addition to being a Special Environmental Protection Area, Patara SPA is also a first-degree natural protected area due to its rich biodiversity, as well as an archaeological protected area because of the presence of ancient cities, such as Patara and Letoon. Patara Beach is *c.* 12 km in length and consists of two subsections (Patara and Karadere).

### Measurement of climatic variables

We downloaded daily sea surface temperature (SST; °C), precipitation (1 mm = 1 kg/m<sup>2</sup>), atmospheric temperature ( $T_a$ ; °C) and relative humidity (%) data from 2019 to 2023 from the



**Figure 1** Satellite view of Patara Specially Protected Area. The yellow line is the border of protected areas.

Turkish Ministry of Environment, Urbanization and Climate Change, General Directorate of Meteorology. The data were obtained from the closest local meteorological station which is in Çavdır (36°21'N, 29°20'E) at an elevation of 10 m a.s.l. and is 10 km away from the Patara nesting beach.

We also utilized a datalogger (LYK 20E) to gauge the  $T_a$  (°C) and humidity (%) at Patara Beach. The device has a resolution of 0.1°C for temperature and 0.1% for humidity. The datalogger was synchronized to record these readings at 60-min intervals from the beginning of May to the end of October.

In order to ascertain the internal thermal conditions of the nests (nest temperatures:  $T_n$ ) and forecast their sex ratios, we additionally positioned Tinytalk dataloggers (manufactured by Orion Components, Chichester, UK) at the centre of the nests during ovulation or within a few hours afterwards. The Tinytalk dataloggers have a resolution of 0.05°C and were synchronized to record temperatures at 30-min intervals.

### Reproductive output data collection

Nest conservation and monitoring activities were conducted from early May to late October using standard protocols in line with the decisions approved by the Turkish Sea Turtle Science Commission, which is affiliated with the Ministry of Agriculture and Forestry, General Directorate of Nature Conservation and National Parks. Teams of trained volunteers, accompanied by experts, performed the fieldwork to collect nest information and provide field control. Regular fieldwork conducted during both day and night guaranteed that no nesting activity was missed.

We grouped the reproductive output data into two main categories. The first is Patara Beach's potential parameters for loggerhead turtle nesting phenology. These were the total number of nests (TNN), non-nesting emergences (NNE), nesting success (NS), nesting density (ND) and the percentage of nests completely protected (PNP). The second category pertains to the content of these nests. These were the incubation period (IP), clutch size (CS), the number of empty eggshells (EES), the presence of undeveloped eggs (UE), dead embryos (DE), hatching success rate (HSR) and sex ratio (SR). TNN and NNE were recorded during the sea turtle nesting season. NS refers to the proportion of female emergences resulting in egg-laying and was calculated as  $NS = TNN / (TNN + NNE) \times 100$ . Upon obtaining the GPS coordinates of a nest's centre, each nest was protected from predators by a 1 m × 1 m wire cage with 10 cm holes. Prism cages were also used to protect nests in some parts of the beach where sun loungers and umbrellas were densely used. Informational signs were also installed on the uppermost parts of the prism cages to provide further protection. Nests that were at risk of being flooded and partially predated nests were relocated to safer locations using an established nest relocation protocol (Başkale & Kaska, 2005). ND refers to the number of nests per kilometre and was calculated as  $ND = TNN / (12 \text{ km})$ . PNP refers to nests that were not subject to any damage or predation due to protection measures and was calculated as  $PNP = [(TNN - \text{Predated Nests}) / TNN] \times 100$ . IP is referred to as the

number of elapsed days from the nesting date until the first hatchling emergence. Two days following the last emergence of the hatchlings from the nests, the nests were opened and examined to determine the number of hatchlings that remained, EES, UE and DE according to Kaska and Downie (1999). CS refers to the total number of eggs ( $CS = EES + UE + DE$ ). If a nest was partially predated, the number of predated eggs was added to the CS. HSR refers to the percentage of eggs that produced hatchlings and was calculated as  $HSR = EES / (EES + DE + UE) \times 100$ . The HSR data from predated nests were not included in the analyses. SR estimated the proportion of female individuals produced annually and was computed based on the methodology provided by Kaska, Downie, et al. (1998a) and Kaska, Furness, and Baran (1998b) using  $T_n$  during the middle third of the IP.

### Statistical analysis

We assessed the normality of all data, employed Shapiro–Wilk test ( $P > 0.05$ ) and then used parametric tests for further statistical analyses. We determined the variation among years in climatic meteorological factors to compare the RO parameters among years using one-way ANOVA and then employed the Tukey's honestly significant difference test to identify the specific years that exhibited significant differences. Strong positive correlations were observed between atmospheric temperatures recorded from the meteorological station and local atmospheric temperatures (Patara Beach) (Pearson's correlation,  $n = 725$ ,  $r^2 = 0.915$ ,  $P < 0.001$ ) and between humidity recorded from the meteorological station and local humidity (Patara Beach) (Pearson's correlation,  $n = 725$ ,  $r^2 = 0.738$ ,  $P < 0.001$ ) during the nesting seasons. Therefore, local humidity and atmospheric temperatures were used in the related statistical analyses. Pearson's correlation analyses were also performed to establish connections between the emergence activities of sea turtles and CVs during the loggerhead turtle mating, nesting and hatchling emergence seasons (from 1 April to 30 October) at Patara Beach.

Canonical correlation analysis (CCA) was performed to validate the relationship between CVs and RO. Canonical correlations, analogous to correlation coefficients in regression modelling, examine associations between two sets of multivariate data. In addition, we constructed generalized linear models (GLMs) and employed stepwise regression analysis with backward selection to eliminate independent variables with non-significant regression coefficients and to determine the bioclimatic variables that affected RO parameters. The statistical analyses were conducted using Statgraphics Centurion XVI version 16.1.11 software for Windows. The analyses were performed again using SPSS version 29 software to check the accuracy of the results obtained.

