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RESEARCH ARTICLE

Sand addition promotes gharial nesting in a regulated river-reservoir habitat

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Abstract

1. The gharial (*Gavialis gangeticus*) is a critically endangered, long-snouted crocodilian, endemic to the Indian sub-continent. Today, the species' distribution and numbers have reduced by more than 95% in all the large rivers where it was formerly abundant. Living upstream in a reservoir dammed in 1976, the Katerniaghat gharial population has continued to nest along the Girwa River, subject to seasonal flooding in recent decades. In 2010, a natural flood upstream in Nepal resulted in a permanent reduction in the mainstream river flow. As a consequence of reduced flow, the formerly open sand banks and mid-river islands have converted gradually to riverbanks with woody vegetation. Coincident with the increased vegetation growth, gharial nesting sites and nest numbers declined by more than 40% by 2018.
2. In an attempt to reverse the observed decline in nesting, we intervened with vegetation removal (VR) in 2019 and sand addition (SA) in 2020, to augment available nesting opportunities at previous and potential nesting locations.
3. The number of nests increased with SA (n = 36 in 2020) but decreased with VR (n = 19 in 2019), relative to the prior year without intervention (n = 25 in 2018). Furthermore, hatching success increased significantly to 93% with SA, compared to 63% in VR. Creating an artificial sand bank required approximately one-third work hours and cost much less than removing vegetation. Substrate temperatures in and around nests approximated the viable incubation range (29–33.5°C) when vegetation is absent, but were lower in sites covered with woody vegetation and/or dense, high grass.
4. Our study indicates that gharial will respond favourably to newly created sand banks that provide open, sandy riverside nesting areas, in contrast to cut-over sites with dense vegetation removed.
5. Finally, we note that this strategy of augmenting nesting sites is only an interim attempt to solve the 'nesting site' dilemma for the river-adapted gharial. Landscape-level solutions related to resumption of seasonal flooding, and particularly natural

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flow regimes that are dynamic, rather than steady, will likely be needed to avoid local extirpation of gharial in river-reservoir habitats.

KEYWORDS
altered river flow, gharial nesting, habitat restoration, incubation temperature, Katerniaghat Wildlife Sanctuary, reservoir, sand addition, vegetation removal

1 | INTRODUCTION

Freshwater aquatic ecosystems around the world are threatened by habitat fragmentation, over exploitation, invasive species and pollution (He et al., 2017). Artificial constructions such as dams and barrages have profound effects on the dynamics of river ecosystems. A physical barrier impacts the river channel and its floodplain downstream as well as upstream of its location (Liro, 2019; Nilsson & Berggren, 2000; Nilsson et al., 2005; Volke et al., 2019). Alteration of natural flow and sediment transport converts a lotic ecosystem into lentic which affects nutrition cycles, penetration of light and vegetation growth in the ecosystem. Riparian vegetation in altered ecosystems undergo irreversible changes due to absence of regulating factors such as natural flow, scouring and erosion of existing shoreline vegetation, and sediment transport and deposition (Merritt & Cooper, 2000; Vesipa et al., 2017; Wohl et al., 2015).

Karnali River is the only undammed riverine ecosystem inside Nepal. However, when the river enters the flood plains below Chisapani, it is subject to water extraction, diversion and manipulation of channel flow. Furthermore, a flood event in 2010 shifted active flow of the main Karnali at a natural bifurcation below Chisapani, from the eastern Geruwa to the western Karnali channel (Khanal et al., 2016; Vashistha et al., 2021). The immediate effects were reduced water flow and water depth in eastern Geruwa channel. This caused a gradual yet permanent change in riparian vegetation along the eastern channel inside India, known as the Girwa (Geruwa).

Inside India, the Girwa east channel joins the Kaudiyala west channel (flowing into India from the Karnali channel in Nepal) above the Girijapuri barrage to form a large reservoir, with the eastern portion comprising the protected Katerniaghat Wildlife Sanctuary (KWS). A small resident breeding population of gharial inhabits the KWS. Exhaustive surveys in the Karnali River basin in Nepal and India indicate that today, gharial only occur along a 10–20 km stretch of the Girwa River, inside the KWS and within the reservoir (Bashyal et al., 2021; Vashistha et al., 2021). In response to the mainstream channel shift from east to west in the Karnali, a small resident freshwater dolphin population moved into the adjoining Kaudiyala channel where the flow was greater and the water deeper than in the Girwa (Khanal et al., 2016; Khatiwada et al., 2019; Paudel et al., 2015; Shah et al., 2020). Unlike dolphins, the gharials in the Girwa did not shift into the Kaudiyala channel, which lies outside the protected KWS, where anthropogenic activities, including intensive fishing and resource extraction (sand removal and boulder collection), cause frequent disturbances (Bashyal et al., 2021).

Open river banks and sand bars in Girwa have converted to woody vegetation following the channel shift of 2010 (Figure 1(a)). Prior to 2010, there were 22–27 nests, this number increased to 30+ till 2017 but fell back to 25 in 2018 (Vashistha et al., 2021). Before the channel shift of 2010, regular monsoon floods were restructuring the riparian habitat. However, subsequent to the channel shift, the trend has been a unidirectional conversion of riparian habitat to woody vegetation cover, with the resultant loss of suitable nesting sites for gharial. Reduced water flow and magnitude of monsoonal flooding has further facilitated vegetation succession on unvegetated riparian areas. During the years 2016–2019, the number of gharial nesting sites reduced from eight to two and the number of nests reduced by more than 46%. The eventual vegetation succession in the above areas reduced the nesting site and nest numbers (Vashistha et al., 2021).

