

Behavioral responses to spatial heterogeneity in endangered Ganges River dolphins (*Platanista gangetica gangetica*)



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ABSTRACT

Globally, the threat of endangerment and extinction of small cetaceans was highlighted after the recent extinction of the Chinese River dolphin or Baiji (*Lipotes vexillifer*). Species with a small population size and a limited geographic range, such as Ganges River dolphins (GRD), are more vulnerable to extinction. The social and behavioral needs of cetaceans have been identified as potential factors increasing their vulnerability to human disturbance. However, little is known about how GRD adapt their behaviors and diel activity patterns to spatiotemporal variation. In this paper, we examined the underwater behavior of GRDs in Nepal by collecting echolocation clicks from three spatially stratified habitats in the Sapta Koshi River system over a six-month period. Our research found that GRDs behave differently in response to spatial heterogeneity, indicating diverse environmental requirements for GRD persistence. Behavioral activity and duration varied across habitats but not across time of day, suggesting that GRD behaviors are likely to be regulated by habitat structure regardless of the time of day. However, GRD consistently exhibited nocturnal activity peaks even when diurnal activity varied substantially. This indicates that river dolphins may favor nocturnal refuges as a reaction to human disturbance in highly regulated rivers. Managing human disturbances in conjunction with habitat heterogeneity can improve the persistence of riverine cetaceans. Here, we document behavioral and ecological information pertaining to GRD, which is essential to the formation of river dolphin recovery plans that link ecological perspectives to planning and management.

1. Introduction

Cetacean interactions with fisheries are on the rise around the world (Dewhurst et al., 2020; Basran and Rasmussen, 2020; Paudel and Koprowski, 2020a; Tixier et al., 2020). Current research shows that over 300,000 whales and dolphins die annually due to entanglement in fishing gear (International Whaling Commission, 2020), suggesting a need for extensive research efforts to understand cetacean life histories and their likely exposure levels to anthropressure (human activities). The social and behavioral needs of cetaceans must be evaluated as potential factors influencing their vulnerability to human exploitation and disturbance. Survival and reproductive success of cetaceans (ie. fitness) may be influenced by social and behavioral factors, thus making them more

vulnerable to exploitation (Wade et al., 2012). In recent decades, the direct killing of cetaceans has been reduced, but the indirect deaths of small cetaceans have increased (Jefferson, 2019), placing small cetaceans in danger of extinction in some cases. The majority of the ten most endangered cetaceans from around the world inhabit freshwater ecosystems (Jefferson, 2019). Undoubtedly, several small freshwater cetaceans are in danger of extinction due to human activities, and may succumb to the same fate as the Chinese River dolphin (*Lipotes vexillifer*) which became functionally extinct in 2006 (Turvey et al., 2007). It is therefore critical that we understand how susceptible small cetaceans are to anthropressure.

Anthropogenic impacts including habitat degradation, prey depletion, noise pollution, and bycatch (including entanglement), as well as

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behavioral and depredation risks for freshwater cetaceans are recognized as primary drivers behind river dolphin decline (Trujillo et al., 2010; Braulik et al., 2014; Jefferson, 2019; Paudel and Koprowski, 2020a). One well-recognized human activity that influences the lives of river cetaceans is the destruction of habitats supporting vital life history activities such as giving birth, calf rearing, or feeding. Thus, endemic species are often restricted to particularly small habitats. Species such as the vaquita (*Phocoena sinus*), Chilean dolphin (*Cephalorhynchus eutropia*), and South Asian River dolphins (*Platanista gangetica*), are at higher risk due to human disturbance, and will potentially go extinct in modern times unless responsible management actions are implemented. Thus, behavioral and ecological requirements need to be understood to minimize the impacts of anthropressure. One way to reduce impacts on habitat is to understand the behaviors and diel activity patterns of animals, as the proportion of animals active throughout the day influences a wide range of ecological and physiological processes (Vazquez et al., 2019). Therefore, these behaviors can help us understand the overlap between the ecological needs of a species (e.g., foraging, resting, social, or surfacing activities) and human activities (e.g., fishing activity). In this way, human-caused habitat pressure can be addressed. Unfortunately, the limited knowledge we have of river dolphin behavior and activity,

particularly for the Ganges River Dolphins (GRD), which appear to have a narrow range and narrow habitat requirements, impedes conservation efforts intended to reduce the impacts of human pressures.

Previous studies on GRD underwater behavior have primarily occurred in captive environments (Herald et al., 1969; Andersen and Pilleri, 1970; Mizue et al., 1971). Although recent studies have focused on capturing the sound source of free-ranging GRD to characterize annual behavioral patterns (Sugimatsu et al., 2008, 2011; Sasaki-Yamamoto et al., 2012) and click characteristics (Jensen et al., 2013), these studies did not explicitly report on spatiotemporal variation in the underwater behavior or diel activity patterns of GRD. Further, the number of clicks exhibited by GRD also offers the opportunity to understand their underwater movement and surfacing behaviors. The number of clicks changes when behavior transitions from traveling to foraging/diving activity in odontocetes localized in a particular area (Au, 1993; Akamatsu et al., 2005, 2007), offering an opportunity to classify and compare underwater behaviors in relation to human-caused disturbances. Previous work has shown that the number of clicks drastically declines as GRD shift from stationary behavior to travel in the Ganges River, India (Sugimatsu et al., 2005). Similarly, in white-beaked dolphins, the number of clicks tends to increase during foraging/deep diving relative to