## Results

### Climatic variables at Patara Beach

Patara Beach had an average annual  $T_a$  of  $20.9 \pm 0.15^\circ\text{C}$  (range: 6.6–36.5°C). The average annual SST was  $22.3 \pm 0.11^\circ\text{C}$  (range: 12.8–32.1°C). The mean humidity was



60.6 ± 0.88% (range: 30.1–87.5), while the average yearly precipitation was 1.78 ± 0.167 kg/m<sup>2</sup> (range: 0–108.1 kg/m<sup>2</sup>). Statistically significant variation in CVs, except precipitation, was observed during the study period (Supporting Information Appendix S1). Supporting Information Appendix S1 also provides the results of Tukey HSD analyses that show the years in which the differences occurred. The Tukey HSD test found statistical differences between years in SST,  $T_a$  and humidity, but no statistically significant difference in the amount of precipitation. Monthly fluctuations of the specified CVs among years are displayed in Supporting Information Appendix S1. The lowest monthly average  $T_a$  was recorded in January, while the highest monthly  $T_a$  was observed in August. The SST reached its lowest monthly average in March, while it peaked in August. The lowest and highest monthly average humidity were measured in July and December, respectively. Patara Beach had almost no rain between April and November, while January had the highest monthly rainfall.

### Nesting phenology at Patara Beach

Important dates and temporal variations for nesting phenology are given in Table 1. As can be seen, there are minor differences in all parameters among the years. Generally, the earliest adult female emergences began around the second week of May, and, a few days later, the first nest was recorded. We recorded the last NNE in the last week of August, despite the egg-laying season continuing until that week. The duration of the egg-laying season was calculated as 89.2 ± 12.89 days. We observed the peak frequencies of nesting and NNE from the 25th to the 30th week of the year (Fig. 2). By aggregating the cumulative nesting effort across all five seasons, the monthly distribution of nests was as follows: May, 4.4%; June, 41.2%; July, 47.1%; and August, 7.3%. The duration of

the hatchling emergence season was calculated as 78.8 ± 14.93 days.

### Reproductive output at Patara Beach

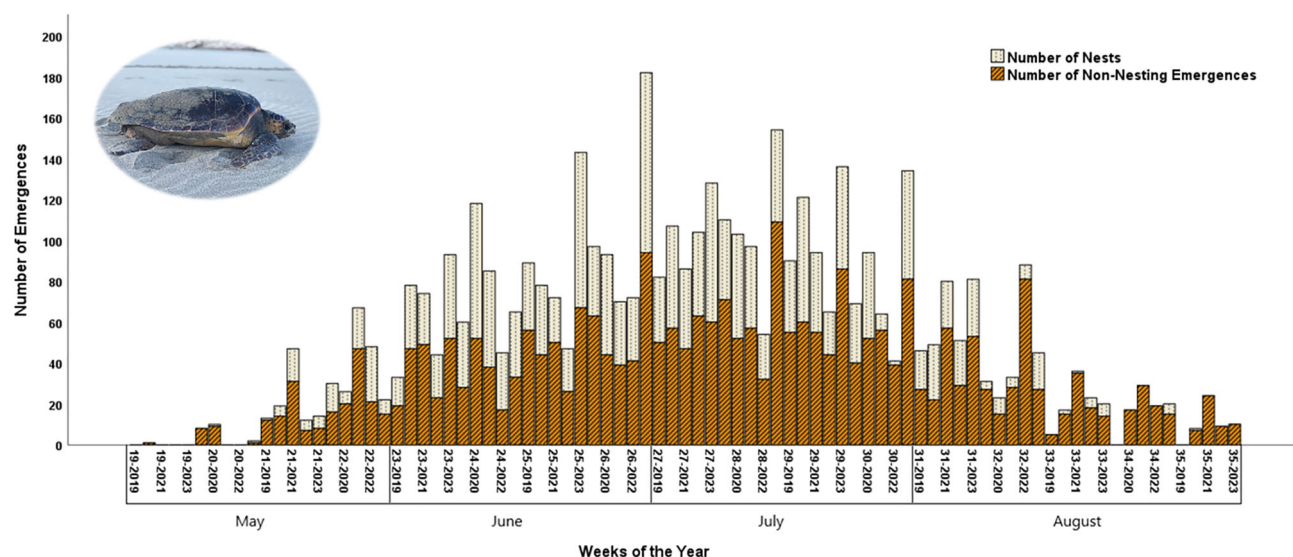
A total of 4654 adult female turtle emergences were observed, and 1813 of them resulted in egg-laying. The annual number of emergences varied from 722 to 1249, with an average of 930.8 ± 208.00 emergences per year. The annual number of nests ranged from 253 to 524, with an average of 362.6 ± 113.14 nests per year (Table 1). NS varied from 32.99 to 45.11%, with an overall mean value of 38.5 ± 4.97% (Table 1). ND ranged from 21.08 to 43.66 nests/km, with an annual average of 30.2 ± 9.42 nests/km over the 5-year period. All these parameters showed a slight increase throughout the years, but these differences were not statistically significant according to correlation analyses ( $P > 0.05$ ).

Although all nests were protected by wire cages, the number of predated nests ranged from 37 (14.6%) in 2022 to 95 (21.9%) in 2020, while the lowest rate was observed in 2023 as 9.7%. The mean number of predated nests was calculated as 63.4 per year (17.5%). In addition, 349 nests (19.24%) were relocated to safer areas to guard against inundation (Table 1).