Our objective in this study was to remedy the loss of suitable nesting sites caused by spread of vegetation cover in Girwa River. We identified accessibility and substrate quality as important factors regulating nesting behaviour of gharials. To improve site access and substrate quality we tested two different approaches: vegetation removal (VR) in 2019 and sand addition (SA) in 2020. We further evaluated (1) how gharial responded to SA and to VR and, we documented (2) the advantages and disadvantages of these interventions for augmenting gharial nesting. Finally, we comment briefly on long-term prospects for the continued well-being and survival of gharial in the KWS. This river-reservoir gharial population not only faces the gradual loss of suitable nesting sites related to the recent river channel changes but also shows little evidence of gharial recruitment into the breeding population, despite decades of releasing hundreds of captive-reared gharials (Vashistha et al., 2021).

2 | MATERIALS AND METHODS

2.1 | Study species and site

The gharial (*Gavialis gangeticus*) is a critically endangered long-snouted crocodilian, endemic to the Indian sub-continent. Presently, gharial distribution and numbers have reduced by more than 95% in major river systems where it was formerly abundant (Lang et al., 2019). Gharial is a specialist species, feeding almost exclusively on fish. It is also a habitat specialist preferring large open free-flowing rivers. It nests in sandy substrates on high, steep river banks and mid-river channel islands and sand bars adjacent to deep water (Lang & Kumar, 2013, 2016;

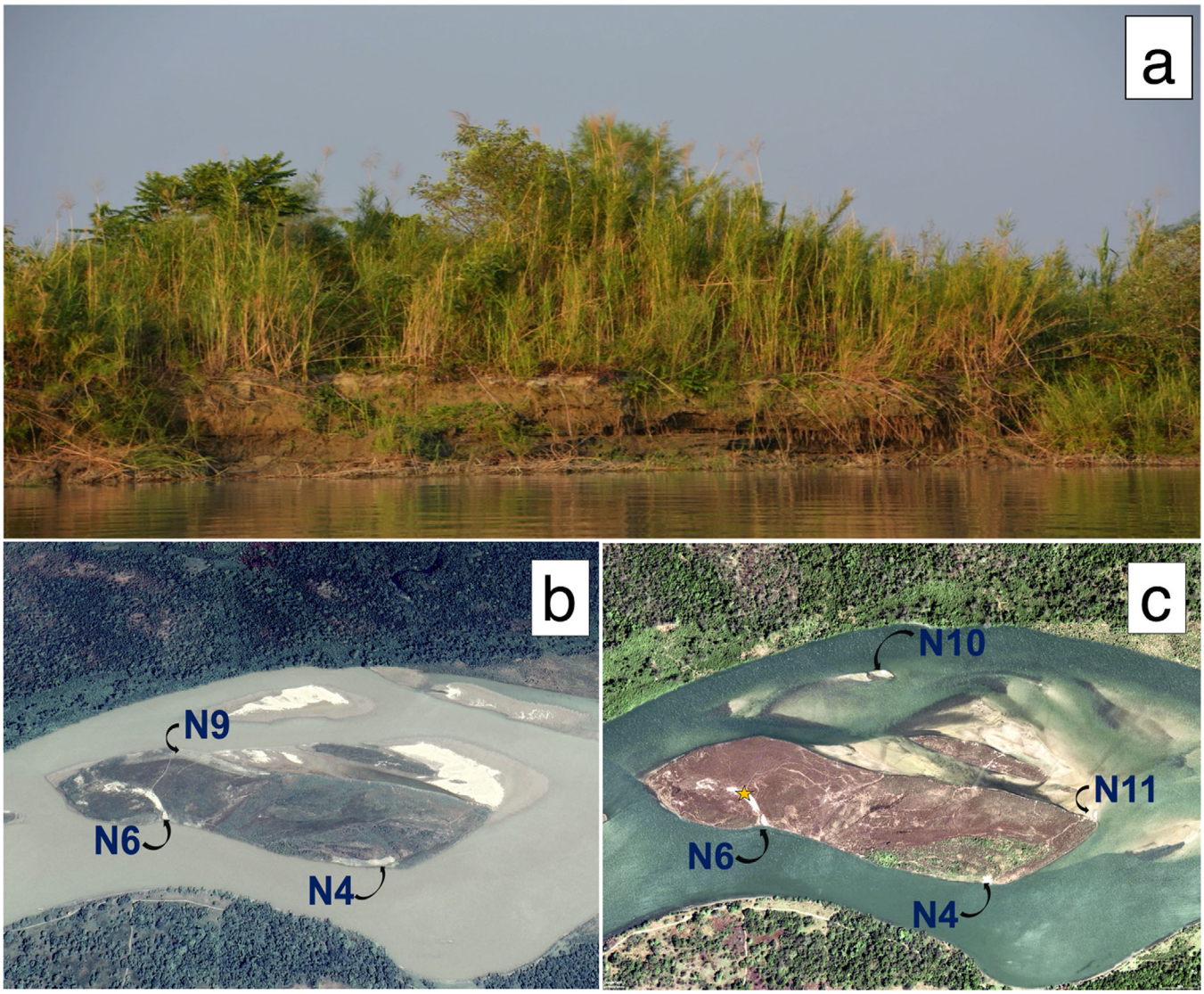

FIGURE 1 Top panel: (a) shoreline view of a vegetated nesting site (site N5; Bhawanipur mid-river sand bar, Katerniaghat Wildlife Sanctuary) illustrating that the entire column of substrate above the water has root penetration. Roots are deep and widely spread in the substrate, especially from grasses such as *Saccharum* and *Phragmites*. Bottom panel: (b) satellite imagery of Bhawanipur mid-river sand bar showing vegetation removal sites in 2019 and (c) satellite imagery showing sand addition sites in 2020. Yellow star marks the site of sand collection in 2020

Bashyal et al., 2019; Lang et al., 2019, and references therein; Khadka et al., 2020, and references therein). Incubation temperature determines sex and several phenotypic traits in gharial hatchlings (Andrews & Whitaker, 2004; Lang & Andrews, 1994). Consequently, nest sites and nesting substrates are critical for successful nesting in gharials.

