Evolutionary Ecology
https://doi.org/10.1007/s10682-025-10340-9

RESEARCH

Nest thermal dynamics and predicted sex ratio in endemic freshwater crocodylian, gharial (*Gavialis gangeticus*) in Chambal River, India

Surya Prasad Sharma[1] · **Suyash Katdare**[1] · **Ruchi Badola**[1] · **Syed Ainul Hussain**[1]

Received: 19 December 2024 / Accepted: 19 April 2025

Abstract

Understanding the thermal dynamics of nests is critical for crocodylians, as they rely on optimal environmental temperatures for physiological processes, developmental success, and sex determination. Each of these factors is critical for maintaining population dynamics and the long-term persistence of species in the wild. In the present study, we assessed the thermal dynamics of the 17 wild gharial (*Gavialis gangeticus*) nests over three nesting seasons (2017–2019). We observed a significant difference in incubation temperature between the monitored nests across the years. The lowest and the highest incubation temperatures were (mean ± standard deviation) 30.3 ± 2.3 °C and the highest was 32.9 ± 2.8 °C, respectively. The predicted hatchling sex ratio based on constant temperature equivalent (CTE) suggests female dominanc (1:3.2) in the monitored gharial nests. Considering the skewed sex ratio and nest temperatures reaching viable upper thermal limit (33.5 °C), it is recommended to implement continuous monitoring of thermal dynamic of the gharial nests. Conservation efforts should therefore prioritize the protection and management of nesting habitats, establishing long-term monitoring of nest thermal dynamics and reproductive success across multiple nesting sites to mitigate temperature-related impacts.

Keywords Optimum environment temperature · Incubation temperature · Nesting ecology · Thermal limits · Sex ratio · Nest protection

---

✉ Syed Ainul Hussain
ainul.hussain@gmail.com

Surya Prasad Sharma
suryapdsharma@gmail.com

Suyash Katdare
suyashk18@gmail.com

Ruchi Badola
ruchi@wii.gov.in

[1] Wildlife Institute of India, Dehra Dun, P.O. Box # 18, Chandrabani 248002, Uttarakhand, India

Introduction

Ectothermic animals attempt to maintain thermal environments around an optimum to maximise physiological performance and development (Barham et al. 2024; Grigg and Kirshner 2015). Deviations in temperature range can impair development, reduce hatching success, and negatively affect growth and survival (Buckley and Huey 2016; Deeming and Ferguson 1989; Lang and Andrews 1994; Somero 2010; Walsh et al. 2019). In species with temperature-dependent sex determination (TSD), elevated temperatures can also skew sex ratio impacting reproductive success and long-term population viability (Deeming and Ferguson 1989; Fukuda et al. 2022; González et al. 2019; Lara et al. 2021). As elevated temperatures can skew sex ratios, and reduce embryonic survival and growth resulting in low reproductive success, nest incubation temperature, therefore, plays a critical role in determining both hatching success and sex ratio (Bodensteiner et al. 2023; Boyle et al. 2014; Charruau 2012). While species can optimize their physiological processes through thermoregulation, they cannot directly regulate the microclimatic environment of the nests (Charruau et al. 2017). Instead, nest temperatures are primarily influenced by environmental factors such as ambient temperature, vegetation cover, and sun exposure (Gatto et al. 2023; Mazzotti et al. 2022). Moreover, species in response to altered environmental conditions, particularly temperature rise may display a range of adaptive mechanisms such as shifts in the timing of oviposition, alteration in nest depth and nesting site selection, that can help regulate sex ratio and improve reproductive success (Mainwaring et al. 2017; Radchuk et al. 2019; Santos et al. 2021).

The gharial (*Gavialis gangeticus*), is a ‘Critically Endangered’ freshwater crocodylian species, facing challenges due to persistent stressors such as habitat destruction, entanglement in passive fishing, and rising environmental temperatures (Hussain et al. 1999; Katdare et al. 2011; Panda et al. 2023; Vashistha et al. 2021). Despite the concerted management interventions that have averted the extinction of gharial, the persistent threats continue to undermine conservation efforts and highlight the need for effective conservation strategies (Nair et al. 2012; Sharma et al 2021). Hence, understanding the thermal dynamics of nests is critical, particularly due to the species reliance on environmental temperature and inability to regulate microclimatic conditions, which may lead to skewed sex ratios and reduced hatching success, ultimately impacting the long-term viability of gharial in the wild (Charruau et al. 2017; Mainwaring et al. 2017). In such circumstances, adaptive management interventions become imperative to alleviate the negative effects of the rise in environmental temperature (Gatto et al. 2023; Vashistha et al. 2021). Nevertheless, the success of such interventions is dependent on understanding the thermal dynamics of the nests. Despite its importance, the thermal ecology of gharial nests remains relatively understudied in comparison to other crocodylians (Charruau 2012; González et al. 2019; Lara et al. 2021; Murray et al. 2016; Viljoen et al. 2023). The present study aims to (a) investigate the thermal dynamics of gharial nests and (b) predict sex ratio using constant temperature equivalents (CTE).

Materials and methods

Study site

The study was conducted between 2017 and 2019 in the Chambal River within the National Chambal Sanctuary (NCS), India. The National Chambal Sanctuary which is a tri-state sanctuary situated in the Chambal River (Fig. 1). The NCS is home to the largest breeding population of gharial and serves as key site for the gharial recovery program. Three gharial nesting sites– Baroli, Nadigaon, and Dangbasai were selected to study the thermal regime of gharial nests (Fig. 1). These sites are crucial for gharial conservation, as wild-laid gharial eggs are collected annually from these sites to support the 'grow and release' program in the Sanctuary and other rivers across India.