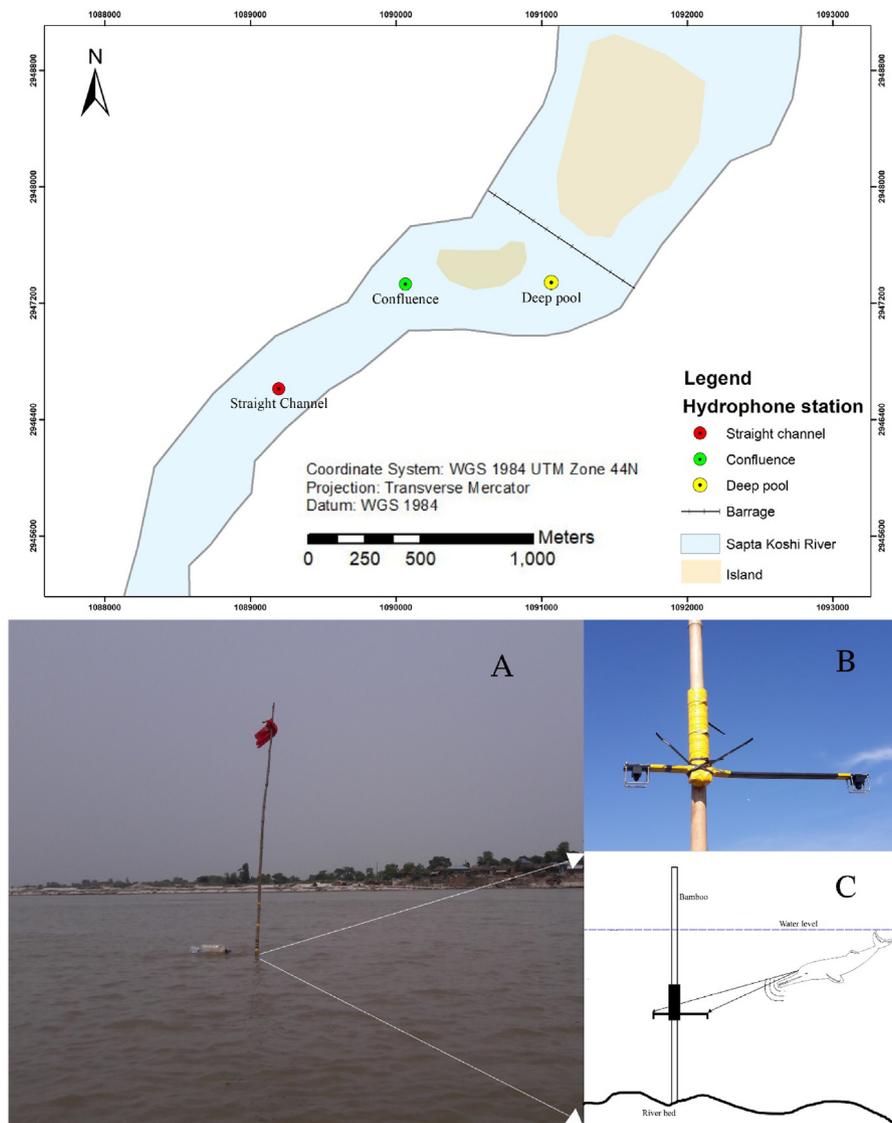


Fig. 1. The study area showing hydrophone locations at three spatially stratified habitats, confluence (CF), deep pool (DP), and straight channel (SC) in the Sapta Koshi River system of Nepal. The insets in the lower portion show the A-tag deployment using bamboo (A), the T-shaped A-tag with two hydrophones at the end of either side (B), and an illustration of how the A-tag captures echolocation clicks when a dolphin is detected (C).

traveling (Sugimatsu et al., 2009). In addition to the number of clicks, trajectory duration can provide insight into the duration of the dolphin's habitat use near the hydrophone area (Sugimatsu et al., 2011), whereby a lengthened trajectory duration is associated with an extended stay in a particular area.

To advance knowledge on the ecology of GRD underwater behaviors and diel activity, we evaluated the movement behaviors and diel activity patterns of GRD using dolphin-emitted echolocation clicks collected by stereo acoustic data loggers from three spatially and temporally stratified habitats in the Sapta Koshi River system of Nepal. Findings of this study help explain the timing of activity peaks (ie. the proportion of the day that animals are active) and significance of spatial heterogeneity to GRD life history activities, which together help broaden our knowledge regarding how human activities compromise the social and behavioral activities of GRD in the Anthropocene.

2. Material and methods

2.1. Study area

This study was conducted in the Sapta Koshi River system of Nepal (Fig. 1). We identified three unique hydro-physically stratified habitats (Table 1) at the study site (Paudel et al., 2015a,b & 2016a,b), each at least 0.5 km apart to ensure independent observation. Multiple authors have already tested and measured the effective detection distance (<500 m) of recording acoustic trajectories using T-shaped A-tags (the same hydrophone system we used). Sasaki-Yamamoto et al. (2012) reported a maximum acoustic distance of 350 m in the Ganges River system on the same species, whereas Li et al. (2009) reported a maximum of 478 m for finless porpoises in the Yangtze River. Considering these effective acoustic detection distances by the A-tag system, we maintained at least a 0.5 km distance between two hydrophone stations to ensure the independence of sampling observations.

The purpose of this experiment was not to study the effects of spatial heterogeneity on GRD behavior, but rather to observe how GRD behavior varies in response to spatial heterogeneity. Further, we consider each habitat as an independent unit of experimentation that explains and controls variation within the experimental unit that arises from sources unrelated to the experiment. This study design provides the opportunity to conduct sampling blocks at different temporal scales. We took this opportunity by recording the GRD's echolocation clicks continuously for a two-month period in each habitat, and assumed that echolocation clicks were directly related to spatial heterogeneity but not to the temporal scale.

We recorded clicks continuously between November 2017 and May 2018 in each habitat (November–January (DP), December–February (CF), and March–May (SC)). As this survey covers the early to late low water season time period, we considered this temporal scale as a season, and included it as an explanatory variable in subsequent analysis.

Table 1
Spatial and temporal characteristics of the study sites, including hydro-physical details of each habitat type.

Habitat type	Location	Survey period	Hydro-physical characteristics
Confluence	26° 31' 29.09" N, 86° 55' 26.33" E	December 6, 2017–February 13, 2018	Meeting point of two small tributaries with 3 m depth; substrate type: silt/clay
Deep pool	26° 31' 31.89" N, 86° 55' 26.11" E	November 6, 2017–January 19, 2018	Straight river channel with 4 m depth; substrate type: small cobbles
Straight channel	26° 31' 18.05" N, 86° 54' 40.33" E	March 22, 2018–May 25, 2018	Straight channel with shallow depth (1.7 m); substrate type: small boulder

2.2. Data collection

Underwater stereo acoustic data loggers (A-tags; MMT, Saitama, Japan) were used to capture the click trains emitted by the GRD. A long-life A-tag with extended battery cases was deployed, which possessed the capacity to capture data continuously for one month. GRD clicks were monitored and captured using a fixed type A-tag; this permitted us to firmly attach an A-tag (T-shaped A-tag with two hydrophones on either end of the "T" structure) on a fixed bamboo stick positioned at half of the depth of the selected habitat (DP, CF and SC) and 4 m away from the riverbank (see detail in Table 1). The A-tag, which consisted of two hydrophones, a passive band-pass filter (55–235 kHz), CPU, flash memory (128 MB), and batteries (two UM-1 batteries), was fixed parallel to the direction of the river flow. Using the maximum theoretical acoustic detection range of 500 m (Akamatsu et al., 2005), hydrophones were placed no closer together than 500 m from each habitat type to ensure independent acoustic observations. Details about the A-tag hardware specification, signal processing (sensitivity range), and auto-removal of noise contamination by A-tags has been documented in detail previously (Akamatsu et al., 2005). The A-tag records intensity of each click, the absolute time of the sound arrival, and the sound source direction of clicks encoded as the time arrival difference between the two hydrophones. When a sound is triggered, either in the primary or secondary hydrophone, an independent high-speed counter begins to measure the sound arrival time difference until the other hydrophone is triggered. As such, only a series of clicks recorded at both hydrophones is considered a valid click train, which also offers the opportunity to exclude extraneous noise. The A-tags sample click trains at 2 kHz, and therefore the time resolution of click detection is 0.5 ms (ms). The hydrophone sensitivity was calibrated in advance and a detection threshold level was set at 132 dB_{p-p} re. 1 μPa. Acoustic sensing distance was estimated using a standard formula (Akamatsu et al., 2005). This estimated sensing distance was further bootstrapped ($N = 10,000$) to obtain the uncertainty on the estimated distance.