The Girwa River within KWS has a resident wild breeding population of gharials currently estimated at about 70 animals (Vashistha et al., 2021). Long-term population assessment (1975–2020) showed that the total population size has increased gradually, but juvenile recruitment has been poor. Gharial nesting habitat is restricted to a less than 10 km stretch of Girwa River, from Pathrahna to Madho nala inside KWS (Vashistha et al., 2021).

Initially, we identified eight nesting sites in the study area (N1–N8), of which six (N2–N6, N8) were under vegetation cover. By 2018, three of the eight initial sites were already abandoned (N5, N7, N8; Vashistha et al., 2021). By late 2018, four additional sites (N2, N3, N4, N6) became inaccessible due to vegetation growth and were unfit for gharial nesting. In 2019, one additional site was identified, N9; and in 2020, two more sites were added, N10 and N11. Nesting sites on the Bhawanipur mid-river (BMR) sand bar in Girwa River have been consistently used for nesting (2015–2018) but were under dense vegetation cover. Therefore, to assess the restoration of nesting sites, we selected sites located on BMR (Table 1).

2.2 | Data collection on nesting and hatching

We conducted morning boat surveys from late March to early April in 2018–2020 to locate trial and actual nests in our study area. We searched river banks and mid-river sand bars to document gharial

TABLE 1 Nest sites at five riverside locations on the Girwa River used by gharials during 2015–2020

Location	Site no./type	2015	2016	2017	2018	2019	2020
Pathrahna	N1/ RB	+	+	3	5	13	–
	N12/SB	0	0	0	0	0	2
Amba ghat	N2/RB	+	+	2	3	–	–
	N3/RB	0	0	2	1	–	–
Bhawanipur ghat	N4/SB	+	+	21	15	6 VR	27 SA
	N5/SB	+	+	1	–	–	–
	N9/SB	0	0	0	0	0 VR	0
	N10/SB	0	0	0	0	0	0 SA
	N11/SB	0	0	0	0	0	0 SA
Cement tower	N6/SB	0	0	0	1	–VR	7 SA
	N7/SB	+	+	1	–	–	–
Madho nala	N8/RB	0	+	2	–	–	–
Total number of nests		NA	35	32	25	19	36

Note: 0 = vacant site; + = nesting (no counts); – = no subsequent nesting. Experimental habitat modification in 2019 = Vegetation removal (VR) and in 2020 = sand addition (SA). Numerical values in each column indicate number of nests observed at each site with or without modifications.
Abbreviations: NA, not available; RB, river bank, SB, mid-river sand bar.

nesting activity based on spoor marks and trial nests. Nest parameters such as GPS coordinates, distance from water, depth, etc. were collected. Egg laying was confirmed by manual search of possible sites. Data on clutch size and hatching was collected in June, only after the nests hatched. Hatching success was calculated as the total number of live hatchlings per total number of eggs laid in a nest.

2.3 | Habitat management

2.3.1 | Vegetation removal (in 2019)

VR was carried out at three sites: N4, N6 and N9, respectively (Figure 1(b), Table 1). A 30 m wide strip with total length of 1 km was marked parallel to the river bank on the three selected sites. This resulted in a total area of 3 ha under VR habitat management. The above-ground vegetation was manually cleared to allow movement of tractors (Figure 2(a)). Some portions of N4 and N6 were burnt to speed up the vegetation clearing process. We used a tractor to loosen the top layer (layer with most fibrous and lateral roots) and moved this entire layer (at least 1.5 ft deep) to the sides of the site (Figure 2(b) and (c)). Harrowing was repeated to loosen the underlying compact sand layer to allow it to dry and attain its natural moisture and texture. Remnants of deep roots from woody plants that remained after harrowing were manually extracted. Shoreline of the VR-managed site had dense vegetation comprising *Saccharum spontaneum* and *Phragmites karka* that were half submerged and on the edges of managed sites. Consequently, gharials did not have access to the newly managed area. Therefore, while creating a slope, we moved the top layer on shoreline towards the river (Figure 2(d)). We did not attempt to remove vegetation in the water at the shoreline. All boat and human activities in the area were stopped after VR was completed.

2.3.2 | Sand addition (in 2020)

Four sites (N4, N6, N10 and N11) were selected for SA (Table 1). N4 and N6 had been used previously for the VR in 2019 (Figure 1(b)) but N10 and N11 were not studied prior to SA (Figure 1(c)). Extensive VR was not carried out during SA in 2020. However, owing to regrowth of vegetation on N4 shoreline, the above-ground vegetation (~0.025 ha) along the river edge was cleared to allow sand deposition. Sand was sourced from a sandy patch at BMR with no vegetation growth (~0.2 ha). Sand was transferred to selected sites in recycled cement packaging bags using a motor boat (Figure 3(a) and (b)). To mimic natural sandy nesting sites, we constructed high sand banks with steep slopes (~0.025 ha area) on the shoreline of each site (Figure 3(c)). After SA was completed, all boat or human movements were stopped on those sites. Within a day or two of cessation of human activities, gharials and mugger crocodiles (*Crocodylus palustris*) started basking on these newly constructed sand banks (Figure 3(d)).

