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Camera Traps Provide First Insights into the Nesting Behavior of the Critically Endangered Northern River Terrapin (*Batagur baska*)

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Abstract. – Camera traps are very useful tools in determining the presence/absence of rare and cryptic species while shedding light on behavioral traits. Passive infrared triggered cameras are routinely used in homeothermic animals, but in ectothermic reptiles, this surveillance method has proven highly unreliable. As part of the conservation goal to provide better understanding and protection for the critically endangered freshwater turtle *Batagur baska*, we investigated their largely unknown nesting behavior and tested video-based motion detection by comparing 2 different camera-trapping systems and their settings under controlled conditions at the Vienna Zoo. A pixel-based video surveillance camera was superior to a camera trap with motion sensor. The surveillance camera allowed reliable motion detection at sensitive settings, and video capture precision could be enhanced by marking the terrapin with reflective tape. This video surveillance camera was then deployed over 2 breeding seasons (2019 and 2020) in the conservation breeding project of the northern river terrapin (*B. baska*, Gray 1830) in Bhawal National Park in Bangladesh. Analysis of video recording demonstrated for the first time that female northern river terrapins nested on average for a period of 1.5 hrs and produced a single clutch per year. Results indicate that females inspect sandbanks and visit suitable nesting sites several times before egg deposition, suggesting that nest-site selection is not random in *B. baska*. In addition, water temperature measurements of the breeding ponds in 2 captive breeding sites of the *B. baska* project showed an annual average temperature decrease to 16°C–18°C during the mating season and an average increase to 28°C–31°C before the nesting season. Temperatures on nesting nights vary between the 2 breeding sites and differ between nesting events within each site, suggesting that overall seasonal temperature shifts initiate the nesting periods, while other physiological and environmental factors might trigger the actual nesting event. With the help of consistent motion-triggered video recording, our study provides a first underpinning of the nesting ecology of *B. baska*.

Key Words. – ectothermic; infrared; motion-based; reflective tape; reptiles

Noninvasive video recordings, with infrared-triggered cameras, are functional and efficient research tools used to study a variety of animal species in their natural habitat (Cutler and Swann 1999; Claridge et al. 2004; Swann et al. 2004; Hariyadi et al. 2011; Maputla et al. 2013). Several studies have assessed questions related to density (Rovero and Marshall 2009), abundance (Soisalo and Cavalcanti 2006; Maputla et al. 2013), activity (Di Bitetti et al. 2006), habitat use, and various types of behavior using camera traps, mostly concerning large terrestrial mammals. However, capturing and studying ectothermic animals with video remains difficult (Welbourne 2013). For example, passive infrared (PIR) camera traps used to survey the large, extremely cryptic Butaan lizard (*Varanus olivaceus*) triggered only when the lizard's surface temperature was higher than the ambient background temperature. Additional photographs were triggered only between 0800 and 1700 hrs (Bennett and Clements 2014), whereby surveillance at night was impossible. Recent studies, however, demonstrated that PIR-triggered camera traps can detect snakes and lizards, including small specimens, and demonstrated that this technique provides effective detection in a temperate environment (Welbourne et al. 2019, 2020). Reliable detection with PIR cameras is challenging, as ectothermic animals rarely vary greater than 3°C from their surrounding environment. Indeed, large-bodied aquatic testudine species such as loggerhead sea turtles (*Caretta caretta*) maintain their body temperature within 1.7°C of that of their environment (Sato 2014). Studies demonstrate that differences of 4°C–5°C (higher or lower than ambient background temperature) are needed to create sufficient radiation contrast between target and background to allow reliable detection (Meek et al. 2012; Welbourne 2014; Welbourne et al. 2016). Hence, camera-based automated surveillance poses a serious compounded technical challenge in providing consistent behavioral information about ectothermic, slow-moving, and nocturnal reptiles. Nevertheless, these systems are one of the few available tools to investigate behaviors without disturbance during critical periods such as breeding or nesting.

We tested 2 types of video surveillance methods to gather information on the nesting behavior of the critically endangered northern river terrapin (*Batagur baska*). Turtles are among the world's most threatened vertebrates. The *Batagur* genus comprises 6 of the rarest species in the world, all of them listed as critically endangered according to the International Union for Conservation of Nature (IUCN) Red List and native to South and Southeast Asia (IUCN 2022). These aquatic species inhabit rivers and estuaries, and all 6 species were considered abundant within their respective ranges in the 19th and 20th centuries (Maxwell 1911; Kuchling et al. 2006). Recent declines caused by the direct consumption of turtle meat and eggs as well as habitat destruction through pollution of river courses, sand mining, and construction have brought the species to the brink of extinction in their natural environments (Kalyar et al. 2007; Platt et al. 2008). In the past decade, local governments have implemented measures to preserve the remaining terrapins. Breeding programs were set up to conserve *B. trivittata* in Myanmar and at the Singapore Zoo. Conservation, legislation, and policy measures are also in place to preserve their natural habitat (Gozde 2017). Both *B. kachuga* and *B. dhongoka* are protected by law in India and are the target of head-start conservation programs established by Uttar Pradesh forest department and Turtle Survival Alliance India (Sirsi et al. 2017). *Batagur borneoensis* is found along the coasts of Sumatra, Borneo, and Malaysia, and numbers are declining. The species' largest nesting site in Aceh is under severe threat, and conservation efforts to hatch the eggs before releasing the juveniles have not been as successful as anticipated (Hernawan et al. 2019).