2.3. Acoustic moving type and its relevance to GRD behavioral activity

Previous studies on underwater behaviors of GRD relied heavily on captive environments (Herald et al., 1969; Andersen and Pilleri, 1970; Mizue et al., 1971) and visual observations (Sinha et al., 2010). We followed the procedure developed by Sasaki-Yamamoto et al. (2012) for underwater movement classification, which assigns three categories based on the relative sound source angle of GRD clicks: Staying (S), Movement A (A), and Movement B (B). Movement A is defined as a straight trajectory in which the relative sound source angle constantly changes to the either positive or negative direction, representing animals traveling in either direction (upstream or downstream), whereas movement B is defined as a tortuous trajectory with at least one flexion point, indicating animals engaging in diving behavior related to foraging or long surfacing activity in a particular area (see details in Sasaki-Yamamoto et al. (2012) regarding the trajectory differentiation). Staying is a trajectory with a very narrow range (i.e., 10–20°) change in the direction of a relevant source of sound.

We further differentiated these movement categories using the pattern of the number of clicks and trajectory duration. We defined two different movement types (A and B) if the trajectory duration and click number were significantly different across the moving types. However, in the case of remaining stationary, we only considered the relative angle of the sound source direction, as its number of clicks and trajectory duration can vary. Before making ecological inferences about underwater behaviors of GRD, we examined the differences in the number of clicks and trajectory durations among all pairs of moving types. Collectively, we refer to all underwater moving types as behaviors of GRD (hereafter behaviors).

2.4. Acoustics click processing and analysis

Recorded clicks were pre-processed in Igor Pro 7 (WaveMetrics Inc., USA) using custom software written by Tomonari Akamatsu for A-tags (Marine Micro Technology, Saitama, Japan). This custom written file is primarily used for noise reduction and to create a time-sequential statistical data set of each click train captured. Dolphins emit series of echolocation clicks that exhibit a click train, which is a series of pulses (or clicks) with click intervals ≤ 100 ms (Au, 1993). To exclude extraneous noises from our datasets, we kept a click train with intervals ranging from 20 to 70 ms with ≥ 5 pulses in a pulse train, which has a high probability of representing signals from the GRD (Sasaki-Yamamoto et al., 2012). Before defining animal movement type, we first identified the acoustic trajectory of the dolphin, separated by > 5 min from previous or subsequent click trains. The time of the first click train in the trajectory was considered as the start time and the time of the last click train was considered as the end time of the trajectory, which enabled us to calculate trajectory duration. Then, within a trajectory, pulse trains were visually analyzed to assign movement type to the trajectory based on the changes in relative angle of the sound source direction. We discarded a trajectory if more than one animal was present to avoid underestimating click and/or inter-pulse intervals. Trajectories in the ranges of $0\text{--}50^\circ$ and $130\text{--}180^\circ$ were also eliminated to avoid the risk of false classification of the movement type. Only valid trajectories were used for subsequent analysis. All analyses were based on the relative angle of the animal's sound production; thus, it only indirectly considered animal body movement.

2.5. Statistical analysis

Due to the unequal sample size and unequal variance in observations across sites, we used Dunnett-Tukey-Kramer pairwise multiple comparison tests (DTK) to compare the pairwise mean of the number of clicks and the trajectory duration among the pairs of habitats and moving types using the DTK package in R-Studio (Dunnett, 1980). We bootstrapped ($N = 10,000$) parameters – number of clicks, trajectory duration, click interval – to report uncertainty on the estimates using the *boot* package in R-Studio.

A chi-square test (χ^2) was used to examine the association between: movement and habitat, movement and time of day (**Twilight** (activity around sunrise and sunset time: 5:00 a.m.–6:59 a.m., 17:00 p.m.–18:59 p.m.; **Day** (activity during day-time): 7:00 a.m.–16:59 p.m.; **Night** (activity during night-time): 19:00 p.m.–4:59 a.m.). The relation between trajectory duration and habitat type was examined by simple linear regression (LR) using the *lm* package in R Studio. Before fitting the model, trajectory duration was normalized using a log transfer.

Due to overdispersion on the number of clicks, we used a negative binomial Generalized Linear Model (GLM) to examine the relationship between the number of clicks and environmental variables using the *glm.nb* function available in the MASS package in R-Studio. Ecological variables (explanatory variables: season (November–February, March–May), habitat type, time of the day, moving type)) that controlled the number of clicks were examined using Poisson GLM by adding trajectory identification number as a random effect in the model to account for the issue of overdispersion on the dependent variable using the *glmer* function available in the lme4 package in R. We built six possible models to explain the variation of click numbers (Table 2) and used Akaike Information Criteria (AIC) to select the best model.

We estimated the overlap coefficient to examine the similarity of click-interval across space, season, and time of the day. Diel activity (the proportion of animals active throughout the day) of GRD was calculated using the time of acoustic detection. We fitted von Mises kernel density to the time of acoustic detection and estimated the overlap coefficient (with bootstrapped $N = 10,000$) to identify similarities or differences in the diel activity pattern across space, season, and time of day. The overlap coefficient was estimated using the *overlap* package in R-Studio.

Table 2

Poisson generalized linear models (GLM) showing the relationships between the number of clicks and explanatory variables. The top model (lowest AIC) shows that the number of clicks was significantly regulated by the interactions of Ganges River dolphin movement type and habitat structure.

Model	Df	AIC	Delta AIC
Number of clicks ~ Moving type*Habitat	10	14462.3	0
Number of clicks ~ Moving type	4	14463.6	1.3
Number of clicks ~ Season	2	14465.6	3.3
Number of clicks ~ Moving type + Habitat	6	14466.4	4.1
Number of clicks ~ Moving type + Habitat + Season	6	14466.5	4.2
Number of clicks ~ Moving type + Habitat + Time of day + Season	8	14467.9	5.6
Number of clicks ~ Habitat	4	14721.3	259
Number of clicks ~ Time of day	3	14730.5	268.2

Differences among parameters were considered significant when the probability (p) was equal to or less than 0.05 in all analyses.