2.3.3 | Control (no management, 2018)

N4 was the only site with consistent nesting through 2018–2020. Except for small-scale vegetation clearing between nests and water in 2018, N4 had not received any management intervention prior to 2019. The extent of these clearings was limited to creating an approach for female gharials through the vegetation. Therefore, nesting data collected in 2018 from N4 served as control for comparing effects of VR and SA on gharial nesting success. The numbers of nest replicates for evaluating hatching success were 10, 24 and 13, respectively, for VR (2019), SA (2020) and control (no management, 2018).

Sites N9–N11 had no previous history of gharial nesting. We selected these sites for interventions because they were located at

FIGURE 2 Vegetation removal (VR) in 2019
Note: Initially, a local crew cropped the vegetation to clear a path for the tractor (a). Subsequently, a tractor harrowed the substrate, disrupting the underlying layer of roots (b) and (c). Lastly, a steep slope was constructed at the shoreline (d).

FIGURE 3 Sand addition (SA) in 2020
Note: A local crew collected sand in recycled cement bags from Bhawanipur mid-river (BMR) sand bar (a) and transported it by boat to the selected sites (b). Sand was deposited to create artificial sand banks with a slope (c). Gharial and mugger crocodiles basking on artificially deposited sand at site N10 (d).

BMR sand bar where no poaching or illegal human movement has been reported. These sites were easy to monitor as they were located near the forest department's monitoring watch tower. The vegetation cover at these sites was dominated by grasses and was easy to work upon, whereas other vegetated sites, such as N2, N3 and N8, were difficult to access by gharials due to the distance from river bank and the presence of woody species. Vegetated sites such as N2 and N3 were difficult for regular monitoring and were frequented by illegal fishermen with several cases of nest poaching (including those of mugger crocodiles and turtles) reported in previous years.

Our study was subject to disturbances beyond our control. These were noted as follows. During the nest laying period in 2019, two nests were poached at N1. Following this poaching event, all remaining nests from N1 ($n = 11$) were translocated to N4 ($n = 6$) and N6 ($n = 5$) by the state forest department. During hatching, we excavated five nests at N4 and two nests at N6 to facilitate egg hatching. This was on the presumption that these nests were abandoned by the females as they were left unopened even after 3 days of continuous calls from the hatchlings.

2.4 | Soil temperature

Vegetation influences substrate temperature by reducing incident solar radiation. In order to analyze effects of VR on substrate soil temperatures, we installed Ibutton thermochron data loggers (Maxim Integrated, USA, model DS 1921G-F5#) from 24 March to 15 June 2019 to record substrate soil temperature data at non-vegetated and vegetated sites. Data loggers for recording soil temperatures were installed at four sites; N1, N4 and two control sites. These were sandy (sandy river bank near N1) and vegetated (vegetated area on N4). Both sandy river bank near N1 and vegetated areas on N4 had no previous history of gharial nesting. To maintain uniformity in analyzing the effects of vegetation on substrate temperature, data loggers were placed at 60 cm depth in the soil at all the sampling sites at the onset of trial nesting. Loggers were programmed to collect data at an interval of 60 min. We had 3, 2, 3 and 4 replicates of soil temperatures for vegetated, sandy, N1 and N4, respectively. We were unable to install temperature data loggers in 2020 due to the COVID pandemic and associated restrictions imposed.

2.5 | Statistical analysis

Statistical analyses were performed in R version 1.3.1056 (R Core Team, 2020). Normality of data distribution was tested with a Shapiro–Wilk test. Differences in means of non-parametric data (hatching success) were analyzed with a Kruskal–Wallis test followed by a pairwise Wilcoxon test with Bonferroni correction. Differences in means of normally distributed soil temperature data were analyzed with a one-way analysis of variance (ANOVA) followed by Tukey's post hoc test. Effects of nest distance from water on hatching success were analyzed using Kendall's rank correlation coefficient (τ).

3 | RESULTS

3.1 | Nesting

SA resulted in almost twice as many nests laid in 2020, relative to the number of nests laid in 2019 when vegetation was removed from nesting banks. Nest numbers increased from 19 in 2019 to 36 in 2020 (Table 1). Nesting took place at three sites in 2020, of which N4 and N6 were managed sites under SA. VR had a detrimental effect on nesting. Nest numbers reduced from 25 in 2018 to 19 in 2019 (Table 1). In that year, gharial nesting took place at two sites, N1 and N4. At the time of hatching, in seven nests under VR management gharial eggs were damaged by vegetation roots (Figure 4(a)). Four nests had signs of egg damage by both root penetration and compression by elephant movement (Figure 4(b), Table 2). Overall in 2019, 11 of the 19 nests monitored were damaged. In contrast in 2020 with SA, no eggs were damaged due to vegetation root penetration or elephant movements (Table 2).

3.2 | Hatching success

SA in 2020 was associated with significantly increased hatching success ($\chi^2 = 26.20$; $p < 0.01$). No differences in hatching success were observed between the control (2018) and VR (2019) (Figure 5(a)). Hatching success was inversely correlated with distance of the nests from water (Kendall's rank correlation $\tau = -0.44$, $p < 0.01$; Figure 5(b)). This suggests that successful hatching is more likely when gharial nests are closer to water.

3.3 | Soil temperature

Vegetated areas had lower soil temperature compared to non-vegetated areas ($F_{6, 210} = 96.75$, $p < 0.01$, Figure 6). N4 (managed under VR and SA) had similar soil temperature as the unmanaged N1. Temperatures recorded at all the data points, except at vegetated sites, fluctuated across the viable development temperature range of 29–33.5°C (Lang & Andrews, 1994; Figure 7). Temperatures in vegetated sites were below the viable range throughout the thermosensitive period. A fluctuation of 0–5.5°C was recorded in daily soil temperatures.