Data collection

We deployed 72 iButton data loggers across 24 nests at three nesting sites viz. Baroli (BA), Nadigaon (NG) and Dangbasai (DG) to study the thermal regime of the gharial nest and one data logger for recording ambient air temperature. The search for suitable gharial nests to deploy the data loggers began following the trial nesting by females at the studied nesting sites at the end of February each year. Subsequently, these sites were monitored every day to ensure that all nests were located on the same day of oviposition. Upon locating nests key characteristics including nest depth, distance from the shoreline, vegetation cover, and clutch size were recorded. Dataloggers to record ambient environmental temperature were

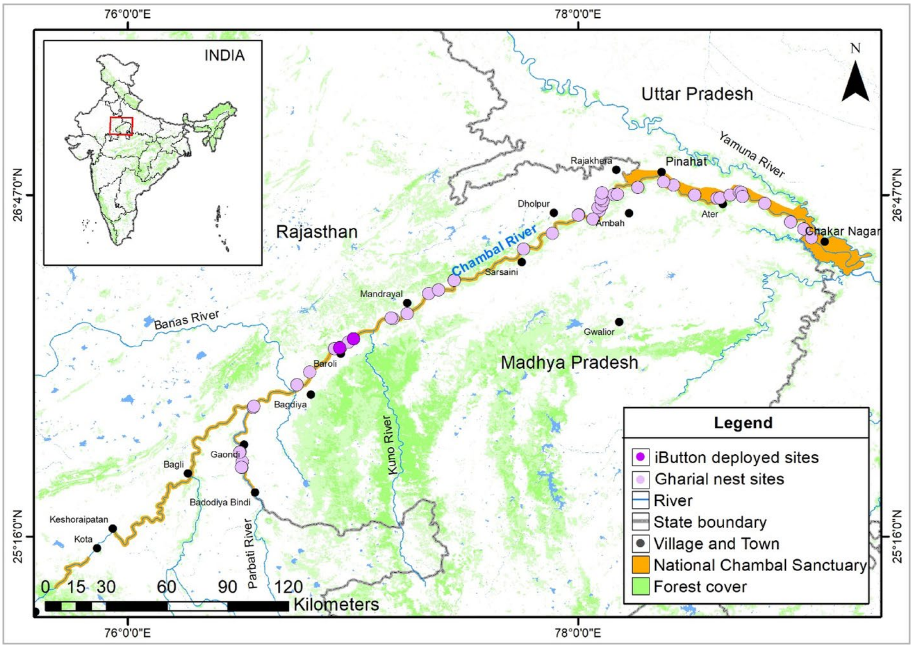

Fig. 1 Map of the nesting sites of the gharial (*Gavialis gangeticus*) within the National Chambal Sanctuary along the Chambal and Parbati rivers

deployed at two sites, Baroli and Dangbasai. Since both nesting sites, Baroli and Nadigaon, are located in close proximity (< 10 km apart), a single datalogger was used during the study. The iButton temperature data loggers (Model: DS1921G#F5; Temperature range (°C):–40 to + 85; Accuracy (°C): ±1; Maxim Integrated Products Inc. USA) were then deployed within 24 h oviposition to minimize any disturbance to the eggs. In each nest, three data loggers were placed each nest at the top, middle and bottom of the nest (Fig. 2). The data loggers were programmed to record the temperature at 90-minute intervals. The 90-minute interval was set to balance the number of data points each logger could record over the 60-day incubation period while ensuring adequate data points to accurately characterize the thermal regime of gharial nests. Following the deployment of data loggers, the nesting sites were regularly monitored for the next 55–60 days until the eggs were relocated to the Deori Gharial Rearing Center (DGRC) facility for rearing. Each nest was labelled in a structured format, where: the first two letters represent the nesting site (BA for Baroli, NG for Nadigaon, and DG for Dangbasai). The next two digits indicate the year of observation and the final three characters specify the nest ID. For example, in BA17 N01, BA refers to Baroli, 17 denotes the year 2017, and N01 identifies Nest 01. The data loggers placed inside the nests were retrieved before the relocation of the eggs along with the outside nest data loggers were also retrieved. The hatching success of each nest was calculated by dividing the number of eggs that successfully hatched by the total number of eggs in the nest and then multiplying the result by 100 to express it as a percentage.

Data analysis

The temperature data obtained were trimmed to remove a few initial and final readings before the nest was opened to retrieve the data loggers to establish a common reference point. The mean, minimum and maximum incubation temperature for each layer (top, middle and bottom) and entire nest were calculated. The daily temperature variation was determined by subtracting the minimum from the maximum temperature for each day. We performed Welch's ANOVA test to examine differences in mean nest temperature and ambient air temperature. Following a significant result, pairwise comparisons with Bonferroni

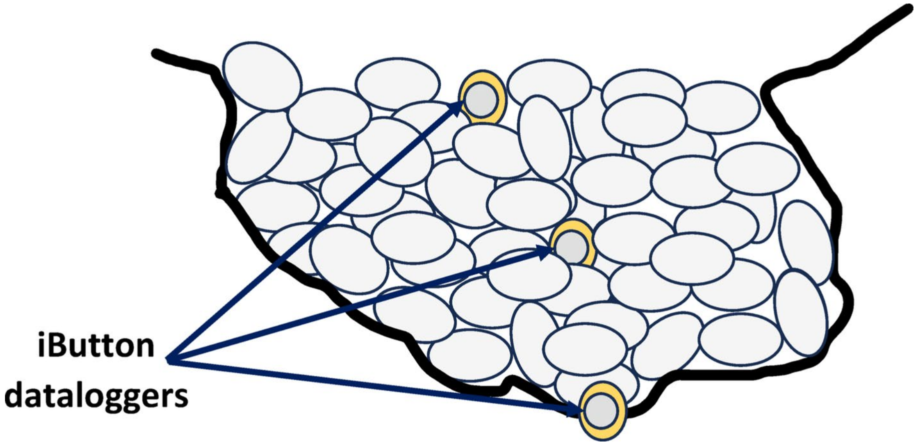

Fig. 2 Illustration depicting the placement of iButton dataloggers within the gharial nests

correction were conducted to identify differences between mean nest temperature across years and sites, as well as between ambient temperature and mean nest temperatures.