3. Results

3.1. Trajectory characteristics and moving type

Acoustic recordings were made over 4110 h (deep pool 1405 h; confluence 1266 h; straight channel 1439 h), in which the total number of valid trajectories recorded was 1413 (confluence-99, deep pool-1042, straight channel-234) that represents a total of 861 h. The average trajectory duration of confluence (mean = 57.50 min, bias = 0.14, SE = 6.86) and deep pool (mean = 39.66 min, bias = 0.002, SE = 3.40) was substantially higher than for the straight channel (mean = 15.05 min, bias = 0.002, SE = 1.54, Fig. 2). We detected pairwise differences in the trajectory duration among all habitat pairs, except deep pool and confluence (DTK test, $p = 0.05$). We found habitat type to be a significant contributor to the trajectory duration (LR, $R^2_{Adj} 0.04$, $F = 33.55$, $p < 0.001$).

Disproportionate distribution of movement types across habitats reveals that movement type is dependent on habitat ($\chi^2 = 123.17$, $p < 0.001$; Fig. 3). Average trajectory duration of diving was longer than remaining stationary and traveling, respectively (Fig. 2, Table 3). Trajectory duration differed among all the movement type pairs (DTK test, $p = 0.05$). The proportion of each movement type was evenly distributed across time of the day ($\chi^2 = 0.89$, $df = 4$, $p = 0.92$, Fig. 3).

Average number of clicks was considerably higher in the deep pool than in the confluence and straight channel (Fig. 4, Table 3). The number of clicks was higher for diving than stationary and traveling behaviors (Table 3). Average number of clicks differed among all pairs of habitat and movement types (DTK, $p = 0.05$). The number of clicks was higher during nighttime ($N = 607$, mean = 100.31, 95% CI 22.89) compared to daytime ($N = 540$, mean = 171.33, 95% CI 70.56) and twilight hours ($N = 228$, mean = 136.40, 95% CI 36.29). The number of clicks did not differ among any pairs across time of day (DTK, $p > 0.05$).

Our results showed no relationship between number of clicks and click interval (GLM, $\beta = -1.002$, SE = 0.03, $Z = -0.07$, $p = 0.94$). Variation in the number of GRD clicks was controlled by the additive effect of habitat and movement type (Table 2); however, habitat type had a weaker effect than movement type. While GRD shift from traveling to diving behaviour, the number of clicks increases ($\beta = 3.78$, SE = 0.73, $Z = 1.82$, $p = 0.05$) and decreases when stationary ($\beta = -0.70$, SE = 1.02, $Z = -0.33$, $p = 0.73$). The second-best model included only movement type with a slight decrease in AIC without habitat type.

A shorter average click-interval length was recorded in straight channel ($N = 234$, mean = 31.80 ms, 95% CI 1.41) than in deep pool ($N = 1042$, mean = 33.38 ms, 95% CI 0.85) or confluence ($N = 99$, mean = 51.54 ms, 95% CI 3.69) habitats, respectively. Average click-interval duration differed among all pairs of habitats, except for straight

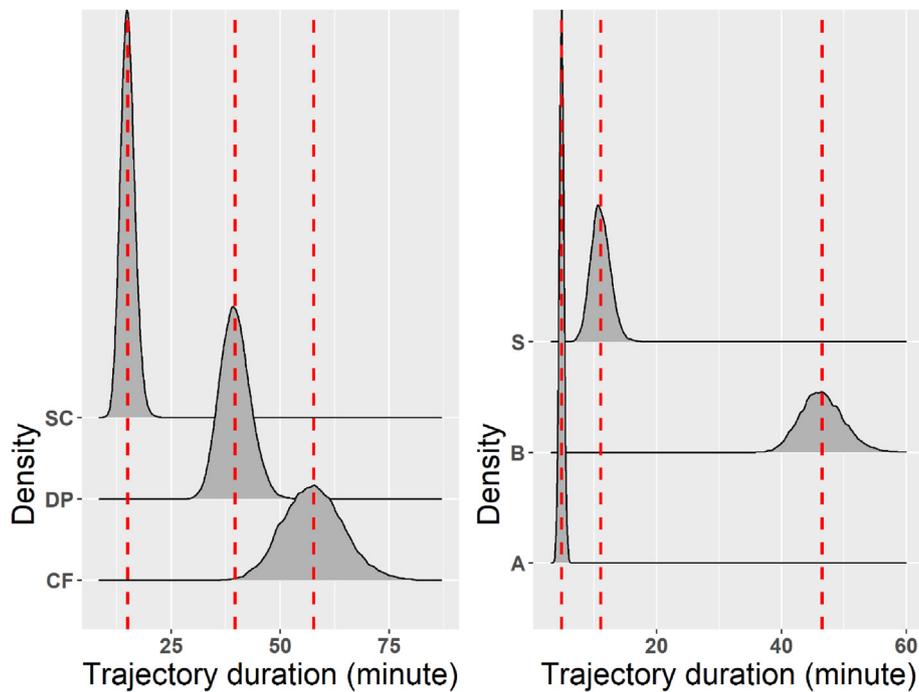


Fig. 2. Density graphs showing trajectory duration distribution across habitats (confluence (CF), deep pool (DP), and straight channel (SC)) and moving types (A-movement A, B-movement B, S- staying) depict significant differences in the trajectory duration across space and moving type indicating different preferences and behaviors adopted by Ganges River dolphins across habitats. The dashed red vertical line indicates the average trajectory duration.

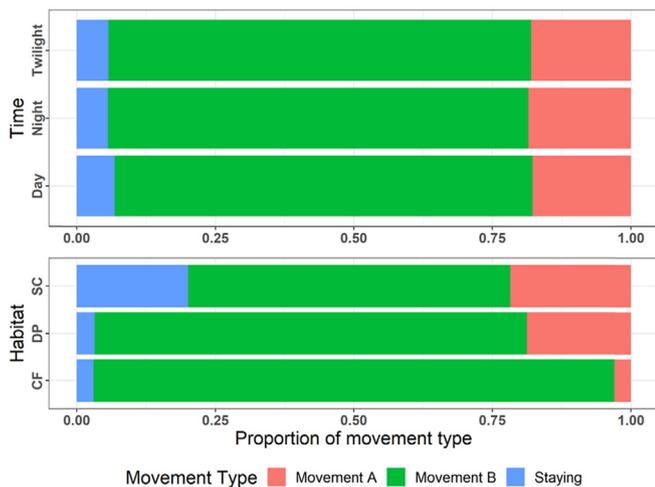


Fig. 3. Moving type (movement A-traveling; movement B- diving)) distribution across habitat and time of the day (twilight, day, and night) depicts significant differences in the moving type of Ganges River dolphins across the habitat but not during the day length. This pattern indicates variability in Ganges River dolphin behavior is habitat-driven.