The reproductive output parameters are summarized in Table 2. A total of 125 801 eggs were laid on Patara Beach, and 101 604 (80.76%) of them produced hatchlings. The mean number of eggs was 25160.2 per year; of these, 20320.8 (80.76%) produced hatchlings. The mean IP was 49.3 days (range: 42–65 days). HSR was calculated as 91.2% (range: 27.2–100%), but this rate decreased to 78.1% when the number of eggs in predated nests was included in the calculation. Table 2 shows that all RO parameters demonstrated statistically significant differences among years. Both the climatic factors and the physiological conditions of the individuals in the

**Table 1** The nesting phenology of loggerhead turtles at Patara Beach, Türkiye, during the nesting seasons from 2019 to 2023

Years	2019	2020	2021	2022	2023
Total number of female emergence	763	962	958	722	1249
Number of nests	286	434	316	253	524
Nesting Success (%)	37.48	45.11	32.99	35.04	41.95
Nesting density (km/nest)	23.83	36.10	26.33	21.08	43.66
Number of predated nests	61 (21.3%)	95 (21.9%)	73 (23.1%)	37 (14.6%)	51 (9.7%)
Number of relocated nests	96 (33.6%)	75 (17.3%)	76 (24.0%)	33 (13.0%)	69 (13.2%)
Date of the first non-nesting emergence	15 May	12 May	23 May	22 May	13 May
Date of the first nest	25 May	17 May	24 May	24 May	15 May
Date of the last non-nesting emergence	14 August	30 August	31st August	31st August	30 August
Date of the last nest	06 August	30 August	14 August	19 August	22 August
Date of the first hatchling emergence	24 July	18 July	16 July	24 July	13 July
Date of the last hatchling emergence	22 September	25 October	01st October	03 October	08 October
The number of days in egg-laying season	73	105	82	87	99
The number of days in hatchling emergence season	60	99	77	71	87
Elapsed days from the first female emergence to the last hatchling emergence	130	166	131	134	148



**Figure 2** Weekly distribution of nesting and non-nesting emergences of loggerhead turtles at Patara Beach, Türkiye, among studied years.

breeding population that year may have contributed to these differences.

### Relationships between climatic variables and reproductive output parameters

Daily graphical patterns between female emergences and CVs during the nesting season are shown in Fig. 3. As shown in this figure, the number of nesting and non-nesting emergences increased in parallel with  $T_a$  and SST on those days of the year. In contrast, the number of nesting and non-nesting emergences decreased on rainy and/or high humidity days. According to Pearson's correlation analyses, the number of nests variable exhibited positive associations with  $T_a$  ( $n = 365$ ,  $r^2 = 0.121$ ,  $P < 0.05$ ) and SST ( $n = 365$ ,  $r^2 = 0.156$ ,  $P < 0.01$ ), but no significant relationships were found between the number of nests and either humidity or precipitation ( $P > 0.05$ ). Similar results were found for NNE (for  $T_a$ : Pearson's correlation,  $n = 491$ ,  $r^2 = 0.189$ ,  $P < 0.01$ ; for SST: Pearson's correlation,  $n = 491$ ,  $r^2 = 0.155$ ,  $P < 0.01$ ). From all these, it could be concluded that, with increases in  $T_a$  and SST and decreases in humidity and precipitation, nesting female loggerhead turtles on Patara Beach were able to temporarily make minor adjustments to their nesting periods from year to year.

On the other hand, of all CVs, humidity, precipitation and  $T_a$  correspond to the IPs of each nest examined for their relationships with RO, covering SR, HSR, IP, EES, DE and UE. Only  $T_a$  exhibited a statistically significant positive association with EES in the nest (Pearson's correlation,  $n = 306$ ,  $r^2 = 0.224$ ,  $P < 0.01$ ). Although not statistically significant, we found that IP and UE were negatively related to  $T_a$ , and HSR and DE were positively related to  $T_a$  ( $P > 0.05$ ). This situation was exactly the opposite for humidity. In addition,  $T_a$  exhibited a strong statistically significant positive association with  $T_n$  (Pearson's correlation,  $n = 35$ ,  $r^2 = 0.953$ ,  $P < 0.001$ ) while humidity showed a strong statistically significant negative relationship with  $T_n$

(Pearson's correlation,  $n = 35$ ,  $r^2 = 0.892$ ,  $P < 0.001$ ). At the same time, the female-biased SR (%) was positively correlated with  $T_a$  and negatively correlated with humidity, but these correlations were not statistically significant ( $P > 0.05$ ). All this means that, while higher  $T_a$  reduced the IP, resulting in the production of more female hatchlings, increased humidity extended the IP, resulting in increased production of males.

We performed canonical correlation analysis (CCA) to examine the combined impacts of CVs and RO parameter relationships. Nevertheless, as SST did not have any impact on the nest characteristics, we removed it from the analysis. Similarly, we excluded SR from the analysis because of its strong correlation with humidity,  $T_a$  and  $T_n$ . According to CCA, CVs and RO parameters demonstrated statistically significant relationships, and three sets of linear combinations were generated (Table 3). All these sets had statistically significant correlations at the 95% confidence level, and the first set of the linear combinations of CVs and RO parameters is shown in Fig. 4.

Furthermore, we also performed the GLM analysis by fitting a multiple linear regression model to describe the relationship between CVs and RO. The  $r^2$  statistics indicated that there were no statistically significant relationships between precipitation and RO parameters ( $P > 0.05$ ), while the fitted models explained 52.53% of the variability for  $T_a$  ( $F = 7.53$ ,  $P < 0.001$ ) and 35.51% of the variability for humidity ( $F = 13.57$ ,  $P < 0.001$ ). According to this analysis, the IP, HSR, DE and EES were significantly influenced by  $T_a$ , while IP and EES were significantly influenced by humidity (Table 4).