We estimated the CTE: the temperature above and below which half of embryonic development is estimated to have occurred (Georges et al., 1994, 2004). The CTE was estimated for the thermosensitive period (TSP) i.e. 20–40 days (TSP: interval of time when the variation of temperature is shown to have significant effect on sex ratio). The TSP in crocodylians is known to be the middle third of the incubation period (Lang and Andrews 1994). For an incubation period of 60 days, the period between 20 and 40 days is the middle third of the incubation period (Lang and Andrews 1994 and Murray 2016). The CTE was estimated following the model developed by (Georges 1989) as described in Georges et al. (2004) and Murray et al. (2016). In the absence of gharial-specific developmental rates, we have used developmental rates derived for American alligator (*Alligator mississippiensis*) (Deeming and Ferguson 1989; Lang and Andrews 1994) assuming these rates to be conserved among the crocodylians.

The sex ratio of each nest was then predicted based on the available information on the thermal pattern of sex determination in gharial (Lang and Andrews 1994). The CTEs calculated for each nest layers were averaged to obtain an overall nest CTE, which was subsequently used to determine the sex ratio. For instance, if a nest has CTE values of 33 °C for the top layer, 32 °C for the middle layer, and 31 °C for the bottom layer, the overall CTE for the nest would be 32 °C. Based on information available on the thermal pattern of sex determination in gharial (Lang and Andrews 1994) the eggs incubated at 32 °C produced 89% male and 11% female. Therefore, a nest containing 27 eggs would produce 24 males and 3 females. We performed a paired t-test to determine whether there was a significant difference between CTEs and mean nest temperature. Finally, we assessed the correlation between mean incubation temperature, CTEs and nest characteristics. All statistical analyses and computations were carried out using Microsoft Excel and R Studio.

Results

Nest features

Between 2017 and 2019, a total of 250 gharial nests were located in three nesting sites, of which the thermal regime of 24 of nests was monitored (Table 1). The mean clutch size of the 24 monitored nests was 34.2 ± 7.0 eggs (mean ± standard deviation) and ranged from 17 to 49 eggs (Table 2). The average nest depth among the monitored nests was 47.3 ± 10.3 cm and ranged between 30.0 cm and 65.0 cm. The shallowest nest (BA18N02; 35 cm) was observed at the Baroli site, while the maximum depth (65 cm) was recorded for the

Table 1 Number of nests observed in the study sites between 2017 and 2019. TN = Total number of nests detected; sn = number of successful nests; un = nummer of nests lost due to predation

Site Name	2017			2018			2019		
	TN	SN	UN	TN	SN	UN	TN	SN	UN
Baroli	11	11	0	18	18	0	32	32	0
Nadigaon	40	33	7	25	10	15	43	31	12
Dangbasai	31	31	0	20	16	4	30	23	7
Total	**82**	**75**	**7**	**63**	**44**	**19**	**105**	**86**	**19**

Table 2 Summary of gharial nest characteristics at Baroli and Nadigaon nesting sites along the Chambal River. Parameters include number of eggs, distance to water, nest depth, hatching success and incubation period (Nest ID nomenclature: BA = baroli nest site, 17 = year 2017, N01 = nest 01)

Nest ID	No. of eggs	Distance to water (m)	Nest depth (cm)	Hatching Success (%)	Incubation period	Data logger position		
						Top	Middle	Bottom
BA17 N01	37	3	35	94.6	62	+	+	+
BA17 N02	35	6	35	100.0	61	+	+	+
BA17 N03	40	6	40	100.0	60	+	+	+
BA18 N01	31	7	35	100.0	64	–	–	+
BA18 N02	37	6	38	–	–	–	–	–
BA18 N03	27	4.2	40	92.6	64	+	–	–
BA19 N01	27	8	40	100.0	65	+	+	+
BA19 N02	31	7	35	100.0	62	+	+	+
BA19 N03	31	4	38	100.0	63	+	+	+
NG17 N01	17	4	55	100.0	64	+	+	+
NG17 N02	32	5	60	96.9	60	+	+	+
NG17 N03	32	5.3	60	100.0	63	+	+	+
NG18 N01	34	4	46	94.1	62	+	+	
NG18 N02	41	5	52	100.0	62	+	–	–
NG18 N03	39	5.3	55	97.4	65	+	–	+
NG19 N01	43	5.3	63	100.0	60	+	+	+
NG19 N02	39	4.5	55	100.0	60	+	+	+
NG19 N03	49	5	65	95.9	62	+	+	+
DG18 N01	32	8	47	–	–	–	–	–
DG18 N02	30	7	55	–	–	–	–	–
DG18 N03	38	3	45	–	–	–	–	–
DG19 N01	22	4	38	–	–	–	–	–
DG19 N02	41	8	53	–	–	–	–	–
DG19 N03	35	5	50	–	–	–	–	–
Mean	**34.2**	**5.4**	**47.3**	**98.3**	**62.3**			
SD	**7.0**	**1.5**	**9.8**	**2.5**	**1.7**			

NG19N03 nest at the Nadigaon site. The average nest distance from the shoreline was 5.4 ± 1.3 m and ranged between 3.0 and 8.0 m. The average incubation period of the nests at the studied sites was 62.3 ± 1.7 days and hatching success ranged between 92.6% and 100%.

Nest temperature regime

Of the 72 data loggers deployed across 24 nests, temperature data from 43 data loggers from 17 nests were successfully retrieved, while the remaining data loggers ($n = 29$) were either lost due to predation or malfunctioned. Temperature data from all the data loggers placed outside the nest were successfully retrieved. We retrieved all three data loggers from 12 nests (50.8%), two data loggers from 2 nests (8%), and only one datalogger from 3 nests (13%). All of the data loggers deployed at the Dangbasai were either lost or malfunctioned. Therefore, the data analysis includes only two sites, i.e., Baroli (BA) and Nadigaon (NG) and for ambient temperature the data logger deployed at the Baroli site was used.