Batagur baska is restricted to regions from coastal northeast India and adjacent Bangladesh to the Ayeyarwady and Bago estuaries in Myanmar (Praschag et al. 2007, 2008). Formerly known as a single species, *B. baska* today comprises at least 2 genetically distinct species (Praschag et al. 2007). Populations of river terrapins occurring in Southeast Asia that were previously viewed as conspecifics are now considered to be a subpopulation of the southern river terrapin, *B. affinis*, a distinct but closely related species. There are currently 3 breeding programs in Malaysia to ensure the survival of *B. affinis*, one of which has managed to increase overall numbers of *B. affinis* in the Terengganu River (Brook 2015; Moll et al. 2015). Conservation breeding programs are also in place for the northern river terrapin, *B. baska*, in India (Mallick et al. 2021) and Bangladesh (Weissenbacher et al. 2015), and 2 ex situ populations exist at the Vienna Zoo and the nongovernmental organization Turtle Island in Austria. These breeding programs have generated baseline knowledge on egg development, incubation periods and temperatures, and hatching rates of these elusive terrapins. Information on nesting behavior and ecology remains scarce, and further investigations constitute an essential next step in this species' conservation.

Nesting is triggered by rainfall in several tropical and subtropical freshwater species, such as *Chelodina expansa* (Australia), which nest during or after storms (Bowen et al. 2005), and *Podocnemis expansa* (South America), which nest when rainfall and river levels are at the lowest, exposing sandbanks for nesting (Alho and Pádua 1982). Nesting in marine turtles is also clearly linked to temperature. An increase in water temperature leads to shorter internesting intervals in both *Chelonia mydas* and *Caretta caretta* (Hays et al. 2002). The onset of nesting can be accelerated by higher temperatures, leading to earlier nesting (Weishampel et al. 2004). Previous observations of species within the *Batagur* genus showed that peak nesting activity varies for the different species. *Batagur kachuga* and *B. dhongoka* appear to nest when the water levels of the rivers they inhabit are at the lowest (Sirsi et al. 2017). *Batagur borneoensis* nests on marine beaches and was observed to nest at low tide (Duli 2009), while nesting of *B. affinis* occurs during the dry season from November through March. Several observations in Malaysia demonstrated that 1 subpopulation of *B. affinis* (*B. affinis edwardmolli*) lays more than once during the same nesting period, presumably returning to nest and depositing the rest of the clutch (Duli 2009; Chen and Wong 2015). Different populations of *B. affinis* show different nesting behaviors. For example, in 1 population, females nest solitarily and are seen to renest, while in another, females synchronize their nesting and excavate mock nests to confuse predators (Moll et al. 2015).

Comparably little information exists on the closely related species *B. baska*. The study species has declined to such an extent that today the terrapin can be considered ecologically extinct, making it impossible to investigate its behavior in its natural habitat. Nest abundance information from the Bangladesh conservation project suggests that females nest once from March to April. However, genetic analyses of juveniles hatched in 2012 and 2013 in this breeding project showed that 1 female was the source of 2 nests, while other females did not deposit eggs at all (Spitzweg et al. 2018). This report raises the question of whether each female primarily deposits only 1 or several nests, revisiting the beach on the same or different nights. Additionally, no knowledge exists about the time spent on the beach to nest or nest-site selection. Equally unknown are environmental factors promoting nesting, such as whether water temperatures influence the laying period of these ectothermic animals.

Observing and monitoring nesting remains difficult, especially because the nesting period is restricted to only a few nights every year. In particular, nocturnal nesting behavior, which may provide protection from predators by being less detectable (Alho and Pádua 1982) and/or reduce the energetic cost of nesting by avoiding heat exhaustion (Spotila and Standora 1985), poses additional visual monitoring challenges. The potential to answer these questions using noninvasive video motion-detection cameras is evident. Automated surveillance could provide consistent information and contribute new findings on nesting behavior and activity of the species. The present study tested video-based detection of the northern river terrapin by comparing different camera trapping systems and settings under controlled conditions at the Vienna Zoo. Subsequently, with the help of motion-based video surveillance, nocturnal nesting behavior was recorded for the first time in 2019 at the breeding site in Bangladesh and quantified in 2 consecutive nesting periods. To understand the influence of temperature on nesting period, we additionally investigated breeding pond water temperatures in 2 different conservation sites in Bangladesh. We report here our first set of observations of *B. baska* nesting behavior and draw conclusions on the nesting ecology of this critically endangered terrapin.

METHODS

Study Species and Location. — The critically endangered northern river terrapin (*B. baska*) is a large aquatic turtle with females larger than males, with a carapace length up to 60 cm (Weissenbacher et al. 2015). The study species is currently managed in conservation breeding sites in Bangladesh, India, and at the Vienna Zoo and Turtle Island in Austria. The Vienna Zoo houses 3 females and 3 males in its Rainforest House. In 2010, a conservation breeding program consisting of 4 sexually active females and 3 males was established in Bhawal National Park (NP; lat 24°5′45″N, long 90°24′14″E) in Bangladesh, a nature reserve located 40 km N of the capital, Dhaka. In 2016, a second breeding group consisting of 4 females and 5 males was established in Karamjal (lat 22°25′26″N, long 89°35′21″E) in Bangladesh, a forest station located in the Sundarbans, near the Bay of Bengal, 315 km S of Bhawal NP. The breeding groups live in fenced ponds (682 m^2 in Bhawal NP and 2904 m^2 in Karamjal) with adjacent nesting beaches resembling the sandbanks they nest on in the wild. The nesting beach in Bhawal NP is 14 m long, including a 3-m-wide flat upper area and a 6-m-wide slope (steepness: 22%–28%; 12°–16°) leading to the pond, and is enclosed by a boundary wall. The brackish water of the pond in Karamjal (pH = 8.3, conductivity = 4.73 msec/cm) has higher salinity than the pond in Bhawal NP (pH = 7.25, conductivity = 42 μsec/cm). The terrapins are fed a mixture of green leaves, fruits, and vegetables ad libitum 3 times a week and shrimp twice per month.