## Discussion

### Nesting phenology

Phenological shifts in sea turtle nesting season due to increased temperature have been reported globally (Patel et al., 2016; Pike et al., 2006; Robinson et al., 2014; Weishampel

**Table 2** Reproductive outputs of loggerhead turtles at Patara Beach, Türkiye, throughout the nesting seasons from 2019 to 2023

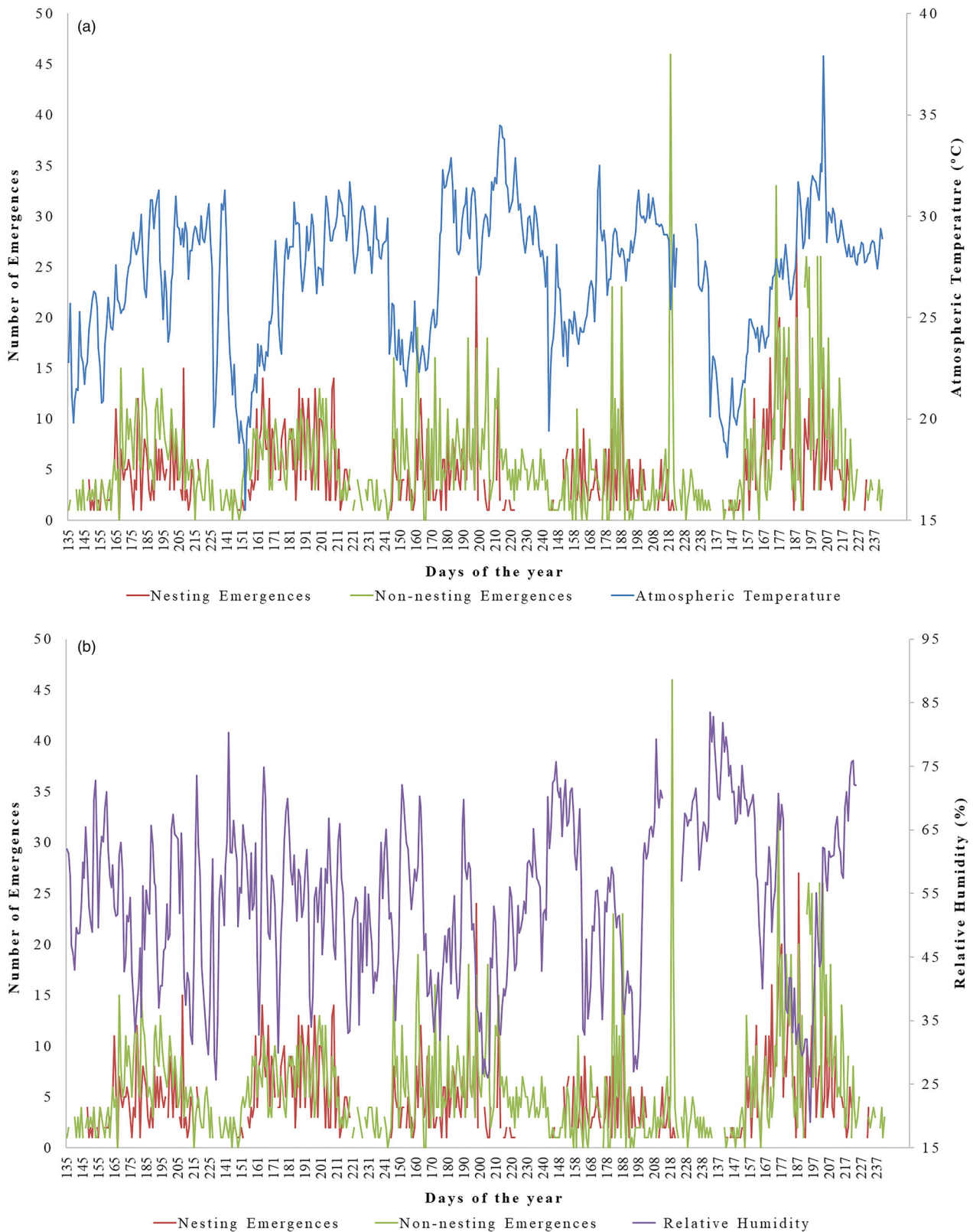
Parameters	Years	N	Minimum	Maximum	Mean	SE	d.f.	F	Sig.
Incubation period <sup>a</sup>	2019	225	42	63	49.48	0.271	4	80.57	<0.001
	2020	339	45	65	51.54	0.209			
	2021	243	45	62	50.823	0.339			
	2022	216	45	62	49.38	0.314			
	2023	473	44	64	46.82	0.133			
	Total	1496	42	65	49.31	0.114			
Hatching success rate <sup>a</sup>	2019	225	49.4	100	89.95	0.379	4	35.55	<0.001
	2020	339	36.1	100	88.38	0.416			
	2021	243	36.8	100	90.76	0.377			
	2022	216	45.6	100	94.58	0.362			
	2023	473	27.2	100	92.44	0.331			
	Total	1496	27.2	100	91.18	0.180			
Clutch size	2019	286	32	166	76.30	0.992	4	24.431	<0.001
	2020	434	25	135	67.12	0.818			
	2021	316	35	112	70.01	0.573			
	2022	253	43	103	68.37	0.604			
	2023	524	32	148	67.62	0.504			
	Total	1813	25	166	69.39	0.326			
Dead embryos <sup>a</sup>	2019	225	0	15	6.70	0.217	4	111.01	<0.001
	2020	339	0	33	4.06	0.212			
	2021	243	0	12	3.56	0.149			
	2022	216	0	9	1.50	0.113			
	2023	473	0	22	2.41	0.123			
	Total	1496	0	33	3.48	0.086			
Empty eggshells <sup>a</sup>	2019	225	51	119	72.51	0.714	4	37.38	<0.001
	2020	339	27	102	62.45	0.669			
	2021	243	25	96	65.97	0.451			
	2022	216	26	98	65.63	0.685			
	2023	473	25	135	63.16	0.478			
	Total	1496	25	135	65.21	0.282			
Undeveloped eggs <sup>a</sup>	2019	225	0	76	1.49	0.343	4	16.47	<0.001
	2020	339	0	62	4.52	0.327			
	2021	243	0	43	3.20	0.236			
	2022	216	0	22	2.17	0.143			
	2023	473	0	64	2.94	0.216			
	Total	1496	0	76	3.01	0.124			
Sex ratio <sup>b</sup>	2019	6	63.94	87.61	72.77	4.243	4	5.932	<0.001
	2020	13	55.95	89.57	73.01	3.332			
	2021	13	28.64	92.79	59.15	6.283			
	2022	12	15.48	89.43	58.00	8.481			
	2023	10	76.96	100	93.52	2.497			
	Total	54	15.48	100	70.11	3.096			