The lowest mean incubation temperature was recorded in NG17 N01 (30.3 ± 2.3 °C) and the highest was recorded in the BA18 N03 (32.9 ± 3.0 °C) and BA17 N01 (32.9 ± 2.8 °C)

(Fig. 3 and Table S1). The bottom of the nest consistently recorded the lowest temperature and variability compared to other layers in the majority of the nests (Fig. 4 and Table S1). Similarly, the top layer was consistently the warmest and most variable. Interestingly, we observed exceptions to the general temperature pattern at two nests BA17 N02 and NG17 N01. The BA17 N02 showed no temperature difference between the bottom and middle layers, while NG17 N01 exhibited warmer temperatures at the bottom than in the middle (Table S1). The mean ambient air temperature and mean incubation temperatures showed a gradual increase as the incubation period advanced, punctuated by brief instances of temperature drop (Fig. 4). In 2017, we observed two instances of temperature drops, the first occurring 15–20 days post oviposition and the second at 30–35 days (Fig. 4). Similarly in 2018, three instances but at different periods, first at 25–30 days, second at 35–40 days and finally at 50–55 days of oviposition. While, in 2019, two instances of drop, first at 25–30 days and

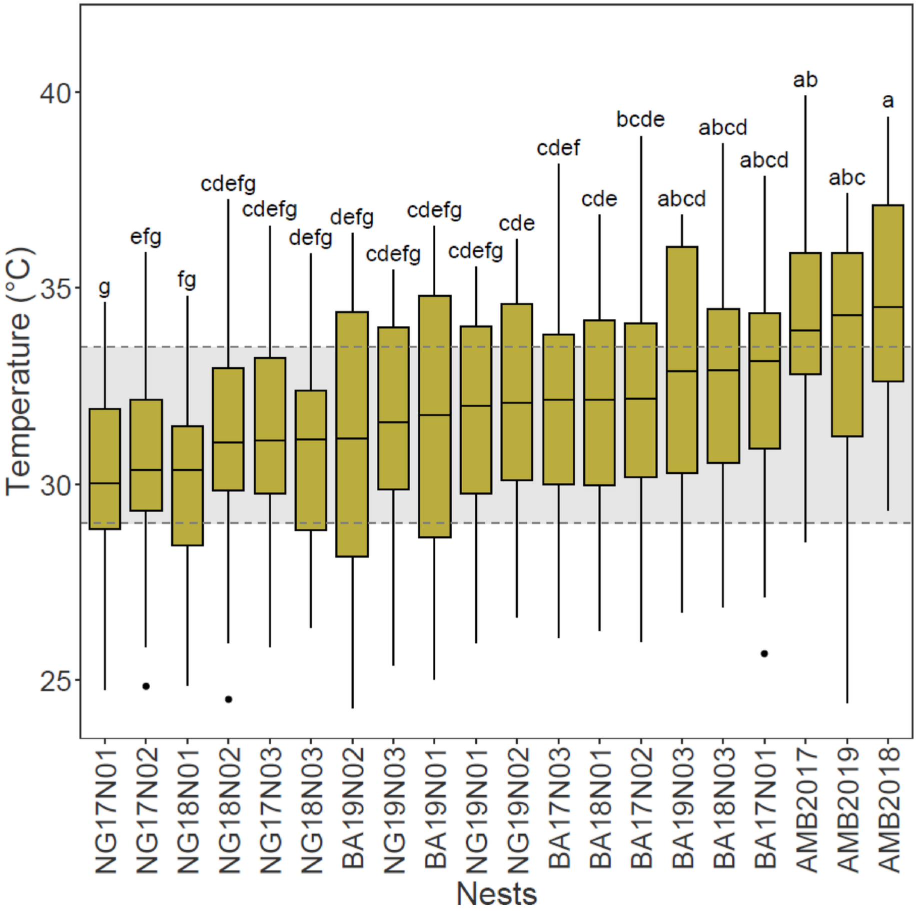

Fig. 3 Box-plot of the mean incubation temperature of the gharial nest and ambient air temperature recorded at Baroli and Nadigaon nesting sites during three nesting seasons (2017–2019). Grey shaded areas indicate temperatures range between 29 °C and 33.5 °C, which is optimum for the growth of crocodylian embryos. The alphabet above the whiskers indicates significant differences ($p \leq 0.05$)

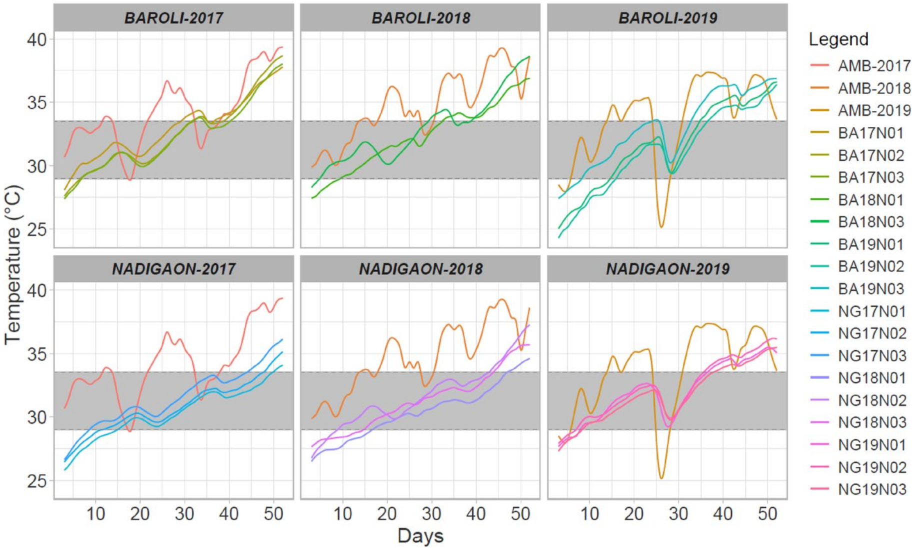

Fig. 4 Line graph of mean incubation temperature and ambient temperature recorded at Baroli and Nadigaon nesting sites between 2017 and 2019

second at 40–45 days (Fig. 4). The mean daily mean variation in temperature within the nests ranged between 8 and 15.5 °C (Fig. 5).

The comparison of mean incubation temperature and mean variation among the monitored nests showed varied results (Figure S1). We observed a significant difference in the mean nest temperature $F\ (19, 387) = 10.05$, $p < 0.001$) across nests. Further, out of the 190 pairwise comparisons made between nests across the nesting sites and nest temperature and ambient air temperature, 51 (26.8%) of these pairwise comparisons showed significant differences in mean incubation temperature.