Motion Detection Experiment (Vienna Zoo). — To monitor the northern river terrapin during nocturnal nesting, we tested different camera traps at the Vienna Zoo. Cameras were set up in a room (5 × 2 × 3.2 m) in the Rainforest House with a constant temperature of 22°C and 80% humidity. All openings or possible light sources were closed with tarps to completely darken the room (illuminance = 0 lx; $n = 10$). To investigate commercially available heat-triggered motion-based cameras, we compared 2 different cameras: a Panasonic WV-S1531LN (PANA) video surveillance camera (Panasonic, Kadoma, Japan) and a DÖRR WildCam Black IRX42 (DORR) video/photo camera trap (Dörr, Neu-Ulm, Germany). In addition, we performed trials with reflective tape (Rovtop 5x300xm; Rovtop-Tech, Shenzhen, China) and an additional infrared-emitting light (Kkmoon IVA1188667372472AR; Shenzhen Tomtop Technology Co Ltd, Shenzhen, China) to potentially enhance detection.

We first tested the DORR camera, which has a 10-MP resolution and is equipped with a motion sensor (45° angle detection at a distance of 20 m) and 42 infrared light-emitting diodes (LEDs) with infrared flash (IR960 nm). We used each of the camera's 3 standard programs to trigger the motion detector: Quick-Set 1 (Q1) takes 3 pictures with 8-MP resolution and a delay of 30 sec, Quick-Set 2 (Q2) takes 1 picture with a resolution of 8 MP and a delay of 30 sec, and Quick-Set 3 (Q3) records a 10-sec video in high definition with 1280 × 720 and a 30-sec delay. The DORR camera was placed on a tripod on 1 side of the room, protected by a wooden barrier to avoid disruption by the animal. The terrapin was placed on the other side of the room. In a second step, we fitted the northern river terrapin with reflective tape (5 × 20 cm) on both sides of its carapace (48 × 36 cm) for enhanced reflection (Fig. 1). To further enhance detection through increased reflection by the tape, an infrared-emitting spotlight, with 96 LEDs and a 10- to 60-m range according to specifications, was installed on an overhead board at 3-m height in the middle of the ceiling. To test detection of the terrapin by the DORR camera, each of the 3 settings was tested for a period of 10 min with and without the additional infrared spotlight. The data were saved on an integrated SD card.

We then tested the pixel-based motion detection PANA camera with a 1/3-inch CMOS Frame-sensor, a 2.8- to 10-mm lens. Light sensitivity for color was 0.01 lx, and for black-and-white it was 0.006 lx. The lens captured a horizontal angle from 31° to 112° and a vertical angle from 17° to 60°. It is equipped with a ×3.6 optical zoom, 1 Power over Ethernet (PoE) LAN and 3 alarm inputs, 1 audio in and 1 audio out, 1 SDXC slot (limited to 128 GB), motion detector, multistream, and integrated infrared light with a range of 40 m. The surveillance camera was fixed on an overhead wooden board at 3 m in the middle of the ceiling and was connected to a computer in an adjacent

Figure 1. Photos from the Panasonic surveillance camera taken during experiments with a female northern river terrapin (*Batagur baska*). The carapace size of the terrapin is 48 × 36 cm. Pictures were taken from a height of 5 m. (A) With reflective tape (5 × 20 cm); (B) without tape.

room. The computer with a LINUX operating system was connected via PoE LAN cable and a PoE switch, and Ffmpeg 3.3 "Hilbert" (ffmpeg, Paris, France) software was used for recording data. To increase the pixel-based motion detection sensitivity of the PANA camera, 15 steps of sensitivity level and 10 steps of detection size can be adjusted in the program settings. Detection size determines how much change in the adjusted frame represents motion, with a value of 1 responding to small change (e.g., moving insect) and providing the highest sensitivity. Motion detection sensitivity provides a contrast setting, determining how much change in contrast is reported, and the largest value of 15 provides the highest sensitivity. Detection size and sensitivity settings were adjusted stepwise to assess the best settings or minimal stimuli necessary to trigger recordings. For both camera systems, we tested the motion-triggered detection of a female *B. baska* with and without reflective tape on the carapace. The data were saved on an integrated SD card.

For data analyses, we compared the number of triggered recordings with the observation of actual movement observations at different settings of the PANA with cross tabulations. Results from Fisher's exact test are reported. The statistical analyses were performed with SPSS 23 (IBM Corporate Released 2015; IBM Corp, Armonk, NY).

Nesting Behavior (Bangladesh). — To monitor the nesting behavior of *B. baska*, the PANA camera was set up at the boundary wall of the breeding beach in Bhawal NP. To obtain the widest possible shot of the area, the camera viewed the beach sidelong. We used the camera settings detection size 3 and sensitivity 15. The camera was activated daily by the station staff after the first terrapin tracks of the season were noticed on the beach. The camera was started at 1730 hrs by connecting to a commercial car battery, and the recording was stopped the next morning at 0600 hrs. Individuals were recorded during the breeding seasons of 2019 and 2020. In 2019, each of the 4 females was marked with a white number painted on their carapace for individual identification 2 mo prior to nesting. In 2020, individual markings were renewed using reflective tape. For individual identification, the tape was put on the carapace as horizontal or vertical lines as well as in the form of a cross or 3 dots. The respective symbols were covered by a thin layer of epoxy glue for better attachment. The data were saved on an integrated SD card.

From the resulting video footage, we selected the recording nights where egg clutches were detected the next morning by the station staff and all recordings of females observed digging on the sand beach. During nesting nights, we recorded the following parameters: number of times an individual came up to the beach, time spent on the beach, and type of activity (walking around, digging, laying, covering up nests, and interactions with other terrapins). Temporal measurements during the nesting event (time spent digging, depositing eggs, and covering up the nest) were collected in minutes. Digging was recorded from the first observed digging activity, when the individual sways and waves its back feet, kicking up sand, until the last. The subsequent behavior was categorized as egg deposition. The deposition time ended on the first observed covering-up action, clearly identifiable by the side-to-side motion of the individual.