<sup>a</sup>The data of predated nests were excluded from the descriptive statistics and one-way ANOVA.

<sup>b</sup>Sex ratio of the nests were calculated from the temperatures during the middle third of the incubation period of the nests.

et al., 2004, 2010), potentially allowing species to maintain favourable climatic niches (Rees et al., 2016). Earlier onset of nesting has been reported for Mediterranean loggerhead turtles, and modelling suggests that these shifts could help maintain climatic niche suitability (Almpanidou et al., 2016; Mazaris et al., 2008, 2013; Patel et al., 2016). However, no study has examined the potential impacts of phenological shifts on the ability to satisfy the conditions from the first female emergence to the last hatchling emergence that determine reproductive output. The first non-nesting emergences started in mid-May, and, a few days later, the first nests were recorded on Patara

Beach. Sea turtles have the ability to alter their behaviour in order to maintain appropriate nesting conditions, and they may adapt to variation in temperature at their nesting sites by either shifting their nesting locations or modifying the nesting period to ensure the successful development of their eggs (Almpanidou et al., 2018; Weishampel et al., 2010). Fuentes et al. (2024) expressed that phenological shifts alone will not be sufficient to mitigate the effects of projected temperature changes, and turtles may require additional adaptive responses to mitigate the impacts of temperature changes on hatching success, sex ratio and overall populations. Similarly, Patel



**Figure 3** Relationships between climatic variables and the number of nesting and non-nesting emergences of loggerhead turtles in relation to days of the year. (a) Atmospheric temperature; (b) relative humidity; (c) sea surface temperature; (d) precipitation.