3.4 | Implementation

Compared to VR in 2019, SA in 2020 required approximately 62.5% less time to accomplish, and took 52% fewer work hours to implement. Taken together, the four sites where sand was added totalled less area (5%) in comparison with the area cleared of vegetation, yet these SA sites had approximately six times higher number of nests (nest $n = 34$) than sites in VR ($n = 6$). Other operational features comparing SA versus VR are detailed in Table 3.

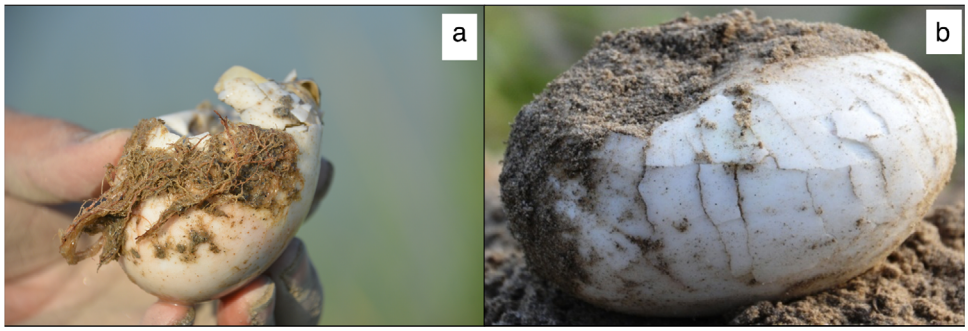

FIGURE 4 A gharial egg damaged by vegetation roots (a). Vegetation roots damaged the outer shell and penetrated the inner egg membrane, which exposed the embryo to external temperature and humidity, resulting in death of the embryo. A gharial egg damaged by compression from elephant movement (b). Compression damaged eggs had lateral cracks around the shell, with egg membrane remaining relatively intact. However, exposure to external factors, such as temperature and humidity, leads to infection, ant predation and ultimately death of embryo

TABLE 2 Gharial nesting in Girwa River after site management in 2019–2020

Nesting parameter	VR (2019)	SA (2020)
Total number of nests	19	36
Nests at managed sites	6	34
Mean clutch size (sampled nest)	30.2 ± 7.39 (15)	30.08 ± 6.071 (24)
Mean incubation period (in days)	69.07 ± 5.09	75.29 ± 2.61
Mean nest distance from water (in m)	12.27 ± 4.65	7.63 ± 1.79
Mean hatching success % (sampled nest)	62.61 (10)	92.53 (24)
Number of dead hatchlings	12	4
Unhatched eggs	128	24
Nests with vegetation roots at hatching	11	0
Eggs damaged by vegetation roots	24	0
Eggs damaged by vegetation roots and elephant movement	39	0

Note: Unhatched eggs = damaged eggs+ infertile eggs+ embryonic deaths.Abbreviations: SA, sand addition; VR, vegetation removal.

4 | DISCUSSION

SA significantly increased gharial nest numbers and hatching success compared to VR. SA is easier to implement as it only requires one third the labour and time compared with VR. SA provided relatively small nesting areas with sandy substrate at the shoreline. In contrast, VR required managing large areas, both above and below ground to restore a vegetated site for nesting. SA provided vegetation free

TABLE 3 Difference in managed site use by gharials and resources used for site management

Parameters	Vegetation removal	Sand addition
Duration of completion	1st week of January to 1st week of March 2019	4th week of January to 2nd week of February 2020
Site use upon completion	Delayed	Immediate
Overlap with gharial breeding	Yes	No
Site used for basking	N4	N4, N6, N10, N11
Site used for nesting	N4	N4, N6
Time required in completion (days)	40	15
Approx. work hours	5200	2500
Approx. nesting area created (in ha)	3	0.1

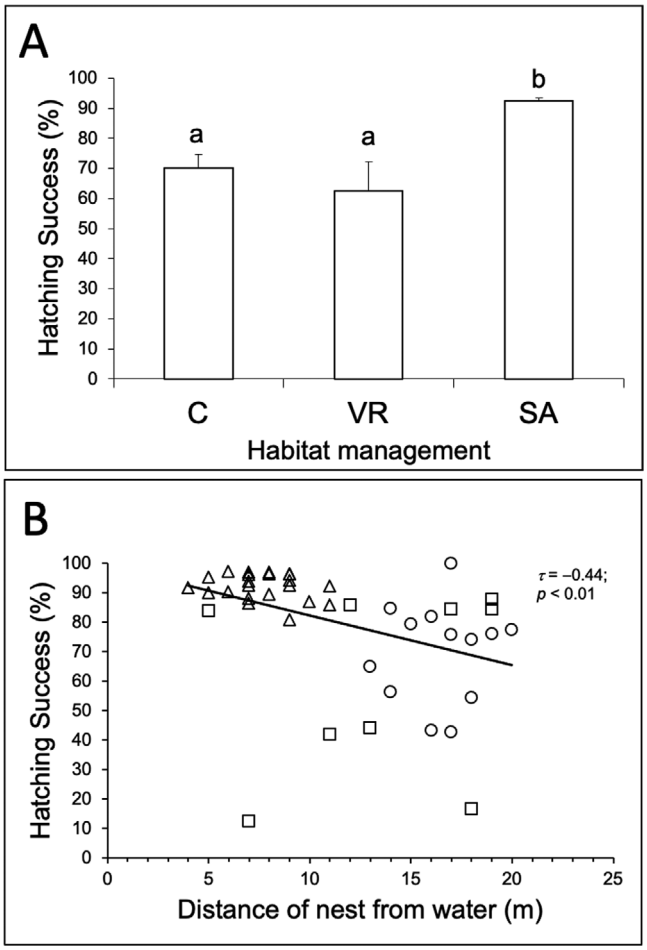

FIGURE 5 Top panel: (a) hatching success (%) of gharial eggs at managed site N4 in three subsequent years, 2018 (control), 2019 (vegetation removal) and 2020 (sand addition). No difference was observed between the control and vegetation removal, but hatching success was higher with the sand addition treatment. Error bars indicate standard error of the mean. Different letters above the bars indicate significant differences in a Wilcoxon pairwise test with Bonferroni correction, $p \leq 0.05$. Bottom panel: (b) hatching success (%) of gharial eggs at the same managed site, N4, under the treatments regimes shown above, showing an inverse relationship with distance from water (bottom panel, horizontal axis), indicating higher hatching success when eggs were closer to water
Abbreviations: C, control; SA, sand addition; VR, vegetation removal.
Data year labels: circle = 2018; square = 2019; triangle = 2020