channel and deep pool (DTK, $p = 0.05$). Average click-interval duration was longer while diving ($N = 1040$, mean = 35.08 ms, 95% CI 0.95) than when remaining stationary ($N = 85$, mean = 32.74 ms, 95% CI 2.14) or traveling ($N = 250$, mean = 32.24 ms, 95% CI 1.45). The average click intervals differed only between traveling and diving, except for the pairs of traveling and stationary and diving and stationary (DTK, $p = 0.05$). The average click interval of all movement types was higher in the deep pool (except diving) compared to straight channel and confluence, respectively. The estimated average acoustic sensing range of GRD was 25.817 m (range = 0.64874.55, 95% CI 25.24,826.40). The higher average sensing distance was recorded in confluence ($N = 99$, mean =

Table 3
Characterization of trajectory duration (minutes) and number of clicks by habitat and movement type of Ganges River dolphins.

	Habitat type			
	CF	DP	SC	Overall
	(N = 99)	(N = 1042)	(N = 234)	(N = 1375)
Trajectory duration (min)				
Mean (SD)	57.5 (67.3)	39.7 (111)	15.1 (23.1)	36.8 (98.9)
Median [Min, Max]	30.4 [0.410, 352]	11.4 [0.173, 1960]	7.73 [0.402, 220]	11.4 [0.173, 1960]
Number of clicks				
Mean (SD)	95.7 (151)	155 (648)	55.9 (113)	134 (569)
Median [Min, Max]	41.0 [6.00, 909]	32.0 [1.00, 15,900]	26.5 [6.00, 1280]	31.0 [1.00, 15,900]
Acoustic movement type				
	Moving A (N = 250)	Moving B (N = 1041)	Staying (N = 84)	Overall (N = 1375)
Trajectory duration (min)				
Mean (SD)	4.74 (4.30)	46.5 (112)	11.0 (14.0)	36.8 (98.9)
Median [Min, Max]	3.52 [0.173, 39.3]	16.4 [0.287, 1960]	6.89 [0.455, 69.1]	11.4 [0.173, 1960]
Number of clicks				
Mean (SD)	16.8 (17.5)	171 (649)	28.1 (40.3)	134 (569)
Median [Min, Max]	11.0 [6.00, 187]	45.0 [1.00, 15,900]	12.5 [6.00, 228]	31.0 [1.00, 15,900]

38.66 m, SE = 1.39) than in deep pool ($N = 1042$, mean = 25.03 m, SE = 0.32) and straight channel ($N = 234$, mean = 23.85 m, SE = 0.53) habitats, respectively. A marginal difference was recorded on sensing distance across movement types (A: $N = 250$, mean = 24.19 m, SE = 0.55; B: $N = 1041$, mean = 26.30 m, SE = 0.36; S: $N = 84$, mean = 24.57 m, SE = 0.81).

The average click interval was 34.43 ms (95% CI range 26.61835.96), with a moderate degree of overlap of click intervals across movement and habitat types (Fig. 5). Considerable overlap was observed among all pairs of movement types (traveling–diving: estimate = 0.77, bias = -0.01, SE = 0.03; traveling–stationary: estimate = 0.64, bias = -0.03, SE = 0.06;

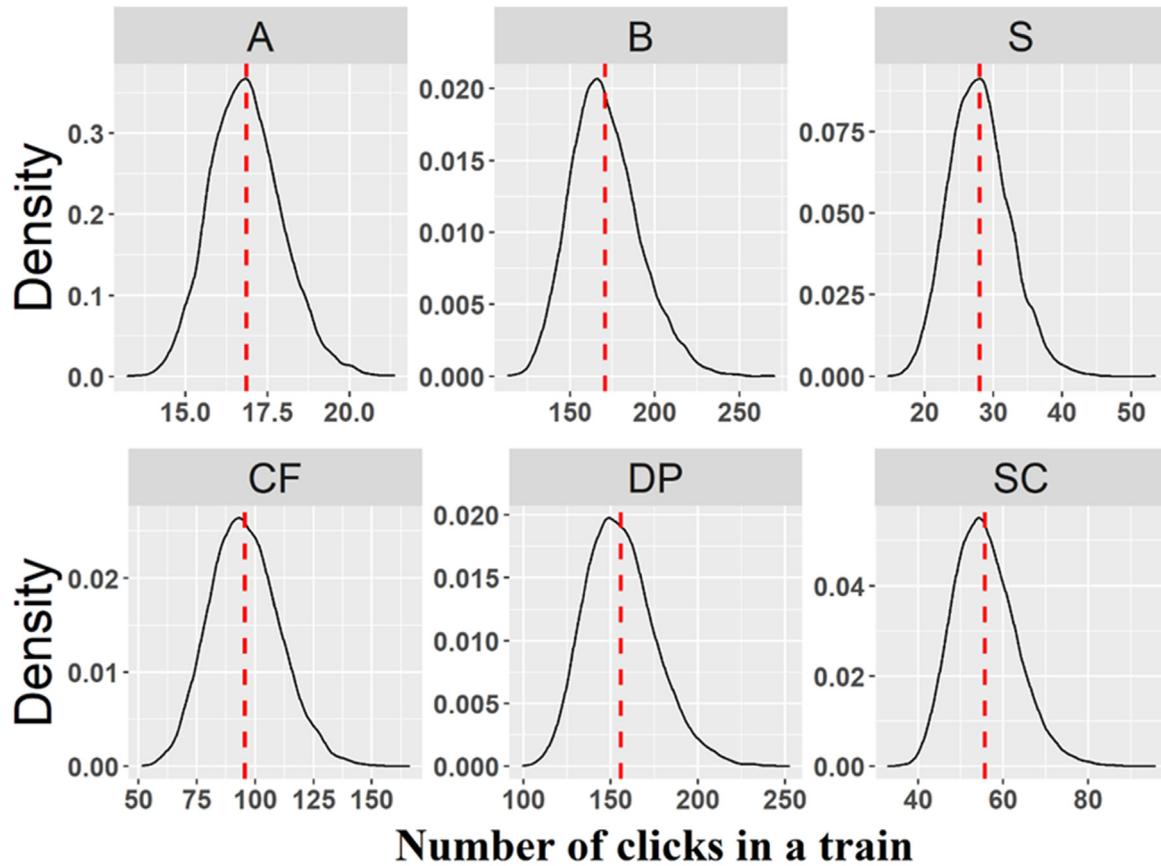


Fig. 4. The number of clicks distribution in a train across movement (A-movement A, B-movement B, S- staying) and habitat types (confluence (CF), deep pool (DP) and straight channel (SC)). This graph reveals differences in the number of clicks over space and moving type, indicating that Ganges River dolphins behavioral activity varies in response to spatial heterogeneity. Further, the considerable variation in click numbers across moving types suggests different behavioral activity adopted by Ganges River dolphins. The red vertical dashed line indicates an average click number.