Temperature Measurement and Analysis. — Year-round water temperature was recorded from the breeding ponds in both Bhawal NP and Karamjal using temperature loggers (HOBO Pro v2 U22-001; Onset, Bourne, MA) fixed approximately 5 cm under the pond surface. Temperatures were recorded every 2 hrs from 2014 to 2020 in Bhawal NP and from 2016 to 2019 in Karamjal. Additionally, oviposition dates of all nests laid in the breeding project are available from both conservation sites (Bhawal NP: 2012–2020; Karamjal: 2017–2020).

To test whether the onset of nesting corresponds to specific water temperature changes, we compared temperatures (recorded every 2 hrs from 1300 to 2400) of the first oviposition nights of each breeding season from 2015 to 2020 in Bhawal NP and from 2017 to 2019 in Karamjal. Temperature comparisons across breeding sites were performed using Mann-Whitney U-tests, and comparisons within the respective breeding site were tested using Kruskal-Wallis tests for nonnormal distributed data, followed by multiple pairwise Dunn's post hoc tests adjusted with Bonferroni corrections in SPSS version 22.

RESULTS

Motion Detection. — The DORR camera did not detect movement of the northern river terrapin. None of the camera's quick-set programs (photo or video format) recorded data of the terrapin with or without reflective tape. Trials with the additional infrared spotlight also failed to detect the animal.

On the other hand, the PANA surveillance camera recorded 100% of movements of an unmarked female terrapin at detection sensitivity 15 and detection size 3 (Table 1; no reflective tape). Similar detection probability was recorded at the lower detection sensitivity setting of 14 (Fisher's exact test, $p = 0.182$, $n = 11$), but less activity was recorded when the sensitivity setting was further reduced to 13 (Fisher's exact test, $p = 0.015$, $n = 11$).

Table 1. Movement detection of the northern river terrapin (*Batagur baska*) equipped with and without reflective tape on the carapace by a Panasonic surveillance camera in percent (%) at different detection-sensitivity and detecting-size settings.

	Detecting size			
	No tape	Tape		
Detection sensitivity	3	3	4	5
15	100 (n = 6)	71 (n = 7)	67 (n = 6)	83 (n = 6)
14	60 (n = 5)	100 (n = 6)	40 (n = 5)	40 (n = 5)
13	20 (n = 5)	43 (n = 7)	—	—

When the terrapin was marked with reflective tape on the carapace, detection of movement was not enhanced. Movement was detected similarly at high sensitivity or contrast settings of 15–13 at a detection size of 3 (Fisher's exact test, $p > 0.05$). However, decreasing detection sensitivity (< 14) and increasing detection area (> 3) settings yielded less than 50% motion detection of the actual movements of the terrapin in the room (Table 1; tape). The high sensitivity settings of detection size 3 and detection sensitivity 15 provided the best detection result of an unmarked terrapin and were chosen for further monitoring during the nesting seasons in the conservation breeding site in Bangladesh.

The PANA camera recorded an average of 343.5 videos (SD = 56.12; time range = 1–185 sec) per night (n = 20) during the nesting seasons in Bhawal NP. Most video recordings were triggered by insects but also by heavy rain, lightning, and several other animals, including birds, amphibians, reptiles, and mammals. Both the paint and the reflective tape markings were prone to abrasion. The terrapins marked with tape were, however, easier to identify from greater distances (7–14 m from the camera).

Nesting Behavior. — In 2019, 4 nesting events were recorded, with each female nesting once. Owing to low visibility during 1 nesting event, only 3 of the 4 could be analyzed in detail. In 2020, 3 nesting events were recorded, as 3 females nested once, and 1 female did not nest. The female that did not nest was observed excavating and covering up 3 potential nests in 1 night without depositing eggs. This female walked onto the beach at 1940 hrs and spent 7 hrs 12 min on the beach before returning to the pond. The first nesting attempt was on the edge of the nesting beach slope, and the second was farther up, on a flat portion, close to where 2 other females nested that same year and the third was 1 body length (~ 50 cm) away from the second excavation. All 7 recorded nests in 2019 (n = 4) and 2020 (n = 3) were laid between 2030 and 0130 hrs. On each nesting night, the individuals came up on the beach and returned to the water at least once before nesting. In 2019, the 3 females for which nesting events could be analyzed visited the beach twice (for periods of 10 and 13 min, 10 and 11 min, and 36 and 9

Figure 2. Screen shot from the Panasonic surveillance camera displaying 2 female *Batagur baska* nesting in close proximity to one another in March 2019 in Bhawal National Park, Bangladesh.

min, respectively) before nesting. During the nesting night of 2020, 1 female visited the beach briefly 4 times (2, 5, 4, and 3 min), another visited 4 times for longer periods (7, 6, 24, and 9 min), and the third female visited only once (6 min) before egg deposition. Brief beach visits consisted of walking to the flat area of the beach and either returning immediately to the pond the same way or walking in a circle across the beach back to the water. During more extensive visits ($>$ 10 min), the females walked up and down the slope and circled the beach, stopping only briefly before continuing in another direction. There was no obvious pattern in the females' visits to the beach prior to nesting.

Nesting time in 2019 lasted on average 89.5 min (n = 3, SD = 29.45, range = 69–133 min), and the mean total time spent on the beach during these nesting events was 112.5 min (SD = 26.56, range = 78–138 min). On average, females were digging for 49.3 min (SD = 37.82, range = 27–93 min) followed by 16.7 min (SD = 3.05, range = 14–20 min) for egg deposition and covering up the nest for a period of 28.3 min (SD = 9.71, range = 26–39 min).

Similar times were recorded in 2020. The total nesting was on average 83.3 min (n = 3, SD = 9.50, range = 74–93 min), and the mean total time spent on the beach during those events was 92.3 min (SD = 7.64, range = 84–99 min). The females spent, on average, 31.3 min digging (SD = 3.21, range = 29–35 min), 22.7 min laying (SD = 5.03, range = 18–28 min), and 29.3 min covering up the eggs (SD = 10.69, range = 17–36 min).