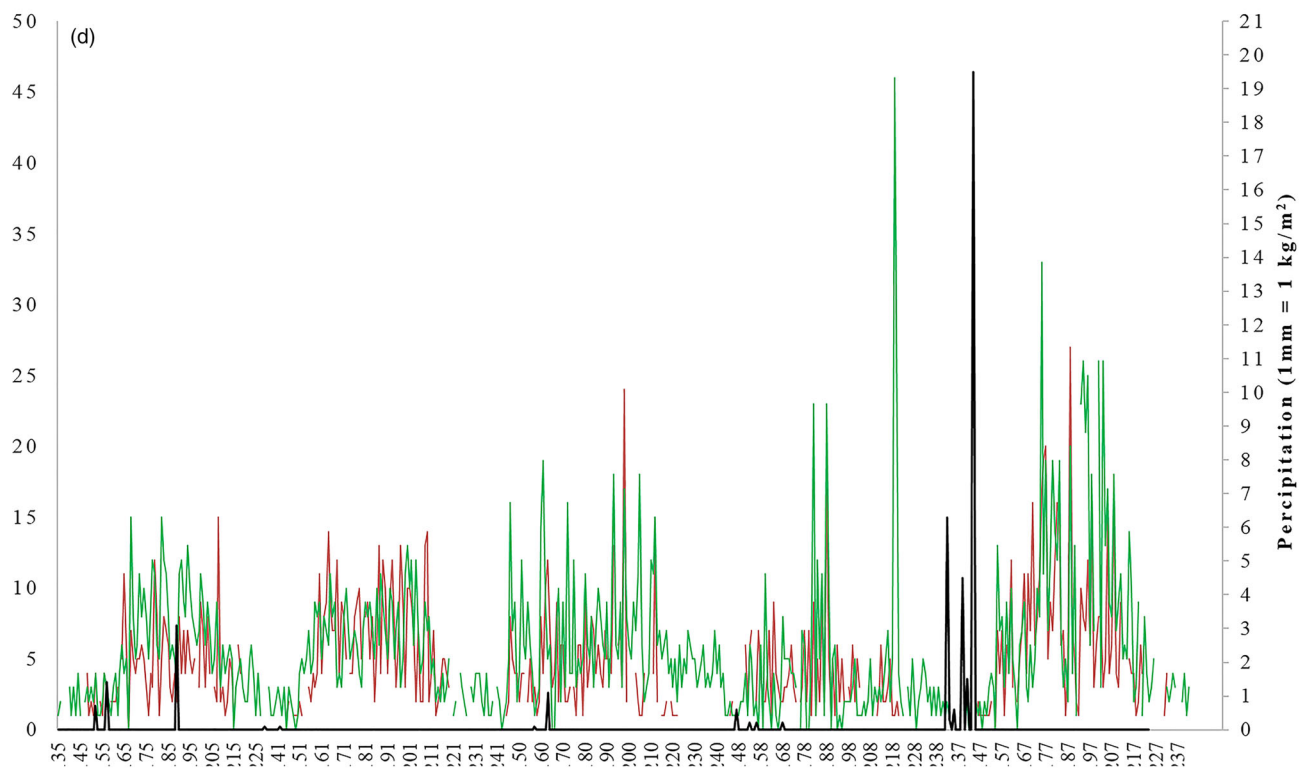
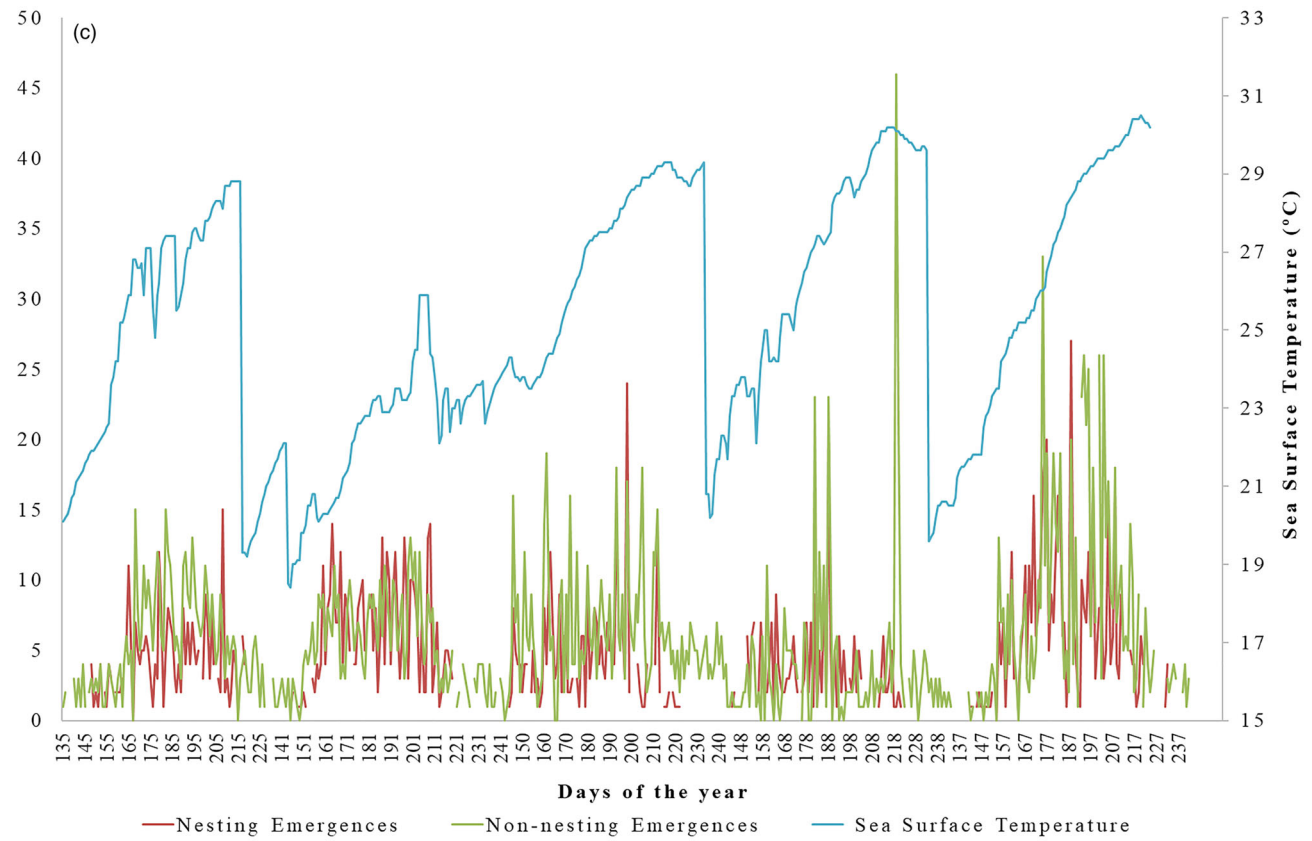
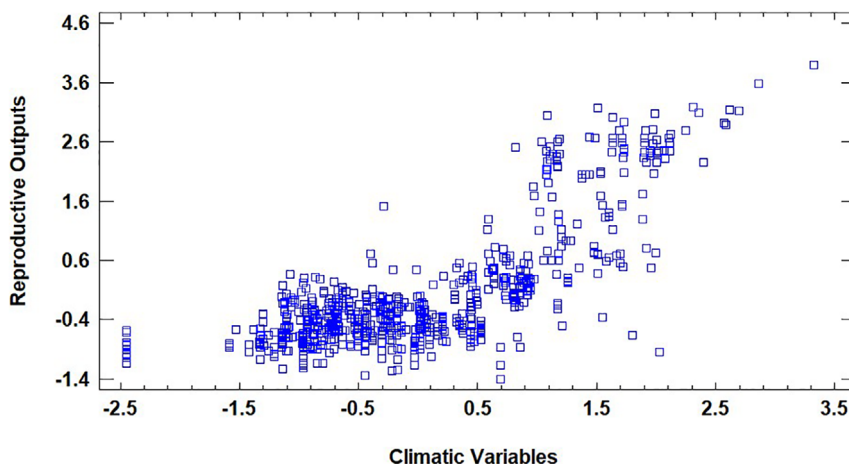


Figure 3 (Continued)



**Table 3** Results of canonical correlation analysis between climatic variables and reproductive output parameters

Number	Eigenvalue	Canonical correlation	Wilks Lambda	Chi-square	d.f.	P-value
1	0.585632	0.765266	0.354269	782.944	9	0.0000**
2	0.102331	0.319892	0.854963	118.228	4	0.0000**
3	0.026824	0.163779	0.952426	36.7765	1	0.0027**