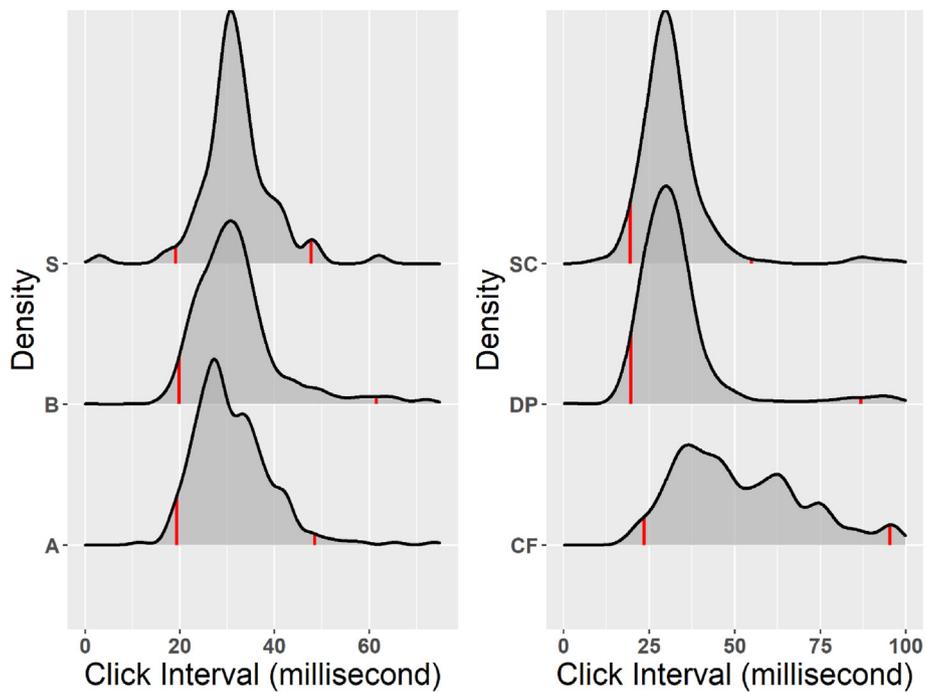


Fig. 5. The click interval across movement (A-movement A, B-movement B, S- staying) and habitat types (confluence (CF), deep pool (DP) and straight channel (SC)). High overlap of density distribution of the click-interval across space and moving type indicates similar click-interval distribution of Ganges River dolphin bio-sonar clicks across space and moving type. The vertical red lines indicate lower and upper 95% confidence intervals of click interval.

diving-stationary: estimate = 0.69, bias = -0.03, SE = 0.05). Across habitats, the pair of deep pool-straight channel (estimate = 0.81, bias = -0.03, SE = 0.03) had substantially more overlap of click intervals compared to confluence-deep pool (estimate = 0.28, bias = -0.001, SE = 0.02) and confluence-straight channel (estimate = 0.26, bias = -0.008, SE = 0.03). Season did not influence the duration of click intervals (LR, $F = 0.18$, $R^2_{Adj} = -0.0005$, $p = 0.66$).

3.2. Diel activity pattern

Diel activity of GRD substantially overlap across space (straight channel-deep pool: estimated overlap = 0.841, bias = -0.015, SE = 0.029; straight channel-confluence: estimated overlap = 0.783, bias = -0.016, SE = 0.042; deep pool-confluence: estimated overlap = 0.869, bias = -0.024, SE = 0.031) (Fig. 6) and season (seasonal overlap: estimated overlap = 0.838, bias = -0.0162, SE = 0.028) (Fig. 7). Across all habitats, GRD consistently demonstrated bimodal nocturnal activity with peaks before sunrise and after sunset, avoiding human activity (mostly fishing activity) during the day for the majority of time (Figs. 6 and 7). But in confluences, GRD showed trimodal peaks, with a short duration highest peak immediately during afternoon and two peaks before sunrise and after sunset.

Seasonal diel activity patterns of GRD displayed similar nocturnal activity with bimodal peaks before sunrise and after sunset. However, the diurnal density of activity was substantially less in the post dry season (March-May) compared to peak dry season (November-February) (Fig. 7). A higher proportion of activity was recorded during night hours ($N = 1238$, mean = 0.450, 95% CI 0.43180.469) compared to twilight ($N = 437$, mean = 0.158, 95% CI 0.14580.173) and day hours ($N = 1075$, mean = 0.390, 95% CI 0.37280.409).

4. Discussion

Trajectory duration and the number of clicks in a train differed among movement types (Figs. 2 and 4), which supported our assumptions of the movement classifications based on echolocation recordings. We confirm that movement A refers to traveling, and movement B indicates diving or surfacing activity in a particular area for a long duration. A substantial difference in trajectory duration across habitats indicated that GRD use habitats disproportionately. GRD appear to occupy deep pool and confluence habitats for longer periods of time, possibly for diving and stationary purposes. Further, we found that movement type is unevenly

distributed across habitats but not across the time of day, which suggested that variability in GRD behaviors may be regulated by habitat structure irrespective of the sunrise and sunset time or the time of day. This result is consistent with the interpretation that variations in light intensity did not influence the GRD's echolocation behaviors (Herald et al., 1969). Our results also predict that habitat type correlates with trajectory duration.

As our results reveal that habitat heterogeneity plays an influential role in shaping GRD behavior, a previous study emphasized that habitat heterogeneity may improve survival and recruitment in species by mediating life-history strategies in complex riverine ecosystems (Stoner, 2009). The use of deep pools and confluences by riverine dolphins (Herald et al., 1969; Pavanato et al., 2019) has been reported frequently, but the site specific underlying ecological significance remains unexplored. In a few studies, such habitats were reported to benefit river cetaceans due to their high biological productivity, which in turn increases prey availability and facilitates easier prey capture (Smith et al., 1998; Biswas and Boruah, 2000). However, the primary underlying mechanism for selecting such hydro-physical habitats is likely associated with improved diving physiology facilitated by suitable hydro-physical attributes of such habitats (Skrovan et al., 1999; Paudel and Koprowski, 2020a). As the diving and swimming activity of river cetaceans is energetically costly, GRD may access certain habitats to conserve energy and limit blood oxygen loss to ultimately improve their foraging efficiency by extending the duration of their dive (Skrovan et al., 1999; Williams et al., 1999). Our model shows that underwater behavior at a particular point is heavily influenced by habitat structure, so hydro-physical attributes of habitat, such as larger cross-sectional area combined with appropriate depth and velocity, likely enhance the energetic efficiency of dolphins by maximizing the useable area (Williams et al., 1999).