Constant temperature equivalent and predicted sex ratio

The constant temperature equivalent (CTE) calculated for the thermosensitive period ranged between 30.5 °C and 34.0 °C (Table 3). Consistent with the average nest temperature the lowest and the highest CTEs were observed in the bottom and top layers of the nests, respectively (Table 3). The t-test indicated a significant difference between the mean incubation temperature and CTEs (t (42) =–12.58, $p < 0.001$). Using CTEs to predict nest sex ratio, we found a strong female bias, with a global sex ratio of 1 male per 3.2 females (1:3.2). Over 35% of the nests exhibited higher female-producing temperatures, and in 30% of the nests, all offspring were female. In addition, using the average nest temperature we obtained a global sex ratio of 1:2 (Table S2). We observed a negative correlation between nest depth and CTE (r =–0.41, $p < 0.001$). However, no significant correlation was found between other nest characteristics and CTEs.

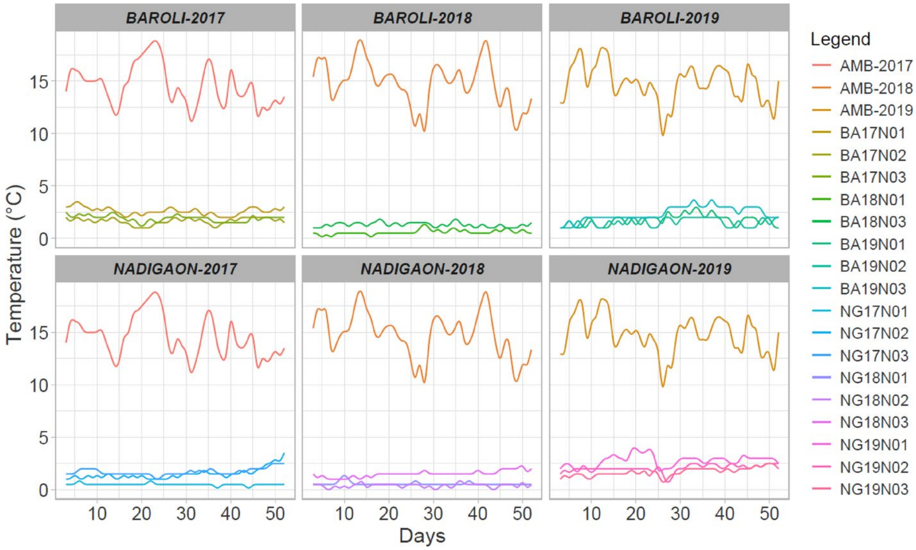

Fig. 5 Line graph of the variation in daily mean variation within the nest and ambient air temperature recorded at Baroli and Nadigaon sites between 2017 and 2019

Discussion

Environmental temperature plays a crucial role in influencing behavioural and morphological traits (Charruau 2012; González et al. 2019), sex determination (Lang and Andrews 1994) and reproductive success in ectotherms (Murray et al. 2016). For temperature-dependent sex determination (TSD) climate-induced alterations in thermal regimes during incubation can have profound consequences (Hulin et al. 2009). The combined effects of developmental stress and sex ratio distortion pose significant threats to the long-term viability of populations (Charruau 2012; Lockley and Eizaguirre 2021). Rising environmental temperatures may influence the timing of egg-laying, incubation duration, and hatchling emergence, potentially reducing reproductive success. While some populations may temporarily buffer the impact of climate-induced temperature rise through behavioural adaptations, such as nest site selection and altered incubation behaviours (Doody et al. 2006; González et al. 2019; Roosenburg 1996), long-term monitoring of thermal dynamics in gharial nests is essential to assess the extent of these impacts and inform conservation strategies (Du et al. 2023; González et al. 2019).

In the present study, we found that the average incubation temperatures of gharial nests ranged between 30.3 and 32.9 °C, consistent with that observed in other crocodylians, such as *Crocodylus acutus*: 30.1 to 34.7 °C (Lara et al. 2021), 29.6 to 34.2 °C (González-Desales et al. 2016), 29.8 to 33.1 °C (Charruau 2012), and *Alligator mississippiensis*: 29.1 to 33.8 °C (Lang and Andrews 1994; Rhodes and Lang 1996). Previous studies on gharial have reported successful embryo development at incubation temperatures between 29 and 33.5 °C (Lang and Andrews 1994). We also found that the daily mean incubation temperature was well within the suggested viable thermal limits (29–33.5 °C) reported for the successful development of embryo in gharial. This was further supported by high hatching suc-

Table 3 Summary of the constant temperature equivalent during the thermosensitive period (CTE), clutch size, and predicted sex ratio for 17 gharial nests along the chambal river, India, during 2017–2019

Nest ID	Data logger Position	CTE	Mean CTE	Clutch size	Male %	Female %	Male Offspring	Female Offspring
BA17 N01	Top	34.0		37.0	17	83	6	31
	Middle	33.5	33.5					
	Bottom	33.0						
BA17 N02	Top	33.5		30.0	18	82	6	25
	Middle	33.0	33.0					
	Bottom	33.0						
BA17 N03	Top	33.5		29.0	28	72	8	21
	Middle	32.5	33.0					
	Bottom	33.0						
BA18 N01	Top	–		31.0	15	85	5	26
	Middle	–	33.0					
	Bottom	33.0						
BA18 N03	Top	33.5		27.0	15	85	4	23
	Middle	–	33.5					
	Bottom	–						
BA19 N01	Top	32.5	32.0	27.0	37	63	10	17
	Middle	32.0						
	Bottom	31.5						
BA19 N02	Top	32.0		31.0	30	70	9	22
	Middle	31.5	31.5					
	Bottom	30.5						
BA19 N03	Top	34.0		31.0	28	72	9	22
	Middle	33.5	33.5					
	Bottom	32.5						
NG17 N01	Top	31.0		17.0	0	100	0	17
	Middle	30.5	31.0					
	Bottom	31.0						

Table 3 (continued)

