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Ecological and environmental factors affecting the foraging activity of the White-bellied Heron *Ardea insignis* (Hume, 1878) in Bhutan

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Summary

White-bellied Heron *Ardea insignis* (WBH) is critically endangered, but we lack data on many aspects of its basic ecology and threats to the species are not clearly understood. The goal of this study was to analyse WBH foraging microhabitat selection, foraging behaviour, and prey preferences in two river basins (Punatsangchhu and Mangdechhu) in Bhutan which are likely home to one of the largest remaining populations of WBH. We also explored the relationship between the relative abundance of the WBH and prey biomass catch per unit effort within four foraging river microhabitats (pool, pond, riffle and run). Prey species were sampled in 13 different 100-m thalweg lengths of the rivers using cast nets and electrofishing gear. Riffles and pools were the most commonly used microhabitats; relative abundance was the highest in riffles. The relative abundance of WBH and prey biomass catch per unit effort (CPUE) also showed a weak but significant positive correlation ($r_s = 0.22$). The highest biomass CPUE was observed in riffles while the lowest was found in the ponds. From the 97 prey items caught by the WBH, 95% of the prey were fish. The WBH mainly exploited three genera of fish (*Garra*, *Salmo*, and *Schizothorax*) of which *Schizothorax* (64%) was the most frequently consumed. This study provides evidence in support of further protection of critical riverine habitat and fish resources for this heron. Regular monitoring of sand and gravel mining, curbing illegal fishing, habitat restoration/mitigation, and developing sustainable alternatives for local people should be urgently implemented by the government and other relevant agencies. Further study is also required for understanding the seasonal variation and abundance of its prey species in their prime habitats along the Punatsangchhu and Mangdechhu basins.

Keywords: diet, foraging ecology, White-bellied Heron, *Ardea insignis*, *Schizothorax*, Bhutan

Introduction

The White-bellied Heron *Ardea insignis*, hereafter WBH, is classified as 'Critically Endangered' with an estimated global population of 50–249 mature individuals (BirdLife International 2018), and a relatively restricted range. However, recent counts can only account for approximately

60 individuals: 28 in Bhutan, 23 in Myanmar, eight in India and one in China (Price and Goodman 2015). It is now extinct in Nepal and possibly extinct in Bangladesh (BirdLife International 2018). The causes of its population decline and extirpation are largely undocumented, but attributed to rapid loss and degradation of its natural habitat which is mostly caused by development projects such as hydropower construction and mining activities, illegal fishing, deforestation and human-induced forest fires across the range countries (Kushlan and Hafner 2000, BirdLife International 2018, Dema *et al.* 2020, WWF 2019).

The WBH is probably a specialist piscivore which spends its daylight hours along riverbanks comprised typically of sand and gravel bars, hunting for fish. The only evidence about the diet of the WBH was from a single stomach analysis that contained crayfish (Baker 1926). Hancock and Kushlan's (1984) examination of its bill morphology predicted that they feed on large-sized fishes, amphibians, small mammals, and reptiles, while RSPN (2011) supposed that it might feed on many fish species.

The WBH breeds in a conifer *Pinus roxburghii* as well as broad-leaved trees (Acharja 2020, Khandu *et al*. 2020a). Nesting takes place in the temperate forest within 400–1,430 m asl (Acharja 2020). Also, they have been reported in a wide variety of wetlands, lakes, marshes, and large or small rivers with sand and gravel bars (Choudhury 2000, King *et al.* 2001, RSPN 2011). The paucity of ecological information such as diet and preferred feeding habitats has impeded the effective implementation of conservation actions (Price and Goodman 2015, Heath 2019). Given the current trend in prey depletion due to illegal fishing and aquatic habitat loss and degradation, an assessment of prey types is crucial for ensuring the availability and abundance of preferred prey in their feeding habitats, determining the characteristics of possible future artificial weirs for enhancing feeding habitats as well as providing baseline diet information for captive-bred animals.

We aimed to understand the relationship between the relative abundance of WBH in four different river microhabitat types relative to prey biomass. We predicted that WBH would prefer microhabitats with a varying stock of prey types and biomass, as seen in *Egretta garzetta* which showed a microhabitat preference based on prey composition (Wong *et al.* 2000). We also investigated the types of prey species and sizes preferred by the WBH and factors affecting their foraging activity. We predicted that WBH would prefer prey types and sizes based on profitability and availability (Maccarone and Brzorad 2002). We hypothesized that microhabitat type, season, time of the day and bird age would affect the foraging activity of the WBH.