In 2019, 2 females nested near each other ($<$ 80 cm; Fig. 2). In 2020, one of those females returned to the same spot as the previous year, and yet another female nested in the exact same area. The females nested not only in the same area but also during the same night, which resulted in a certain amount of competition in both 2019 and 2020. In 2020, 1 female (marked with dots) started digging and was physically disturbed by the second female (marked with horizontal stripes), who was seemingly interested in the first female's spot (Supplemental Video; all supplemental material is available at doi:10.2744/CCB-1543.1.s1). The second female kept investigating the digging female's cavity and circled around the cavity twice before leaving. The first female (marked with dots) left her digging area and returned to the water without depositing eggs. Subsequently, the second female (marked with stripes) took over the same digging area minutes later, started digging, and deposited her eggs. She then covered the nest and returned to the pond. The first female returned hours later that night and resumed digging at the exact same location. This time, the female successfully deposited eggs and covered the nest before returning to the water without disturbance. Egg clutches were found the next morning only 5 cm apart. This nesting area was located 1 m from the boundary wall on a flat portion of the beach, approximately 1.5 m away from the slope (steepness: 22%; 12.4°) leading down to the water. The nesting area was 8 m away from the pond and 1.75 m above the water surface.

In 2019, one of the females that nested on the same spot and during the same night as another female was observed digging and potentially nesting again 19 d later. However, a severe rainstorm began during the presumed laying stage, and video footage was no longer viable, as rain completely obstructed any view of the individual. Egg deposition could not be confirmed, and no eggs were discovered at the designated location by the station staff on the following morning.

Water Temperatures. — The average water temperature of the pond in Karamjal (26.9°C) was higher than

Table 2. Monthly average water temperatures of breeding ponds in the *Batagur baska* conservation stations in Bhawal National Park from seasons 2014–2020 and in the Karamjal center from seasons 2016–2019. Averages of coldest and hottest months are bolded.

Station/ breeding season	Temperature (°C)							
	Mating and egg development							
	November		December		January		February	
	Mean (± SE)	Range	Mean (± SE)	Range	Mean (± SE)	Range	Mean (± SE)	Range
Bhawal/2014–2015	24.0 (± 0.07)	21.15–25.21	19.4 (± 0.06)	17.34–21.25	17.4 (± 0.02)	16.92–18.60	17.9 (± 0.05)	17.15–20.44
Bhawal/2015–2016	23.4 (± 0.08)	20.13–31.23	19.6 (± 0.12)	15.68–21.82	16.4 (± 0.03)	14.96–17.34	19.7 (± 0.12)	15.92–23.40
Bhawal/2016–2017	23.1 (± 0.12)	20.53–26.72	18.9 (± 0.04)	18.30–20.77	16.8 (± 0.05)	15.15–18.60	18.4 (± 0.06)	16.89–20.84
Bhawal/2017–2018	23.4 (± 0.06)	20.58–24.68	19.3 (± 0.03)	18.37–20.58	15.2 (± 0.06)	14.31–18.49	17.1 (± 0.06)	15.01–18.96
Bhawal/2018–2019	24.7 (± 0.05)	22.73–25.72	19.4 (± 0.08)	16.58–30.22	16.9 (± 0.02)	16.03–17.87	17.4 (± 0.06)	16.18–20.08
Bhawal/2019–2020	24.7 (± 0.05)	22.73–25.72	19.4 (± 0.08)	16.58–30.22	16.9 (± 0.02)	16.03–17.87	17.4 (± 0.06)	16.18–20.08
Bhawal 2015–2020	23.5 (± 0.03)	20.01–31.23	19.2 (± 0.03)	15.68–30.22	**16.6 (± 0.02)**	**14.31–18.60**	17.8 (± 0.03)	15.01–23.40
Bhawal 2017–2019	23.2 (± 0.05)	20.01–26.72	19.0 (± 0.03)	16.03–20.77	**16.0 (± 0.03)**	**14.31–18.60**	17.7 (± 0.04)	15.01–20.84
Karamjal/2016–2017	23.7 (± 0.10)	21.22–28.52	19.4 (± 0.08)	13.93–32.33	17.6 (± 0.05)	15.44–20.22	21.9 (± 0.08)	18.42–24.15
Karamjal/2017–2018	24.9 (± 0.09)	20.20–25.82	19.9 (± 0.04)	18.79–21.65	16.0 (± 0.06)	15.22–19.25	20.5 (± 0.10)	16.61–24.48
Karamjal/2018–2019	26.0 (± 0.07)	23.67–28.49	21.3 (± 0.08)	17.72–24.10	19.0 (± 0.04)	28.01–21.56	21.8 (± 0.09)	19.75–26.21
Karamjal 2017–2019	24.8 (± 0.05)	20.20–28.52	29.6 (± 0.03)	13.93–32.56	**18.0 (± 0.05)**	**15.22–21.56**	21.4 (± 0.06)	16.61–26.21

recorded in the breeding pond in Bhawal NP (24.7°C). Water temperatures in both breeding sites decreased during the mating period in November and December, reaching the lowest average temperatures in January (Bhawal NP = 16.6°C, Karamjal = 18.1°C; Table 2). Subsequently, temperatures increased continuously, and eggs were consistently laid in March and April (Fig. 3). The warmest water temperatures were recorded in May and June at both breeding sites (Table 2).

Comparison of recorded water temperatures during all documented nesting nights of the conservation project showed that the average water temperature when first nests were laid was 22.4°C in Bhawal NP (SD = 1.23; range = 21.7°C–25.4°C; 2015–2020) and 25.4°C in Karamjal (SD = 1.23; = range 23.1°C–26.3°C; 2017–2019). Water temperatures during these first nesting nights differed significantly across the years within the respective breeding site (Bhawal NP: Kruskal-Wallis test: $\chi^2_5 = 67.243$, $p < 0.001$; Karamjal: Kruskal-Wallis test: $\chi^2_2 = 31.236$, $p < 0.001$; Fig. 4). In 2017, 2018, and 2019, the first nests were laid 10, 16, and 7 d earlier, respectively, in Karamjal than in Bhawal NP. The pond temperature during these earlier nesting nights in Karamjal was on average 2.2°C higher than temperatures in the breeding pond in the Bhawal NP several days later (Mann-Whitney U-test: U = 1152, $p < 0.001$).