Habitat-driven behaviors and disproportionate distribution of trajectory duration across space are indications that riverine cetacean persistence require productive and diverse habitats. There is past evidence of patchy occupancy of GRD in the region (Smith et al., 1998; Paudel et al., 2015a,b) which provides further support for the notion that diverse habitats are necessary for river cetaceans to persist. Similar heterogeneity in habitat was reported in common bottlenose dolphins (*Tursiops truncatus*) and Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) (Ingram and Rogan, 2002). The majority of small cetaceans in the western Ligurian Sea and southwestern Mediterranean short-beaked common dolphins (*Delphinus delphis*) also exhibited specific preferences

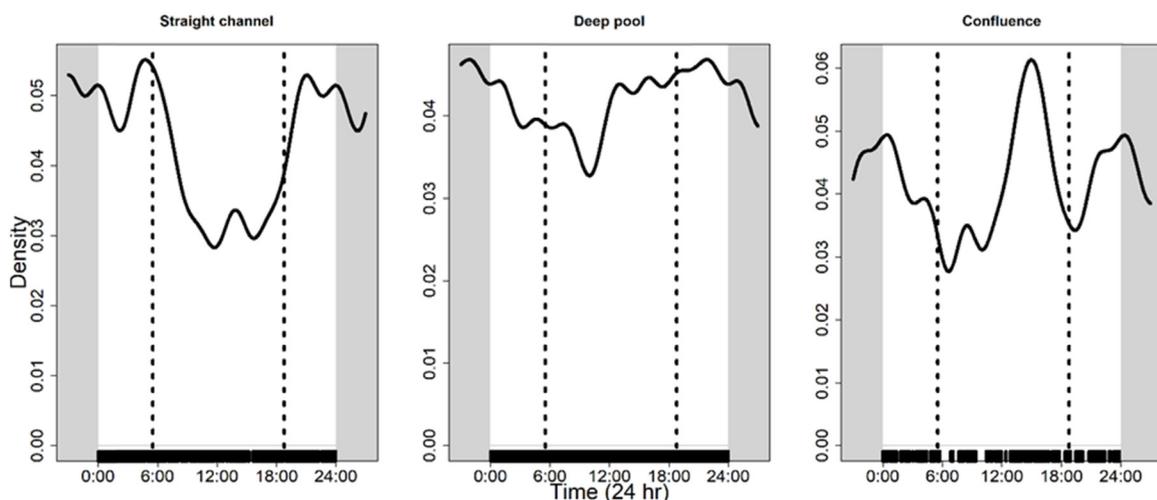


Fig. 6. Diel activity patterns (density plot of the active period) of Ganges River dolphins across habitats throughout the survey period (six months). The diel activity patterns indicate that Ganges River dolphins are highly active during nighttime hours, avoiding daytime hours when human disturbances are highest. The black dashed lines indicate sunrise (5:30 a.m.) and sunset (18:30 p.m.) times, respectively, on a 24-h time scale.

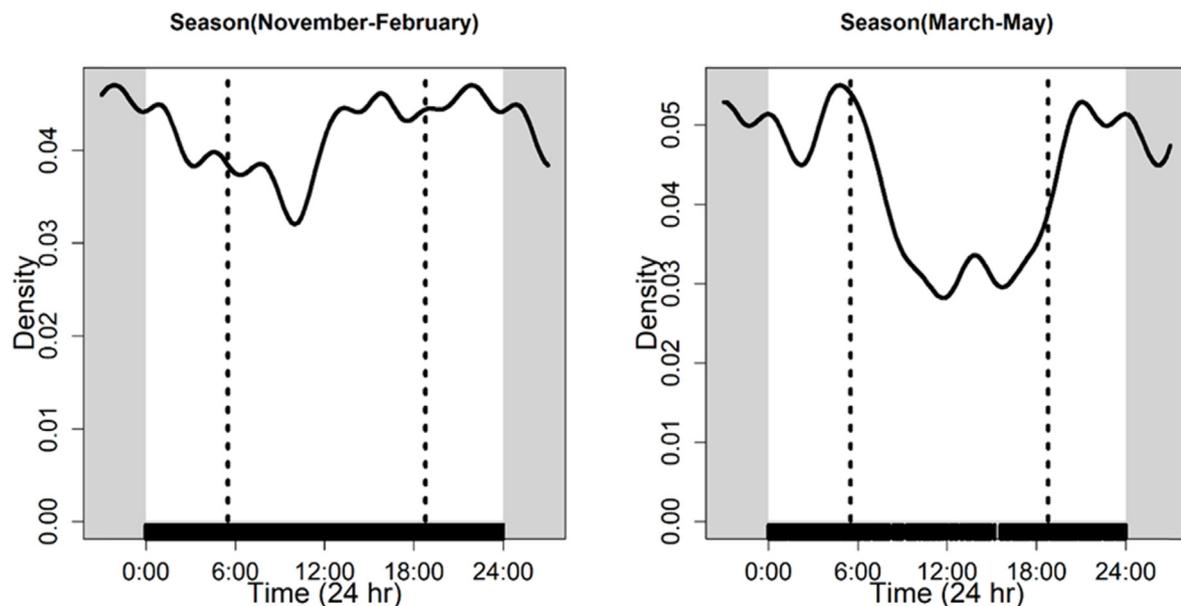


Fig. 7. Seasonal diel activity patterns of Ganges River dolphins indicate that daytime avoidance intensified during the late dry season (March–April) compared to peak dry season (November–February). The black dashed lines indicate sunrise (5:30 a.m.) and sunset (18:30 p.m.) times, respectively, on a 24-h time scale.

for physical habitats (Azzellino et al., 2008; Cañadas and Hammond, 2008). Such specific habitat preferences were often linked to heterogeneity in habitats (Samuel et al., 1985). However, incorporating prey availability information with acoustics data can help to provide a better understanding of the underlying drivers of dolphin behavior.

As human pressure increases and riverine habitats are colonized, exploiting diverse habitats and modifying behaviors indicate a degree of plasticity of a species in an altered environment while adjusting to human-induced disturbance. However, such behavioral responses to altered environments may be maladaptive or insufficient to offset the animal's fitness loss (Wong and Candolin, 2015). A recent study indicated that increases in ambient noise level in the riverine ecosystem altered GRD acoustic activity, which may induce metabolic stress (Dey et al., 2019). Even though habitat-driven variation in behavioral patterns is likely to improve their persistence under human pressure, this will likely affect the processes that regulate their population size. The declining population size and recent increase in bycatch of riverine cetaceans indirectly indicate the effects of anthropogenic effects in the long term (Sinha et al., 1992; Dewhurst et al., 2020). Thus, this finding highlights the importance of heterogeneity in the spatial environment for riverine dolphin persistence along with mitigating deleterious impacts on population size. Maintenance of a natural flow regime along with habitat management (creating semi-natural lateral habitats) and protection may offer diverse physical habitats, allowing cetaceans to persist. A similar recommendation to balance the needs for GRD conservation and water based-development was proposed in Bangladesh (Smith et al., 1998).