\*\* $P < 0.001$ .**Figure 4** Relationships between climatic variables (atmospheric temperature, relative humidity, precipitation) and reproductive output parameters (hatching success rate, incubation period, number of dead embryos, number of empty eggshells, number of undeveloped eggs) according to canonical correlation analysis.**Table 4** Results of GLMs analysing the effects of climatic variables on reproductive output parameters of loggerhead turtles

Climatic variable	Parameters	Mean square	F-ratio	P-value
Atmospheric temperature (°C)	Hatching success rate	78.657	14.82	0.0001**
	Incubation period	70.399	13.26	0.0003**
	Number of dead embryos	36.712	6.92	0.0085**
	Number of empty eggshells	108.579	20.45	0.0000**
	Number of undeveloped eggs	9.081	1.71	0.1909
Relative humidity (%)	Hatching success rate	1.77128	0.07	0.7921
	Incubation period	167.132	6.55	0.0105*
	Number of dead embryos	60.678	2.38	0.1230
	Number of empty eggshells	265.526	10.41	0.0013**
	Number of undeveloped eggs	0.878	0.03	0.8528

\* $P < 0.05$ .\*\* $P < 0.01$ .

et al. (2016) suggested that minor phenological adjustments may not be sufficient to sustain existing populations, due to increased skew in sex ratios depending on temperature, drier nest conditions caused by reduced soil moisture, and the projected degradation of foraging grounds.

### Reproductive output at Patara Beach

Loggerhead turtles typically nest every other or every third year, with a small percentage nesting at intervals of less than 2 or more than 3 years, and they usually lay 2 or 3 nests per

season (Bjorndal et al., 1983; Broderick et al., 2003; Wyneken et al., 2013). Intraseasonal nesting intervals are typically 12–14 days and may vary with water temperature (Frazer & Richardson, 1986; Hughes, 1975). In this study, the annual nesting success was calculated as 38.96%, and the nest numbers were highly variable among years. We also witnessed a significant event: a few female turtles laid their eggs on Patara Beach four times, with intervals ranging from 12 to 16 days.

Conservation and monitoring activities began on Patara Beach in 1989, and Canbolat (2004) claimed that this beach is a nesting area of secondary importance, containing 3.5% of the

nests in Türkiye annually. Subsequently, it was reported that the annual number of nests on Patara Beach accounted for 2.5% of the total number of nests in the Mediterranean and 8.38% in Türkiye (Casale & Margaritoulis, 2010). It was also reported that non-nesting emergence density on Patara Beach ranged from 12.25 to 21.8 tracks/km, while nest density ranged from 7.4 to 18.7 nests/km (Erdoğan et al., 2001; Olgun et al., 2016; Öz et al., 2004; Taşkın & Baran, 2001). According to these studies, the annual nest numbers varied from 55 to 224, and the mean number of nests between 2010 and 2014 (except 2011) was 180.5 per year. In our study, the mean number of nests per year was 362.6 (range: 253–524 nests), indicating an increasing trend in the number of nests. This increase in the number of nests over time can be attributed to the effectiveness of long-term conservation studies and the monitoring of larger areas by teams using consistent approaches. In this study, the mean nest density was calculated as 30.2 nests/km (range: 21.08–43.66 nests/km). Casale et al. (2018) reported that the average nest numbers were 52.5 nests/year before 1999 and 117.7 nests/year after 2000 at Patara Beach, an increase of 124.4%, and they defined this area as a nesting beach with ‘high’ activity (100–300 clutches/year). Considering our new findings, Patara Beach should be in the ‘very high’ category (>300 clutches/year) according to the classification by Casale et al. (2018).

### Hatching success and predation

Öz et al. (2004) reported a low rate of successful hatching, primarily due to predation, especially in 2000 when the predation rate reached 63%. The following year, Öz et al. (2004) implemented measures to protect nests from predation using screens, resulting in a decrease in the predation rate to 32%. Subsequently, Olgun et al. (2016) reported that 55% of nests were destroyed by predation and 18 162 loggerhead turtle eggs were consumed by predators in the 2010 and 2012–2014 nesting seasons. In our study, the mean predation rate was calculated as 17.5%, which means that 1496 out of 1813 nests (83%) were completely protected. As reported by the aforementioned studies (Olgun et al., 2016; Öz et al., 2004), the main nest predators are foxes (*Vulpes vulpes*), followed by wild pigs (*Sus scrofa*), and rare predation by badgers (*Meles meles*) and domestic dogs (*Canis lupus familiaris*) were also observed between 2019 and 2023.

The results of our study also showed that the mean hatching success rate for the studied years was 81.8%, with a peak of 91.6% in 2023. Reported HSRs at Patara Beach range from 37% to 44.1% according to various studies (Kaska et al., 2005; Kaska, Furness, & Baran, 1998b; Olgun et al., 2016; Yılmaz, 2006). In addition, the mean HSRs at other nesting beaches in Türkiye have been reported as 22.9% in Göksu (Durmuş et al., 2011), 74.4% in Fethiye (Başkale et al., 2016), 61.7% in Dalyan (Türkozan & Yılmaz, 2008) and 41.8% in Demre (Ergene et al., 2007). Hatching success rates at other Mediterranean nesting beaches have been reported as 66.6% in Laganas Bay (Margaritoulis, 2005) and 83% in Northern Cyprus (Broderick & Godley, 1996). It is obvious

that Patara’s HSR in our study is notably higher than in previous studies. In addition to conducting nocturnal patrols along the beach during the whole nesting season, implementing protective measures such as caging of nests to prevent predation and nest relocation to avoid flooding were crucial aspects that contributed to this success.