Nest ID	Data logger Position	CTE	Mean CTE	Clutch size	Male %	Female %	Male Offspring	Female Offspring
NG17 N02	Top	31.5		32.0	0	100	0	32
	Middle	31.0	31.0					
	Bottom	30.5						
NG17 N03	Top	32.5		32.0	37	63	12	20
	Middle	32.5	32.0					
	Bottom	31.0						
NG18 N01	Top	31.0		34.0	0	100	0	34
	Middle	30.5	31.0					
	Bottom	--						
NG18 N02	Top	--		41.0	55	45	23	18
	Middle	32.0	32.0					
	Bottom	--						
NG18 N03	Top	32.0		39.0	18	82	7	32
	Middle	--	31.5					
	Bottom	31.0						
NG19 N01	Top	33.5		43.0	23	77	10	33
	Middle	32.5	32.5					
	Bottom	31.5						
NG19 N02	Top	33.0		39.0	25	75	10	29
	Middle	32.5	32.5					
	Bottom	31.5						
NG19 N03	Top	32.5		49.0	37	63	18	31
	Middle	32.5	32.0					
	Bottom	31.0						
Predicted Sex Ratio (Male: Female) **1:3.2**							**136**	**433**

cess (> 90%), indicating that the observed thermal conditions were conducive to embryo development and hatchling survival. In contrast to the previous studies that have reported low hatching success in warmer nests exceeding incubation temperature of > 33.5 °C, we observed high hatching success in the monitored nests. The high hatching success could be attributed to multiple factors such as substrate quality, moisture and thermoregulation ability of embryos inside the eggs (Du and Shine 2022; Du et al. 2023; Packard et al. 1987; Zhao et al. 2013). The embryos of oviparous reptiles can actively reposition themselves within the egg by subtle movements, allowing them to seek optimal thermal conditions. This enables embryos to adjust physiologically and behaviorally in response to environmental changes, enhancing their survival (Liu et al. 2023; Zhao et al. 2013).

We also observed a distinct thermal gradient within the nests, with the top layer being the warmest and exhibiting the highest temperature variability, while the bottom layer remained the coolest with the most stable temperature conditions. The warmer temperatures at the top layer can be attributed to its closer proximity to the external environment, where it receives greater solar radiation exposure (Lara et al. 2021). This thermal stratification within the nest may have important implications for embryonic development, influencing factors such as sex determination and hatching success. Crocodylian nests typically experience a daily cycle of temperature variations ranging from 1 to 5 °C, largely driven by fluctuations in environmental temperature (Murray et al. 2016). During the day, increased solar radiation leads to greater heat absorption by the nest, while at night, radiative cooling causes significant heat loss to the surrounding air (Murray et al. 2016). Additionally, the gradual rise in the mean nest temperature from oviposition to hatching corresponds with the seasonal increase in ambient temperatures as the summer progresses.

The sex ratio predicted using the CTE indicated female dominance 1:3.2 (male: female) in the monitored gharial nests. However, we were unable to validate the predicted sex ratio against the actual sex of the hatchlings, necessitating cautious interpretation of the results. Notably, the dominance of female hatchlings is supported by previous studies on crocodylians that have reported female dominance in the population (González et al. 2019). In species exhibiting a female-male-female (FMF) pattern of sex determination, the temperature range that produces females is generally broader than that for males. Consequently, a higher proportion of female offspring is expected (Katselidis et al., 2012). Further, rising environmental temperatures are predicted to exacerbate sex ratio imbalances and reduce survival rates, potentially altering population dynamics (Hays et al. 2017). In sea turtles, it has been observed that even when the sex ratios are female-biased, the impact on the population viability was less severe than previously anticipated due to the ability of males to maintain the operational sex ratio by mating with multiple females (Hays et al. 2017). A similar scenario may be occurring in the gharial population of the Chambal River, where despite a female bias, the population appears to be thriving, as suggested by increasing trends (Sharma et al. 2024, In review). While a female-skewed sex ratio may initially seem beneficial due to the higher potential for reproductive output, a disproportionately low number of males can reduce the effective population size (Ne), potentially leading to inbreeding and reduced genetic diversity over time (Mitchell et al. 2010). However, similar female-biased ratios have been reported in other crocodilian species with temperature-dependent sex determination (TSD), such as the American alligator and some caiman species (González et al. 2019). These populations have persisted, possibly due to behavioural or life-history trait modifications such as multiple mating by males that help maintain a functional operational sex ratio

(Hays et al., 2017). Whether such mechanisms are sufficient to buffer against demographic or genetic risks in gharial remains unclear. Furthermore, in the absence of gharial-specific developmental rates, the use of cross-species developmental rates as a reference may not fully account for potential differences, and the estimated sex ratio might differ from the actual demographic composition.

Multiple factors influence the thermal environment of crocodylian nest, including the substrate, nest depth, distance from the shoreline, and solar radiation (González et al. 2019). Empirical studies indicate that these factors are largely dependent on individual choice, with female individuals attempting to select the most suitable nest sites based on availability (Bodensteiner et al. 2023; Du et al. 2023). Nest-site selection is critical for reproductive success, and female crocodiles evaluate various environmental parameters before choosing a nesting location, including substrate texture, shadiing, accessibility, distance to water, and slope. This process is commonly referred to as ‘trial nesting’. Studies have suggested that species can mitigate the negative effects of climate change through phenotypic plasticity (Santos et al. 2021). Species in responce adapt to natural changes that occur over time, such as turtles avoiding areas prone to tidal inundation, and early or delayed oviposition due to temperature rise (Du et al. 2023).

The change in precipitation patterns may also influence nesting site selection and nest construction, affecting nest success (Charruau et al. 2017). Increased frequency and intensity of extreme weather events may disrupt nesting behaviours and nesting success, leading to population decline. Therefore, it is foreseeable that management interventions will be necessary to mitigate the impacts of rising environmental temperatures. Among the most common interventions is the relocation of eggs to safer locations, either in *in-situ* hatcheries or specialized facilities (Gatto et al. 2023). The success of these interventions is directly linked with the available information on the thermal dynamics of the wild gharial nests, which can inform efforts to replicate these temperatures in managed settings. Notwithstanding that TSD taxa have survived climate warming and cooling over evolutionary timeframes (Mitchell and Janzen 2010), it remains unclear if TSD reptiles can respond quickly enough to the contemporary human-induced climate warming through evolutionary compensatory mechanisms or if they have scope to respond through phenotypic plasticity.