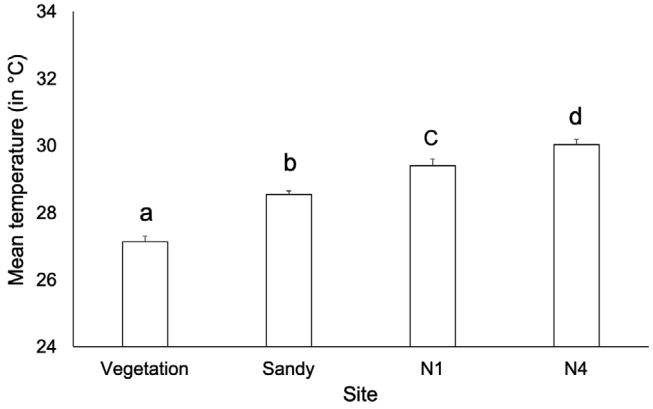

FIGURE 6 Differences in soil temperatures during the estimated thermosensitive period (15–45 days) during egg incubation at gharial nesting sites
Note: Soil temperatures were lower at the vegetated site (left), relative to the other non-vegetated sites (sandy, N1, N4). Error bars indicate standard error of the mean. Different letters above the bars indicate significant differences in Tukey's post hoc test, $p \leq 0.05$

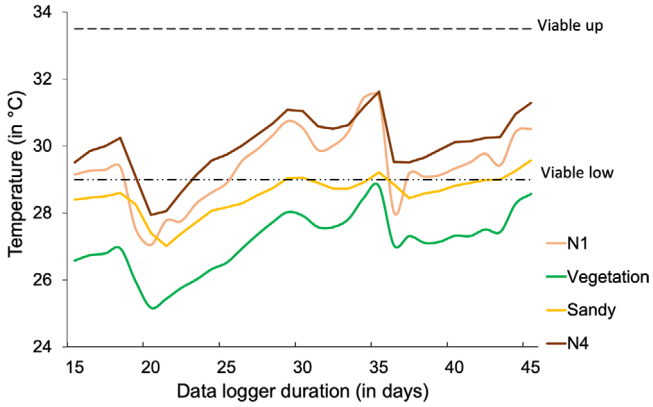

FIGURE 7 Vegetation removal at N4 resulted in higher soil temperature at nest depths that were within the viable range for embryonic development compared to lower soil temperatures at this site with intact vegetation
Note: With intact vegetation, soil moisture and shading resulted in soil temperatures at nest depth that fell below viable range during the thermosensitive period (TSP) for gharials nests (dashed lines). In contrast, soil temperatures at nest depth in open, sandy sites approximated soil temperatures at nest depth recorded when vegetation was removed.

substrates and minimized distances between nests and the nearest shoreline. Proximity of the nests to water may help maintain suitable nest temperatures, moderated by available moisture. It also reduces predation risks by decreasing nest-water distances as well as facilitating guarding behaviours by adults.

Nest-site selection has a critical role in crocodile nesting success. Prior to selection of an optimal nesting site nesting females evaluate a variety of parameters such as substrate texture, shadowing, accessibility, distance to water, slope etc. (López-Luna et al., 2020; Platt et al., 2008; Somaweera & Shine, 2013; Somaweera et al., 2011; Villamarín et al., 2011). Ninety-five per cent of total nests under SA in 2020 were laid at the two managed sites N4 and N6 compared to only 31% of the total nests laid at N4 in 2019 under VR. The distance between nesting area and water at these two sites was greatly reduced under SA compared to VR (Table 2). SA increased hatching success to 93% compared to 71% in the control (2018) and 63% with VR (2019). Gharials prefer to bask and nest close to deep water. Relative to other crocodilians, gharials' ability to move on land is limited (Choudhary et al., 2017; Iijima & Kubo, 2019). Constructed sand banks provide proximity to water

and sand substrate that is free of vegetation. Both features may not necessarily be available on banks where existing vegetation has been removed.

The substrate at BMR sand bar consists of alternate layers of sand, silt and clay, deposited year after year during the monsoon floods. Seed bank and root remnants from previous years have naturalized this substrate for vegetation growth. This was evident from the intense and deep root network of plant species such as *Typha*, *Saccharum* and *Phragmites* (Figure 1(a)). We observed regrowth of vegetation on all the managed sites in 2019. This reduced access of female gharials to nests and resulted in abandoning of seven fully developed nests. Vegetation roots also caused damage to egg shells, exposing the embryo to external factors and ultimately embryonic mortality. A total of 63 gharial eggs from 11 nests were damaged by vegetation roots in 2019 (~14% of total sampled eggs). *Phragmites* is an invasive species which has a high tolerance for adverse habitat conditions and is known to invade and dominate freshwater ecosystems worldwide (Eller et al., 2017). *Phragmites* sp. have been reported to reduce nesting area and incubation temperatures in Diamondback Terrapin (*Malaclemys terrapin*; Cook et al., 2018) and Spiny softshell turtle (*Apalone spinifera*; Bolton & Brooks, 2010).