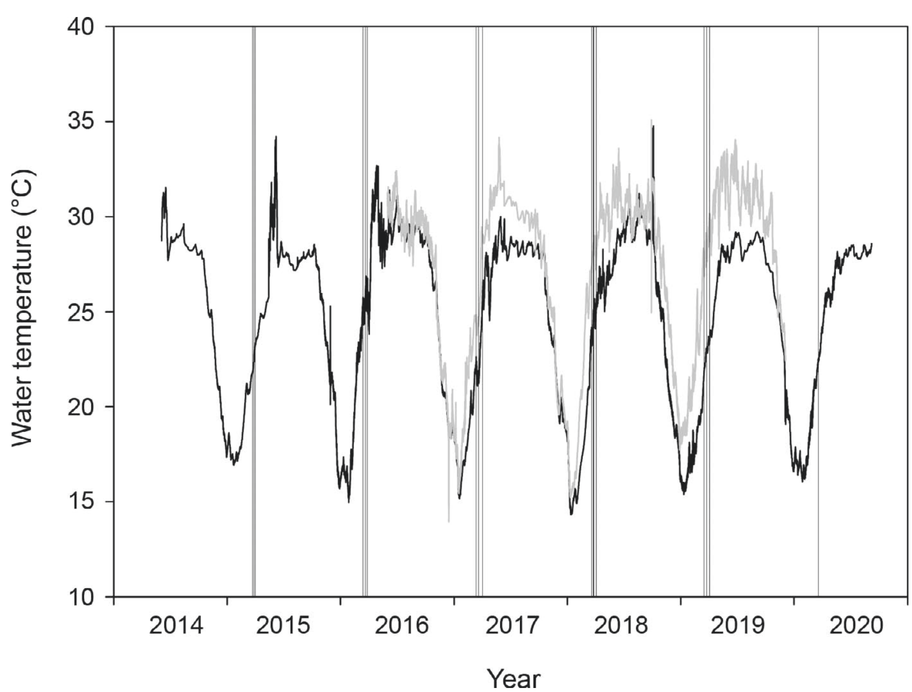

Figure 3. Annual water temperature fluctuations of the breeding ponds in Bhawal National Park from June 2014 to September 2020 (black) and Karamjal from June 2016 to December 2019 (gray). Gray vertical lines represent oviposition nights in both stations.

Table 2. Extended.

Temperature (°C)							
Oviposition and incubation				Hatching			
March		April		May		June	
Mean (± SE)	Range	Mean (± SE)	Range	Mean (± SE)	Range	Mean (± SE)	Range
21.2 (± 0.04)	20.44–23.18	24.5 (± 0.03)	23.21–24.92	27.5 (± 0.12)	24.82–31.82	28.3 (± 0.11)	27.36–34.23
25.1 (± 0.06)	22.35–26.89	30.5 (± 0.13)	23.83–32.67	28.8 (± 0.05)	27.28–32.67	29.5 (± 0.05)	28.54–31.41
21.8 (± 0.07)	19.56–25.09	26.6 (± 0.05)	24.54–28.12	26.9 (± 0.03)	25.02–28.30	28.3 (± 0.03)	27.70–29.89
23.1 (± 0.10)	19.01–25.70	26.3 (± 0.04)	24.12–28.30	26.9 (± 0.03)	25.02–28.30	28.9 (± 0.03)	27.51–29.37
22.0 (± 0.06)	19.41–24.20	25.7 (± 0.03)	23.88–26.26	27.2 (± 0.03)	25.62–28.17	28.0 (± 0.01)	27.16–28.37
22.0 (± 0.06)	19.41–24.20	25.7 (± 0.03)	23.88–26.26	27.2 (± 0.03)	25.62–28.17	28.0 (± 0.02)	27.16–28.37
22.1 (± 0.04)	19.01–26.89	25.7 (± 0.05)	23.21–32.69	27.8 (± 0.03)	24.82–32.67	**28.5 (± 0.02)**	**27.16–34.23**
21.9 (± 0.05)	19.01–25.70	26.0 (± 0.04)	23.28–28.30	27.8 (± 0.03)	25.02–30.02	**28.5 (± 0.02)**	**27.51–29.89**
24.6 (± 0.07)	22.73–29.96	29.3 (± 0.04)	28.59–31.66	31.3 (± 0.05)	30.34–34.18	31.0 (± 0.02)	30.57–31.87
26.6 (± 0.07)	24.51–29.02	29.7 (± 0.06)	27.19–31.79	29.8 (± 0.05)	28.15–32.74	31.1 (± 0.05)	29.72–33.60
27.5 (± 0.10)	22.71–29.32	30.2 (± 0.06)	27.95–32.56	32.3 (± 0.06)	28.30–33.55	32.5 (± 0.06)	29.29–34.07
25.8 (± 0.05)	22.71–29.46	29.6 (± 0.03)	27.19–32.56	31.2 (± 0.04)	28.15–34.18	**31.4 (± 0.03)**	**29.29–34.07**