### Incubation period and sex ratio estimation

Sea turtle species exhibit temperature-dependent sex determination, with higher incubation temperatures leading to female hatchling production (Mrosovsky & Yntema, 1980). Similarly, the length of the incubation period can serve as an indicator of the incubation temperature: longer IPs reflect lower temperatures and result in a higher proportion of male hatchlings, while shorter IPs indicate higher temperatures and lead to a higher proportion of female hatchlings (Mrosovsky et al., 1999). Girondot (2023) reported that the pivotal incubation temperature and duration which produce a 50/50 sex ratio are 28.95°C and 52.80 days, respectively, for Mediterranean marine turtles.

We found that the average IP was 49.3 days, with a range of 42–65 days, for Patara Beach. Furthermore, there were statistically significant differences observed in the IPs among years, and such differences have also been seen in previous studies (Erdoğan et al., 2001; Olgun et al., 2016; Öz et al., 2004; Taşkın & Baran, 2001).

The nest environment generally has a high level of humidity resulting from the transfer of moisture between the eggs and the surrounding sand. Since an increased amount of moisture is inversely related to temperature, moisture mitigates the temperature-related reduction of the IP. Similarly, precipitation can temporarily increase humidity in the nest. However, since the nesting seasons during this study were very dry, no statistically significant relationships regarding precipitation could be detected in the analyses. According to Usategui-Martín et al. (2019), lower incubation temperatures result in the production of larger hatchlings and a longer IP. This finding aligns with an earlier study indicating that lower temperatures lead to a greater conversion of yolk into tissues (Sim et al., 2015). We found a positive correlation between  $T_a$  (atmospheric temperature) and  $T_n$  (nest temperature), which is in accordance with the findings of previous studies (Booth & Limpus, 2008; Hays et al., 1999; Janzen, 1994; Maloney et al., 1990). During the later stages of growth, temperatures increase as a result of metabolic heating (Godfrey et al., 1997; Godley et al., 2001; Van De Merwe et al., 2006; Zbinden et al., 2006). Local climatic conditions may affect the sex ratio and hatching success of sea turtles (Santidrián Tomillo & Spotila, 2020). However, if temperatures reach extremely high levels, the HSR may decline. For instance, Türkozan et al. (2021) reported that declines in HSRs occurred when conditions exceeded the threshold of 33°C for two-fifths of the IPs of green turtle nests. In our study, we could detect statistically significant relationships between  $T_n$  that was recorded as within the seasonal average limits (see Supporting Information Appendices S1 and S2) and either HSR or other nest content

variables. This could be explained by the fact that  $T_n$  during the IP was lower than this threshold temperature (range: 25.88–33.21°C), resulting in a high HSR.

On Patara Beach, Öz et al. (2004) found that the sex ratio was biased towards females, with the calculated percentages of 67% in 2000 and 74% in 2001. We estimated from the  $T_n$  for the SR to have a 70% female bias. Other female biased SRs of loggerhead turtles have been estimated at 81% at Göksu Beach and 61% at Dalyan Beach (Sarı & Kaska, 2015). These estimates for Fethiye Beach ranged between 60% and 65% (Kaska et al., 2006). Similarly, female-biased SRs were estimated at Zakynthos Beach as 68% in 2002 and 75% in 2003 (Zbinden et al., 2007), while Jribi and Bradai (2014) estimated male-biased SRs of loggerhead turtles on the Kuriat Islands, Tunisia, during the 2013 nesting season. In addition, Hays et al. (2017) investigated the population viability of extreme sex-ratio skews at 75 sites around the world. They found that the mean hatchling sex ratio was 73.5% female; for 73% of sites, the SR was more than or equal to 60% female, whereas on just 6.6% of the sites, less than or equal to 40% of the hatchlings were female.

Moreover, the IPs of most nests dropped below the crucial 52.8-day duration (see Giron dot, 2023) during the study period, resulting in a skewed, female-biased sex ratio at Patara Beach. The gradual reduction in IP over time suggests a sustained rise in  $T_n$  and  $T_a$ , possibly influenced by global warming, resulting in an increase in female hatchlings. Furthermore, the increasing feminization of hatchlings may partially explain the observed rise in nest numbers at Patara Beach. An increase in the number of female hatchlings would lead to a larger population of adult female turtles and thereby more nests per season. Comparable examples have been observed at other nesting sites experiencing a rise in nest numbers (Hays et al., 2022; Laloë et al., 2014; Margaritoulis et al., 2023; Sönmez et al., 2023; Sönmez, Elginöz, et al., 2021a).

## Conclusions

This study suggests that successful long-term conservation measures have led to an increase in the number of nests and in HSR, and a decrease in predation rate. Nevertheless, the long-term and successful conservation techniques alone are insufficient to guarantee the species' survival. Due to global warming, sea surface temperatures and  $T_a$  are both increasing every year. Concurrently, annual precipitation and humidity are decreasing. These changes can have direct or indirect effects on the nesting phenology and reproductive output of loggerhead turtles. Rising temperatures led to a decrease in incubation period and an increase in  $T_n$ , resulting in a higher proportion of female offspring, although nesting phenology kept up with minor changes from year to year. Despite the findings of this study, there are still gaps in our knowledge about the effects of global warming on the reproductive biology of the loggerhead turtle; accordingly, new protection strategies need to be created and implemented to reduce the effects of global warming, and more studies are needed on both the Mediterranean and global scales.

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## Conflict of interest

The authors declare that they have no conflict of interest.

## Author contributions

AŞ and EB developed the project, designed the methodology and data collection; EB analysed the data; EB and AŞ led the writing of the manuscript. All authors contributed critically to the drafts of the text, figures and tables, and gave final approval for publication.

## Data availability statement

Data will be made available on request.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Results of a one-way ANOVA analysis of the climatic variables on Patara Beach from 2019 to 2023, with additional descriptive statistics.

**Appendix S2.** Monthly distribution of atmospheric temperature, sea surface temperature, relative humidity and precipitation over a 5-year period (2019–2023) at Patara Beach, Türkiye.