Biosonar clicks dramatically changed when movements shifted from one mode of locomotion to another, such as traveling to foraging (Au, 1993; Rasmussen et al., 2013). In line with this finding, our model also predicted that behavior controls the number of clicks in a train. This result further supports our movement classification hypothesis as well as the findings of previous studies. We also noticed appreciable overlap of the click-interval across space, season, and time of the day. We suggest considering the number of clicks and trajectory duration is a more reliable indicator than click-interval to classify underwater behaviors of riverine cetaceans. In addition, understanding the pattern of click numbers and click intervals across search, approach, and catch phases of cetacean clicks could provide additional perspectives on foraging behaviors (see details in Rasmussen et al. (2013) for more information about phases of clicks).

As fishing activity increases during daylight hours at our study site (Paudel et al., 2020b), diel patterns indicate that human activity may influence GRD behavior and activity such that they occur when anthropogenic activities are lower (Figs. 6 and 7). Clicks are higher during the night, and dolphin activity peaks before sunrise and after sunset, showing GRD undergo diel shifts at night in response to human disturbances. Further, avoidance of humans becomes more intense during the post-dry season (March–April, Fig. 7) when the pressure from artisanal fishing is accelerated (Paudel and Koprowski, 2020a). Similar results were reported by a recent study that examined the temporal activity overlap between GRD and artisanal fishing in the same study area (Paudel et al., 2020b). The study found inverse peaks in GRD activity, reporting that small cetaceans might be avoiding peaks in artisanal fishing activity. Combining acoustic data with prey information, however, may help unravel the factors that govern the nighttime foraging behavior of GRDs in future studies.

Several studies have hypothesized night foraging and echolocation clicks in dolphins to be related to the foraging activity of vertically migrating prey (Sinha et al., 1992; Soldevilla et al., 2010; Sasaki-Yamoto et al., 2012; Cascão et al., 2020). Our results indicating that the night-time foraging activities of riverine cetaceans are likely linked to the consequences of human activities, which shift river dolphin activity towards refuge during the day due to day foraging being riskier than at night. Several recent entanglement incidents in the study area have resulted in dolphin deaths, indicating a negative interaction between fishing and GRD (Paudel and Koprowski, 2020a). Recent findings from a global study that examined the effects of humans on mammalian daily patterns also found that humans significantly altered mammalian nocturnality and daily patterns (Gaynor et al., 2018). Thus, such variation in temporal responses exhibited by river cetaceans in the Anthropocene may alter their diets towards prey that are more accessible at night. Although coexistence between fisheries and riverine cetaceans may be enhanced by increased nocturnal activity, the effects induced by the diel shift in response to human presence may be considerable, and could compromise reproduction and survival (Gaynor et al., 2018). Incorporating knowledge of freshwater cetaceans temporal dynamics into conservation planning through developing temporal zonation seems imperative in the Anthropocene (Paudel and Koprowski, 2020a). Thus, regulating human behavior and resource exploitation with respect to the diel activity or time/habitat specific behavioral responses of cetaceans

may be a means of improving their survival and recovery in areas of heavy human disturbance.

Foraging in close proximity to human activity and fishing gear poses a great risk to cetaceans. Consequently, bycatch has become the leading direct and immediate threat to many riverine dolphin populations around the world. Appropriate conservation measures to mitigate the most common and documented small cetacean's conservation issue-fisheries and cetaceans interactions-have been highlighted globally (Bearzi et al., 2019). Our previous study also revealed that close approaches to GRD by humans, particularly by fishers, likely impede social, feeding, and resting behaviors of GRD (Paudel and Koprowski, 2020a). Similar risks were reported for Indo-Pacific bottlenose dolphins (Cribb et al., 2013), and recently, increased bycatch of GRD in small-scale fisheries has occurred (Dewhurst et al., 2020; Paudel and Koprowski, 2020a). Our identified acoustic sensing distance could facilitate development of regulations by defining minimum approach distance to riverine cetaceans that would minimize potential adverse biological effects to small cetaceans from human disturbances.

5. Conclusions

While many studies have been conducted on GRD echolocation clicks (Andersen and Pilleri, 1970; Sugimatsu et al., 2008, 2011; Sasaki-Yamamoto et al., 2012), the underwater behaviors and diel activity patterns in response to spatial and temporal changes are still poorly understood. To the best of our knowledge, this is the first study that has examined the effect of spatial and temporal variations in click trains emitted by GRD on behavioral and activity patterns. Using GRD, our research supports and informs conservation initiatives for endangered freshwater cetaceans. For example, it is important to identify, delineate, and protect cetaceans' priority habitats (spatial heterogeneity), to regulate activity overlaps so that river dolphins' interactions with the fishing industry are minimized, and to limit humans or fisheries' proximity to river dolphins by using sensing distances. In this study, we demonstrate that environmental heterogeneity plays a significant role in the natural history of riverine cetaceans, enhancing survival and foraging efficiency. Consequently, adjusting to different habitats by widening behavioral plasticity is likely a common behavior among riverine cetaceans in order to maximize their fitness in human-modified habitats. This adaptation may extend their persistence in the short term, however, human disturbances may expose GRD to different morphological and physiological stresses. Identifying priority habitats and defining temporal zoning along with protecting travel corridors that connect geographically proximate protected areas by developing appropriate regulations might help to conserve viable populations of small riverine cetaceans in highly regulated rivers of the region.

Ethical statement

This research was conducted under a research permit issued to the principal author of this paper by the Department of National Parks and Wildlife Conservation (DNPWC), Government of Nepal. All the observation procedures comply with regulations developed by the DNPWC.

Author contributions

Shambhu Paudel: Conceptualization, Formal analysis, Data curator, Funding acquisition, Project Administration, Methodology, Writing-original draft. **John L. Koprowski:** Conceptualization, Writing-reviewing & editing. **Usha Thakuri:** Project administration, Investigation. **Yukiko Sasaki-Yamamoto:** Methodology, Software. **Shiro Kohshima:** Writing- Reviewing and Editing.

Declaration of competing interests

We declare no known, financially competing interests or personal

relationships that could potentially influence the work reported in this paper.

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Further reading

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