DISCUSSION

A commercially available and widely used camera trap system was unable to capture movement of the northern river terrapin in the dark. Sensor detection could not be enhanced with reflective tape or accessory infrared light. A study on Komodo dragons (*Varanus komodoensis*) compared detections obtained from cage traps vs. camera traps, with similarly good detection with both methods (Ariefiandy et al. 2013). Komodo dragons are also ectothermic; however, they can regulate their body temperature to some extent (Harlow et al. 2010) and were detected during daylight while moving rapidly toward baited traps. In contrast, considerably slower *B. baska* movement under nocturnal conditions could not be detected by camera traps with motion detection in the infrared spectrum despite the application of a reflective surface. The pixel-based video surveillance camera, on the other hand, was able to capture movements of a female northern river terrapin under controlled conditions at the Vienna Zoo. Only very sensitive settings allowed reliable motion detection. When the terrapin was equipped with reflective tape, sensitivity settings could be lowered 1 step and still consistently captured movement. However, only 50% or less of the terrapin's movements triggered video motion detection when the camera's detection area setting was simultaneously increased with decreased sensitivity levels, which would yield unreliable and inconsistent data collection under in situ conditions. Reflective tape markings allowed easier and faster individual identification of terrapins than paint marking on video recordings collected at the conservation breeding site in Bangladesh. Consistent with other studies, triggered infrared surveillance at settings providing reliable detection eventually resulted in a considerable amount of false trigger events, especially by insects, when the camera was deployed at the nesting beach in Bangladesh (Welbourne 2014). Similarly,

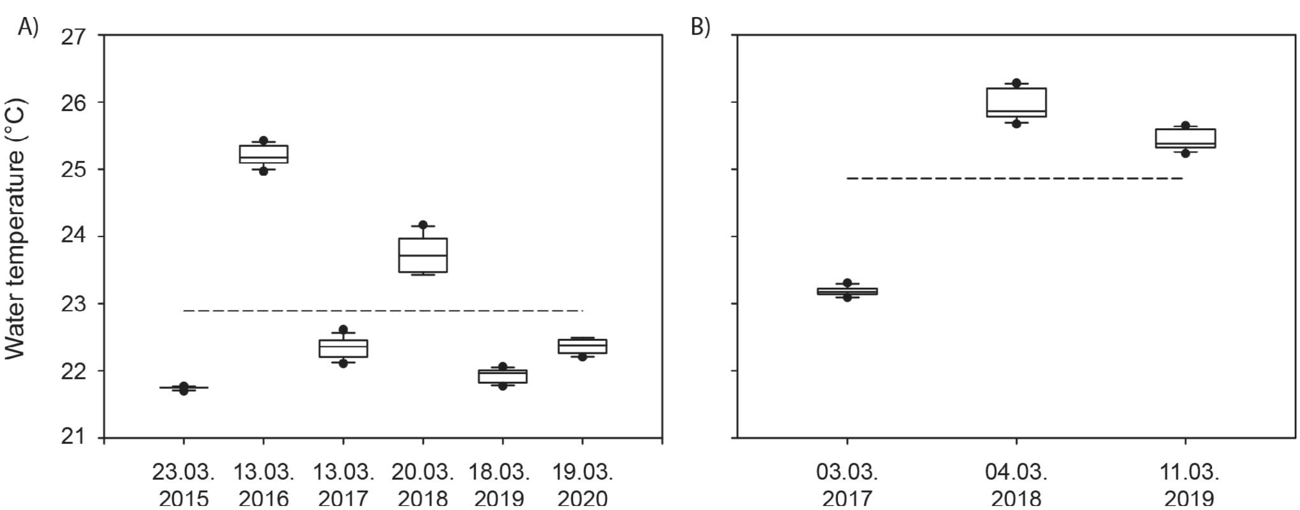

Figure 4. Mean water temperature on the nights when first nests were laid in (A) Bhawal National Park and (B) the Karamjal station. Box plots represent median and percentiles measurements; dots denote outliers. The dashed line represents the mean water temperature of first nesting nights across the years.

light beam barrier–operated detection (Leeb et al. 2013) and an optical trigger method (Hobbs Active Light Trigger; Hobbs and Brehme 2017) were hampered by minimal movement of objects (e.g., leaves, water droplets, and insects), leading to gaps in data collection.

Reliable sampling to inventory and monitor wildlife employing images of animal communities is improving (Hobbs and Brehme 2017), but consistent passive-triggered video monitoring of rare behaviors, particularly of ectothermic and nocturnal animals, remains difficult. A recent study documented basking behavior of several (> 1000) freshwater turtles with an artificial basking platform and camera traps but failed to report whether the night vision and motion sensor was able to detect nocturnal visits (Unger and Santana 2019). So far, detection by motion-sensitive camera traps of elusive reptiles and/or their behavior at night in their natural environment with current technology leads to unreliable results. Successful video trapping studies of ectothermic animal have relied mostly on continuous recording of large-bodied species (Lang and Kumar 2016), but continuous uninterrupted surveillance is inefficient due to the high volume of footage to process. However, with the advent of deep-learning and machine-learning techniques and algorithms, the combination of constant recording or triggered recordings with sensitive settings in combination with concurrent analysis could constitute an interesting path forward (Tuia et al. 2022). Nevertheless, research, development, and investments into new systems are desperately needed to address the multiple questions arising, among many others, from the restoration efforts of turtle populations in Southeast Asia and beyond (Swinnen et al. 2014).

The motion-triggered video surveillance in the conservation breeding program in Bangladesh yielded, for the first time, information on the nesting behavior of the critically endangered terrapin *B. baska*. Investigations demonstrated that female northern river terrapins in the Bhawal NP conservation project nested on average for a period of 1.5 hrs and produced a single clutch per year. These observations are in accordance with previous findings of clutch numbers in relation to reproductively active females in this colony and with ex situ populations of the species (Praschag and Singh 2019; P. Praschag, *pers. comm.*, 2018). In 2019, 1 *B. baska* female excavated a second nest 3 wks after laying the first clutch. A heavy rainstorm interrupted the video recording and erased any signs of digging for the station staff to confirm egg deposition. Thus, renesting events cannot be ruled out in our study population, especially because renesting has been documented once previously by genetic parental analysis of juveniles in this population (Spitzweg et al. 2018). Multiple nesting events were also observed in its close relative, *B. affinis* (Moll et al. 2015). This phenomenon, however, could not be confirmed in the current study.