SA provided a clean, root-free sand substrate which may have influenced nest depth and thermal characteristics of the nest. Sandy substrates are easier to dig and usually have deeper nests. This possibly led to low daily temperature fluctuations compared to vegetated substrates where nests are shallower. Our temperature data revealed that soil temperatures differed significantly between vegetated and non-vegetated sites. Shaded, vegetated areas had lower soil temperatures compared to open unvegetated sites such as N1 and N4 (Figure 6). This was possibly an outcome of reduced solar irradiation (Charruau, 2012; López-Luna et al., 2020). However, it must be noted that we recorded substrate temperature at a fixed depth of 60 cm to analyze effects of VR on substrate soil temperature. Gharial nest depths may vary in different soil types. Consequently, substrate temperatures recorded by us at fixed 60 cm depth is not representative of gharial nest incubation temperature.

Crocodile nests experience a daily cycle of temperature fluctuations ranging from 1°C to 5°C as a consequence of fluctuations in external environmental temperature (Murray et al., 2016). These fluctuations are believed to expose incubating eggs to higher effective pivotal temperature compared to nest's mean incubation temperature. But each egg experiences a different temperature fluctuation due to its location inside the nest and the depth of nest itself. Eggs in the top layer of the nest usually experience highest fluctuations being in closest proximity to external temperature whereas eggs in lower layer experience low fluctuations (Murray et al., 2016).

Deeper nests and more stable incubation temperatures may have resulted in the increased hatching success we observed in 2020 at the SA sites (Table 2). Most crocodilians including gharial have incubation temperature-determined sex determination (TSD; Andrews & Whitaker, 2004; Lang & Andrews, 1994). Nest sites influence the substrate temperatures of crocodilian nests (Bock et al., 2020; Charruau, 2012; López-Luna et al., 2020). Substrate temperatures in turn determine embryonic development as well as hatchling phenotypes including sex. In this manner, overall population composition, and particularly sex ratios of various size/age classes, is affected (Du et al., 2019; Noble et al., 2018; Refsnider, 2016; Rhen & Lang, 2004; Singh et al., 2020; Valenzuela et al., 2019; While et al., 2018) based on incubation temperature, which ultimately depends on features of the nesting substrate.

The BMR sand bar has been used regularly for nesting by gharials and is located in a relatively protected area of KWS where the human interventions are negligible. Although we attempted to control critical variables such as human activity during VR and SA, the time taken to complete VR in 2019 extended into mid-February to mid-March which is the beginning of the breeding season (Lang & Kumar, 2013, 2016). Consequently, we speculate human activities, which extended through February, may have contributed to a reluctance of gharial to fully utilize the VR manipulated sites for nesting in 2019. In contrast in 2020, SA was completed in early February. This may have facilitated the early use of the newly constructed SA sites for basking, prior to the start of nesting. Qualitatively, we observed that gharials were very responsive to SA, utilizing these sites within days of their construction. Consequently, the year-to-year differences in the number of nests constructed in response to VR versus SA may have been influenced by possible disturbance levels related to VR in 2019. Gharials did not use two of the three sites built in 2019 (VR) and two of the four sites built in 2020 (SA).

Nest-site selection was driven by the previous nesting history, substrate quality and accessibility. Selection of potential nesting areas begins in late December through early February, when breeding females start aggregating and basking in these sites. By mid-February, the selection becomes intensified with onset of mating when the dominant males establish dominance over other males and breeding areas. Nest-site selection in gharials is determined by two key factors: availability of adequate sand at minimal height above water and proximity of adjacent deep-water pools at the shoreline of the nesting site. Water levels remained stable during the study years and therefore were not a regulating factor for nesting outputs (Table S1).

There have been several ad hoc attempts in the past to improve gharial nesting at KWS. Nest numbers increased from less than 10 in 2005–2006 to 24–27 nests in 2007–2008 when sand banks were created and vegetation was cleared near the Girwa nesting sites (Chaudhari, 2008; R. Pandey, personal communication, 2020). Similar efforts were carried out at Son Gharial Sanctuary in 2005–2006. Sand was deposited near a deep pool in Jogdah, which was located downstream to Bansagar dam. Female gharials readily used the site for nesting. Sand deposition was continued till 2015–2016 and it was used every year for nesting during this period (S. Katdare, personal communication, 2020).

Comparable studies on other crocodilian species are limited. The best examples we are aware of are for a widely distributed New World coastal dwelling American crocodile (*Crocodylus acutus*). *Crocodylus acutus* nested on canal plugs within hours of construction in the Everglades National Park, Florida (Mazzotti et al., 2007). A total of 94 nests were reported on man-made substrates, of which 74 were on canal banks. Artificial substrates contributed more to increase *C. acutus* nest numbers than natural substrates. Canal banks created several years ago to reduce intrusion of sea water and retain freshwater proved to be a

suitable nesting substrate and nursery for hatchlings (Mazzotti et al., 2007). One of the most successful artificial nesting programmes for *C. acutus* was undertaken in Cispata Bay, Colombia, where artificial shoreline and nesting areas were created in mangroves using nearby soil to counter the effects of sea water flooding. These artificial sites were immediately used for nesting and accounted for 321 nests in 10 years or 64% of total nests, from 2003 to 2012. At least 70% of the total artificial sites was used for nesting. The increased nesting helped in the population recovery (Ulloa-Delgado & Sierra-Diaz, 2013). *Crocodylus acutus* has been reported using spoil bank clay dug from man-made canals for nesting in Placencia Lagoon, Belize (M. Tellez, personal communication, 2020). In Cuba, two artificial nest sites created near existing nest sites and transit areas were adopted quickly, and two to five nests were laid per constructed site for at least two breeding seasons (N. Rossi, personal communication, 2020). These examples suggest that *C. acutus* readily nests in suitable settings, natural or artificial, that provide appropriate incubation conditions even in dynamic habitats susceptible to storms and/or sea-level changes.