The gharial exhibits two pivotal temperatures and follows a female–male–female (FMF) pattern of temperature-dependent sex determination, where females are produced at both lower and higher temperatures, while males emerge at intermediate temperatures (Lang and Andrews 1994). This pattern makes it challenging to predict the consequences of rising temperatures, as the relationship between temperature and sex ratio is non-linear. With observed nest temperatures approaching the upper viable thermal limits, and female-biased sex ratios, there is an urgent need for comprehensive monitoring of the thermal dynamics within gharial nests to assess the implications of rising environmental temperature. Furthermore, the extent to which gharial can adapt their nesting strategies in response to these changes remains poorly understood, highlighting the necessity for further research into their behavioural plasticity and potential for adaptive responses.

In conclusion, our findings highlight the importance of monitoring the thermal environment of gharial nests and its influence on hatchling sex ratio and reproductive success. The observed female-biased sex ratio underscore the potential demographic and genetic risks posed by rising environmental temperatures. Conservation efforts should therefore focus on the protection of nesting sites, establishing long-term monitoring of nest thermal dynamics and reproductive success across multiple nesting sites to better understand spatiotemporal variation in nest temperatures. This information is essential for developing effective, site-specific conservation strategies aimed at mitigating the impacts of rising environmental temperatures on gharial reproduction and population viability.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10682-025-10340-9.

Acknowledgements This study was carried out with funding support from Grant-In-Aid fund of the Wildlife Institute of India (WII), Dehra Dun and through the projects Biodiversity conservation and Ganga rejuvenation" and "Planning & Management for Aquatic Species Conservation and Maintenance of Ecosystem Services in the Ganga River Basin" funded by the National Mission for Clean Ganga (NMCG), Ministry of Jal Shakti, Government of India. We acknowledge the help and support provided by the Director and Dean, WII. We would like to thank the Chief Wildlife Wardens of Government of Madhya Pradesh, Rajasthan and Uttar Pradesh for providing and facilitating timely research permits. We especially thank Dr. A. A. Ansari, Divisional Forest Officer, National Chambal Sanctuary for facilitating this study.

Author contributions Sharma S. P: Data Curation, Methodology, Software, Formal Analysis, Visualization and Writing - Original Draft. Katdare S: Methodology, Data Curation and Writing - Review & Editing Draft. Badola R: Conceptualization, Funding acquisition, Supervision and Writing - Review & Editing. Hussain S. A: Conceptualization, Methodology, Supervision and Funding acquisition and Writing - Review & Editing.

Funding This study was funded by the Grant-in-aid fund of the Wildlife Institute of India, Dehra Dun and the National Mission for Clean Ganga, Ministry of Jal Shakti, Government of India (Grant No. B-02/2015-16/1259/NMCG-WII PROPOSAL and B-03/2015-16/1077/NMCG-NEW PROPOSAL). The funding agency has no role in the design of the study and collection, analysis, and interpretation of data and in writing the manuscript.

Data availability The data that support the findings of this study are openly available in figshare at 10.6084/m9.figshare.26827927.

Code availability No custom codes or software applications were developed or used specifically for this study.

Declarations

Competing interests The authors declare no competing interests.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

References

Barham KE, Dwyer RG, Frere CH, Bentley LK, Baker CJ, Campbell HA, Irwin TR, Franklin CE (2024) Cooling down is as important as warming up for a large-bodied tropical reptile. Proceedings B 291, 20241804

Bodensteiner BL, Iverson JB, Lea CA, Milne-Zelman CL, Mitchell TS, Refsnider JM, Voves K, Warner DA, Janzen FJ (2023) Mother knows best: nest-site choice homogenizes embryo thermal environments among populations in a widespread ectotherm. Philosophical Trans Royal Soc B 378:20220155

Boyle M, Hone J, Schwanz LE, Georges A (2014) Under what conditions do climate-driven sex ratios enhance versus diminish population persistence? Ecol Evol 4:4522–4533

Buckley LB, Huey RB (2016) Temperature extremes: geographic patterns, recent changes, and implications for organismal vulnerabilities. Glob Change Biol 22:3829–3842

Charruau P (2012) Microclimate of American crocodile nests in Banco Chinchorro biosphere reserve, Mexico: effect on incubation length, embryos survival and hatchlings sex. J Therm Biol 37:6–14

Charruau P, Martínez D, Cantón G, de la Méndez F (2017) Additional details on temperature-dependent sex determination in Crocodylus acutus. Salamandra 53:304–308

Deeming DC, Ferguson MW (1989) The mechanism of temperature dependent sex determination in crocodilians: a hypothesis. Am Zool 29:973–985

Doody JS, Guarino E, Georges A, Corey B, Murray G, Ewert M (2006) Nest site choice compensates for climate effects on sex ratios in a Lizard with environmental sex determination. Evol Ecol 20:307–330

Du W, Shine R (2022) The behavioural and physiological ecology of embryos: responding to the challenges of life inside an egg. Biol Rev 97:1272–1286

Du W-G, Li S-R, Sun B-J, Shine R (2023) Can nesting behaviour allow reptiles to adapt to climate change? Philosophical Trans Royal Soc B 378:20220153

Fukuda Y, McDonald PJ, Crase B (2022) Lost to the Sea: predicted climate change threats to saltwater crocodile nesting habitat. Front Ecol Evol 10:839423

Gatto CR, Williamson SA, Reina RD (2023) Mitigating the effects of climate change on the nests of sea turtles with artificial irrigation. Conserv Biol 37, e14044

Georges A (1989) Female turtles from hot nests: is it duration of incubation or proportion of development at high temperatures that matters? Oecologia 81:323–328

Georges A, Doody S, Beggs K, Young J (2004) Thermal models of TSD under laboratory and field conditions. Temperature-dependent Sex Determ Vertebrates 79–89

González EJ, Martínez-López M, Morales-Garduza MA, García-Morales R, Charruau P, Gallardo-Cruz JA (2019) The sex-determination pattern in crocodilians: A systematic review of three decades of research. J Anim Ecol 88:1417–1427