Female *B. baska* performed investigative walks along the beach before the actual nesting events, indicating that females are conscientious of where they nest and search for suitable nesting areas and substrate as observed in other species, such as *Chrysemys picta marginata* (Christens and Bider 1987). Our observations showed that females favored nest sites that were the farthest away from the water (8 m) and on flat terrain, suggesting nonrandom nest-site selection, likely ensuring a drier and unflooded environment for their clutch. One female nested at the same location in both nesting seasons. Interestingly, this nesting site was also used by a total of 3 females over both 2019 and 2020. The female that did not lay in 2020 also dug 2 potential nests in the same spot. Nest-site selection in turtles has direct repercussions on reproductive success of the females and influences incubation length, hatching success, and hatchling size (Valenzuela et al. 1997; Ferreira Júnior and Castro 2010). Nests laid closer to the water often experience higher predation rates than nests laid farther inland (Christens and Bider 1987; Kolbe and Janzen 2002; Spencer 2002).

Several freshwater turtle species also synchronize nesting events, including species of the *Batagur* genus. In Malaysia, *B. affinis edwardmolli* nests en masse, and females synchronize their nesting to the same night (Moll et al. 2015), similar to other freshwater (Ferrara et al. 2014) or sea turtles (Bézy et al. 2020). In 2019, 2 *B. baska* females nested on the same night, and in 2020, 3 females nested on the same night. However, nesting records of the breeding program in Bangladesh have so far documented only 3 further simultaneous nesting events where 2 nests were detected at once in the same breeding season, over a total of 9 seasons in Bhawal NP and 5 in Karamjal in the past years (D.P., *pers. obs.*). We must acknowledge that the detection of nests on the breeding beach might be hampered after occasional heavy rains but still suggest that synchronization of nesting seems unlikely in the study population and that simultaneous nesting could be coincidental and related to favorable environmental conditions on the nesting nights.

To understand the significance of environmental factors influencing nesting, we additionally investigated water temperatures of the breeding ponds that female *B. baska* inhabit on the 2 conservation breeding sites in Bangladesh. The average water temperature on the nights when the first nests were laid in Bhawal NP (2015–2020) was 22.4°C, and, on average, 3°C warmer nesting nights were recorded in Karamjal (2017–2019). Karamjal is in southern Bangladesh at the edge of the Sundarbans mangrove forest compared with the more northern and central Bhawal NP. Water temperatures at both breeding sites varied over the entire reproductive period, decreasing from November to January, which coincides with the mating period, potentially acting as a trigger to search for a mating partner. This period is followed by an increase in temperatures from February to April, with higher average temperatures in Karamjal compared with Bhawal NP, explained by their respective geographic positions. The warmest months were May and June (Bhawal NP: 27°C–28°C; Karamjal: 31°C) at the end of the defined reproductive season, which coincided with incubation or egg development and the hatching periods, likely providing stable conditions for juvenile development.

Females nested earlier in Karamjal than in Bhawal NP, suggesting that increasing water temperatures could act as a threshold to trigger nesting in *B. baska*, similar to temperate-zone turtles (Williard and Harden 2011) and sea turtles (Hays et al. 2002). However, considering the lower water temperatures when nests were laid in Bhawal NP, comparable temperatures were present in Karamjal several weeks prior to when nests were laid, suggesting that nesting theoretically could have occurred sooner. Water temperatures on nesting nights also differed significantly across years within each breeding site, making it difficult to define threshold temperatures prompting nesting events. We therefore suggest that temperature shifts trigger mating and nesting and that further environmental factors apart from water temperature might be relevant for nesting. Overall, nesting of terrapins tends to coincide with rainfall (Wilson et al. 1999; Bowen et al. 2005) but also with low water levels, when the largest portion of sandbanks are exposed (Alho and Pádua 1982). Hence, precipitation may influence nesting by modifying sand quality or moisture. In addition, physiological factors influence egg deposition, as nesting depends on the developmental stage of the eggs within the female's body cavity (Miller 1997; Rafferty and Reina 2014). Further studies should focus on measuring substrate qualities, rainfall events, amount of precipitation, and concomitant microhabitat changes to determine what environmental factors interact to influence nesting and nest-site selection in *B. baska*. Of equal importance is monitoring the impact of climate change on potentially severe water level rise in Bangladesh (Clark et al. 2016) and on temperature, which could have a dramatic influence on mating and nesting periods as well as on temperature-dependent sex determination during egg development (Valenzuela et al. 2019).

The survival of the species of the genus *Batagur* in general and *B. baska* in particular requires consistent efforts from conservation breeding programs in combination with the protection of the species' natural habitat to ensure their survival. Although the present findings result from an assurance colony with restricted beach access, the study provides a first foundation of the nesting ecology of this *B. baska* population. Wider generalizations for the species' nesting behavior and in situ management remain immensely difficult for *B. baska*. The species can be considered ecologically extinct, and in previous release attempts employing satellite transmitters in the natural habitat, the terrapins were monitored for only a few months before being captured in fishing nets of subsistence fishermen (Preininger et al., unpubl. data, 2018–2020). Additional surveys of potential nesting beaches were unable to confirm reproduction of the species during recent years. These uncertainties make constant and sensitive video surveillance to record nesting in the wild unfeasible, at least until nesting beaches can be identified with reasonable certainty and protected during the nesting season. We acknowledge that the current data represent only a limited sample size; however, due to the species' critical status and its likely extinction in the wild, our findings yield immense insights for future studies and help to understand the study species' reproductive biology for in situ and ex situ population management.

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The *B. baska* project in Bangladesh was approved by the Ministry of Environment, Bangladesh, and all project partners commit to an active memorandum of understanding to conserve the critical endangered northern river terrapin. For handling and marking of individuals reported in this article, established animal care protocols were followed that comply with the current laws of the country in which they were performed. The study was financially supported by the University of Veterinary Medicine Vienna, Research Institute of Wildlife Ecology, Department of Integrative Biology (FIWI), and the Vienna Zoo.

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