In other crocodilian species that are widely distributed geographically across a variety of habitats, flexible nesting strategies are utilized (e.g. *C. niloticus* – Cott, 1961; Modha, 1967; *C. porosus* – Magnusson, 1980; Webb et al., 1983a). Among primarily river-dwelling species, the Orinoco crocodile (*C. intermedius*) nests in rocky sites when sandy sites are unavailable, and even modifies its nesting habit from hole-to-mound nesting and vice versa, according to local conditions (Thorbjarnarson & Hernandez, 1993). Although the Australian freshwater crocodile (*C. johnstoni*) typically nests in sandy banks along rivers (Cooper-Preston, 1991; Webb et al., 1983b), the species also successfully nests in dry gravelly substrates with full sun exposure and close to the water's edge in a reservoir habitat in Lake Argyle (Somaweera et al., 2011). However, this particular nesting preference is atypical of the species' nest-site selection in its usual riverine settings. The hydric and thermal characteristics of these rocky sites are suitable for successful incubation of the eggs, and other attributes such as the absence of egg/hatchling predators favour this alternative nesting strategy in the altered flow regime in the reservoir (Somaweera & Shine, 2013).

Based on our observations for augmenting nesting opportunities for gharial in this study, the following recommendations are outlined. Sand banks should be constructed parallel to the direction of river flow on a firm substrate which is higher than the river water level and has a gradual slope for land access. Deep water nearby facilitates guarding opportunities for attendant adults. Gharials appear to have a strong fidelity to traditional nest sites that are routinely used year after year. Managed sites of 2019 (VR) and 2020 (SA) without previous records of nesting were not used for egg laying by gharials. A managed site should remain accessible to female gharials even if the river water level recedes by up to 60 cm. Multiple managed sites provide gharials with opportunities to select the most suitable locations, with sufficient area for nests to be spaced appropriately.

Large rivers inhabited by gharials in India and Nepal have already been altered by dam construction and/or water extraction. Although gharials continue breeding in such modified habitats, nesting sites are often limited and the river-reservoir habitat may impose constraints. One-way downstream movements imposed by dams and barrages may restrict recruitment. The two secondary populations of gharials in which breeding regularly occurs, namely the one in the KWS and the Ramganga River population in the Corbett Tiger Reserve (CTR), raise an important question. Are these populations which are breeding in altered reservoir ecosystems self-sustaining? In other words, will these river-reservoir gharial populations ultimately contribute to gharial survival in the long term? At present there are few studies that analyze long-term status of crocodilian populations now living in reservoirs, for example Nile crocodiles living in Flag Boshielo (Botha, 2005), in Loskop Dam (Botha et al., 2011) and in Pongolapoort Dam (Champion & Downs, 2017). In these settings, nest failure, poor recruitment and/or sources of pollution have been implicated.

To date, the KWS population has been sustained with human interventions such as supplementation and habitat management. Similar comparable baseline data on nesting and hatching success for gharials of CTR is lacking. Our analysis of the KWS gharial population indicates that the number of reproductive adults increased from less than 10 in the late 1970s to close to 50 in recent years. Notably, there was a concomitant increase in nesting from less than 5 nests in the late 1970s to more than 30 in recent years. Importantly for most of the past four decades although nesting increased, recruitment as indicated by the numbers of juveniles and/or yearlings in the smaller size classes has shown little evidence of anticipated increases, in contrast to the recruitment of smaller size classes evident elsewhere, for example Chambal population (Lang et al., 2018; Sharma & Dasgupta, 2013). This is despite annual natural production of wild hatchlings and the cumulative release of more than 1800 captive-reared juveniles (Vashistha et al., 2021). Despite these periodic additions to the resident gharial population in the KWS, the size of the total population has not increased commensurately. Now, with the loss of suitable open sand banks and bars due to the restricted Girwa flow regime, the ability of the resident gharial population to sustain itself in the KWS river-reservoir habitat is in serious doubt.

For the Ramganga river-reservoir in the CTR, the conservation prospect is uncertain. The CTR gharial population is likely to be subject to the same general constraints that have been outlined for the KWS population. Resident gharials are nesting downstream within the reservoir proper in CTR, but most of these sites are marginally suitable. Consequently, hatching success is limited and hatchling survival is low (Chowfin & Leslie, 2013). Nesting also occurs upstream where the source rivers enter into the reservoir or just upstream from the associated river deltas in CTR, for example on the Ramganga, Sona and Palain Rivers (G. Vashistha, 2021, unpublished data). Restocking with captive-reared juveniles as in KWS has not been a regular occurrence at CTR, and the extent of successful recruitment within the existing CTR resident population is not known. Clearly, these river-reservoir gharial populations require more investigation to determine whether they have the ability to be self-sustaining breeding populations, and whether natural juvenile recruitment is sufficient to preclude supplementation of captive-reared animals.

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AUTHORS' CONTRIBUTIONS

G. Vashistha, J.W. Lang and D. Kothamasi conceived the idea and designed the work. G. Vashistha, J.W. Lang and P.M. Dhakate collected the data. G. Vashistha, D. Kothamasi and J.W. Lang analyzed the data. D. Kothamasi, J.W. Lang and P.M. Dhakate arranged all the necessary permissions and funding for the field work. All authors contributed to draft revisions and approved the final version for publication.

DATA AVAILABILITY STATEMENT

Data available from the Figshare repository : https://doi.org/10.6084/m9.figshare.13147700.v2 (Vashistha et al., 2020).

PEER REVIEW

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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