González-Desales GA, Monroy-Vilchis O, Zarco-González MM, Charruau P (2016) Nesting ecology of the American crocodile in La encrucijada biosphere reserve. Mexico Amphibia-Reptilia 37:261–271

Grigg G, Kirshner D (2015) Biology and evolution of crocodylians. CSIRO Publishing. https://doi.org/10.1071/9781486300679

Hays GC, Mazaris AD, Schofield G, Laloë JO (2017) Population viability at extreme sex-ratio skews produced by temperature-dependent sex determination. Proceedings of the Royal Society B: Biological Sciences 284(1848): 20162576

Hulin V, Delmas V, Girondot M, Godfrey MH, Guillon J-M (2009) Temperature-dependent sex determination and global change: are some species at greater risk? Oecologia 160, 493–506

Hussain SA (1999) Reproductive success, hatchling survival and rate of increase of gharial Gavialis gangeticus in National Chambal Sanctuary, India. Biol Conserv 87(2): 261–268

Katdare S, Srivathsa A, Joshi A, Panke P, Pande R, Khandal D, Everard M (2011) Gharial (Gavialis gangeticus) populations and human influences on habitat on the river Chambal, India. Aquat Conservation: Mar Freshw Ecosyst 21:364–371. https://doi.org/10.1002/aqc.1195

Katselidis KA, Schofield G, Stamou G, Dimopoulos P, Pantis JD (2012) Females first? Past, present and future variability in offspring sex ratio at a temperate sea turtle breeding area. Anim Conserv 15(5): 508–518

Lang JW, Andrews HV (1994) Temperature-dependent sex determination in crocodilians. J Exp Zool 270:28–44

Lara RB, Grajales JG, Ramírez EM (2021) Nest temperature assessment in an American crocodile (Crocodylus acutus) population on the central Coast of Oaxaca, Mexico. J Therm Biol 99:103012

Liu S, Zhao B, Gu X, Du W (2023) Behavioral thermoregulation by reptile embryos promotes hatching success and synchronization. Commun Biology 6:848

Lockley EC, Eizaguirre C (2021) Effects of global warming on species with temperature-dependent sex determination: bridging the gap between empirical research and management. Evol Appl 14:2361–2377

Mainwaring MC, Barber I, Deeming DC, Pike DA, Roznik EA, Hartley IR (2017) Climate change and nesting behaviour in vertebrates: a review of the ecological threats and potential for adaptive responses. Biol Rev 92:1991–2002

Mazzotti FJ, Balaguera-Reina SA, Brandt LA, Briggs-González V, Cherkiss M, Farris S, Godahewa A (2022) Natural and anthropogenic factors influencing nesting ecology of the American crocodile in Florida, united States. Front Ecol Evol 10:904576

Mitchell NJ, Allendorf FW, Keall SN, Daugherty CH, Nelson NJ (2010) Demographic effects of temperature-dependent sex determination: will Tuatara survive global warming? Glob Change Biol 16:60–72

Mitchell NJ, Janzen FJ (2010) Temperature-dependent sex determination and contemporary climate change. Sex Dev 4(1–2): 129–140

Murray CM, Easter M, Padilla S, Marin MS, Guyer C (2016) Regional warming and the thermal regimes of American crocodile nests in the tempisque basin, Costa Rica. J Therm Biol 60:49–59

Nair T, Thorbjarnarson JB, Aust P, Krishnaswamy J (2012) Rigorous gharial population estimation in the Chambal: implications for conservation and management of a globally threatened crocodilian. J App Ecol 49(5): 1046–1054

Packard GC, Packard MJ, Miller K, Boardman TJ (1987) Influence of moisture, temperature, and substrate on snapping turtle eggs and embryos. Ecology 68:983–993

Panda AK, Katdare S, Gawan S, Sharma SP, Badola R, Hussain SA (2023) Population status and factors influencing the distribution of critically endangered gharial (Gavialis gangeticus) in a regulated unprotected river system in India. Global Ecol Conserv 46:e02547

Radchuk V, Reed T, Teplitsky C, van de Pol M, Charmantier A, Hassall C, Adamík P, Adriaensen F, Ahola MP, Arcese P (2019) Adaptive responses of animals to climate change are most likely insufficient. Nat Commun 10:3109

Rhodes WE, Lang JW (1996) Alligator nest temperatures and hatchling sex ratios in coastal South Carolina. Presented at the Proceedings of the annual conference of the Southeastern Association of Fish and Wildlife Agencies, pp. 521–531

Roosenburg WM (1996) Maternal condition and nest site choice: an alternative for the maintenance of environmental sex determination? Am Zool 36:157–168

Santos MA, Carromeu-Santos A, Quina AS, Santos M, Matos M, Simoes P (2021) High developmental temperature leads to low reproduction despite adult temperature. J Therm Biol 95:102794

Sharma SP, Ghazi MG, Katdare S, Dasgupta N, Mondol S, Gupta SK, Hussain SA (2021) Microsatellite analysis reveals low genetic diversity in managed populations of the critically endangered gharial (Gavialis gangeticus) in India. Scientific Reports 11(1): 5627

Somero G (2010) The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. J Exp Biol 213:912–920

Vashistha G, Lang JW, Dhakate PM, Kothamasi D (2021) Sand addition promotes gharial nesting in a regulated river-reservoir habitat. Ecol Solut Evidence 2(2): e12068

Vashistha G, Mungi NA, Lang JW, Ranjan V, Dhakate PM, Khudsar FA, Kothamasi D (2021) Gharial nesting in a reservoir is limited by reduced river flow and by increased bank vegetation. Sci Rep 11:4805

Viljoen DM, Webb EC, Myburgh JG, Truter JC, Lang JW, Myburgh A (2023) Adaptive thermal responses of captive nile crocodiles (Crocodylus niloticus) in South Africa. Appl Anim Behav Sci 269:106098

Walsh BS, Parratt SR, Hoffmann AA, Atkinson D, Snook RR, Bretman A, Price TA (2019) The impact of climate change on fertility. Trends Ecol Evol 34:249–259

Zhao B, Li T, Shine R, Du W-G (2013) Turtle embryos move to optimal thermal environments within the egg. Biol Lett 9:20130337