Methods

Study area

Bhutan contains nearly 50% of the known WBH population and the greatest number of breeding pairs compared to other range countries. The study was carried out in two major river basins; Punatsangchhu (chhu = river) basin (27°7′23.55″N, 90°4′13.44″E) falling within the jurisdiction of Punakha, Wangduephodrang and Tsirang districts and Mangdechhu basin (27°9′47.88″N, 90°39′49.33″E) of Zhemgang district, in Bhutan (Figure 1). These are the two major habitats where more than 95% of Bhutan's known population of WBH occurs, yet both river basins have been subjected to four large hydropower projects and numerous small to large scale sand and gravel mining activities. From a single agrometeorological station located in Tsirang district about 30 km from the farthest transect, the total annual rainfall recorded was 1,359 mm, and the temperature ranged from 12°C to 21°C (NCHM 2017). Punatsangchhu basin is an important habitat for large numbers of migratory waterbirds such as *Tadorna ferruginea* and *Phalacrocorax carbo* as well as threatened and near-threatened species such as *Aythya nyroca* and *Haliaeetus leucoryphus*. *Tetrameles nudiflora* and *Syzygium* spp. dominate the riverine forest vegetation found at an elevations of < 370 m along the Punatsangchhu (Ghemiray 2016). Mangdechhu basin falls within Zhemgang district which contains the main habitat of the WBH selected for this study. From a single agrometeorological station located in Zhemgang district near the center of the sampling

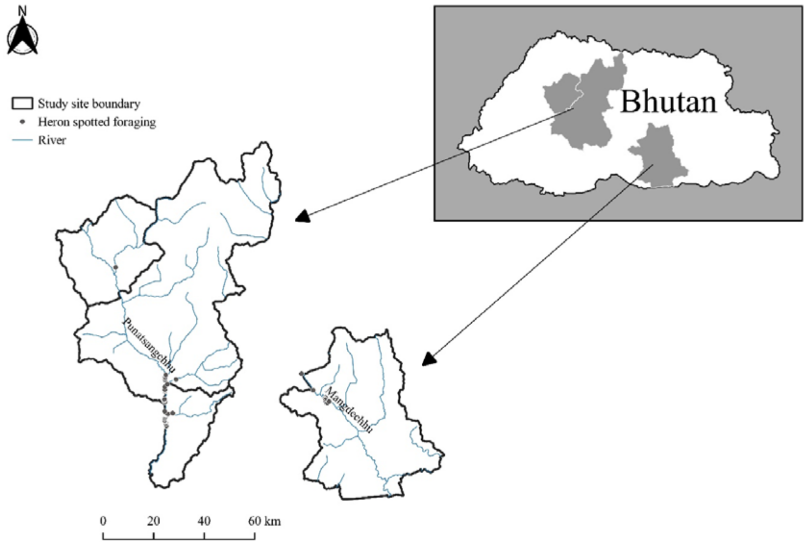

Figure 1. Location of the Punatsangchhu (left) and Mangdechhu (right) basins, Bhutan.

transect, total annual rainfall was 1,438 mm, and the temperature ranged from 14°C to 21°C (NCHM 2017). It supported 10 globally threatened bird species including *Tragopan blythii*, *Aceros nipalensis* and *Spelaeornis caudatus* (Dorji 2011). Mixed broadleaved and conifer forest with *Daubanga grandiflora, Syzygium formusa and Pinus roxburghii* as dominant species are found along this basin (Tshering 2016).

Foraging activity

We conducted surveys for ~ 300 days (25 days/month) from 25 February 2018 until 10 January 2019 to locate and observe WBH. An area count survey (Kushlan 2011) with a systematic approach (Dorge *et al.* 2014, Fu *et al.* 2016) was employed to locate the focal species. With the help of two to four experienced local birdwatchers, we scanned both sides of small and large rivers where the WBH was known to forage, between 06h00 and 17h00. Riverbanks and roads running parallel to rivers were used as transects, covering an average of 4 km along riverbanks on foot and 30 km along roads by vehicle per day. Continuous focal animal sampling was chosen to observe the foraging activity due to its suitability for the study and minimal bias (Altmann 1974, Rose 1999). Only 2-hr observations were videoed per individual per day due to limited battery power. After spotting a bird, observations were made from a hide which was ≥ 100 m from the focal individual considering the wariness of the bird. Binoculars (10 x 42) and a 20–60x monocular spotting scope were used to observe the birds. Foraging bouts were recorded on a prepared worksheet and simultaneously filmed using a 500-mm zoom lens with a 2x converter for future reference and re-evaluation of the data. All observations were made under favourable weather conditions (no rain or strong wind).

The independent variables collected included microhabitat type, season, time of the day and age of the bird. Adapting the habitat classification from Fasola (1994) and Campos and Lekuona (2001), we grouped the foraging habitat into four microhabitats (pool, pond, riffle, and run; Figure 2). A pool was defined as shallow to deep water (0.5–1 m) with a smooth surface and low average velocity of ~ 0.15 mps. Rate of flow or velocity was determined through a float method following Michaud and Wierenga (2005). A pond was defined as a naturally formed temporary water body along the riverbank which was not connected directly to the main river. The water was mostly static and relatively shallow (< 0.5 m). Riffles were defined as shallow water usually consisting of multiple

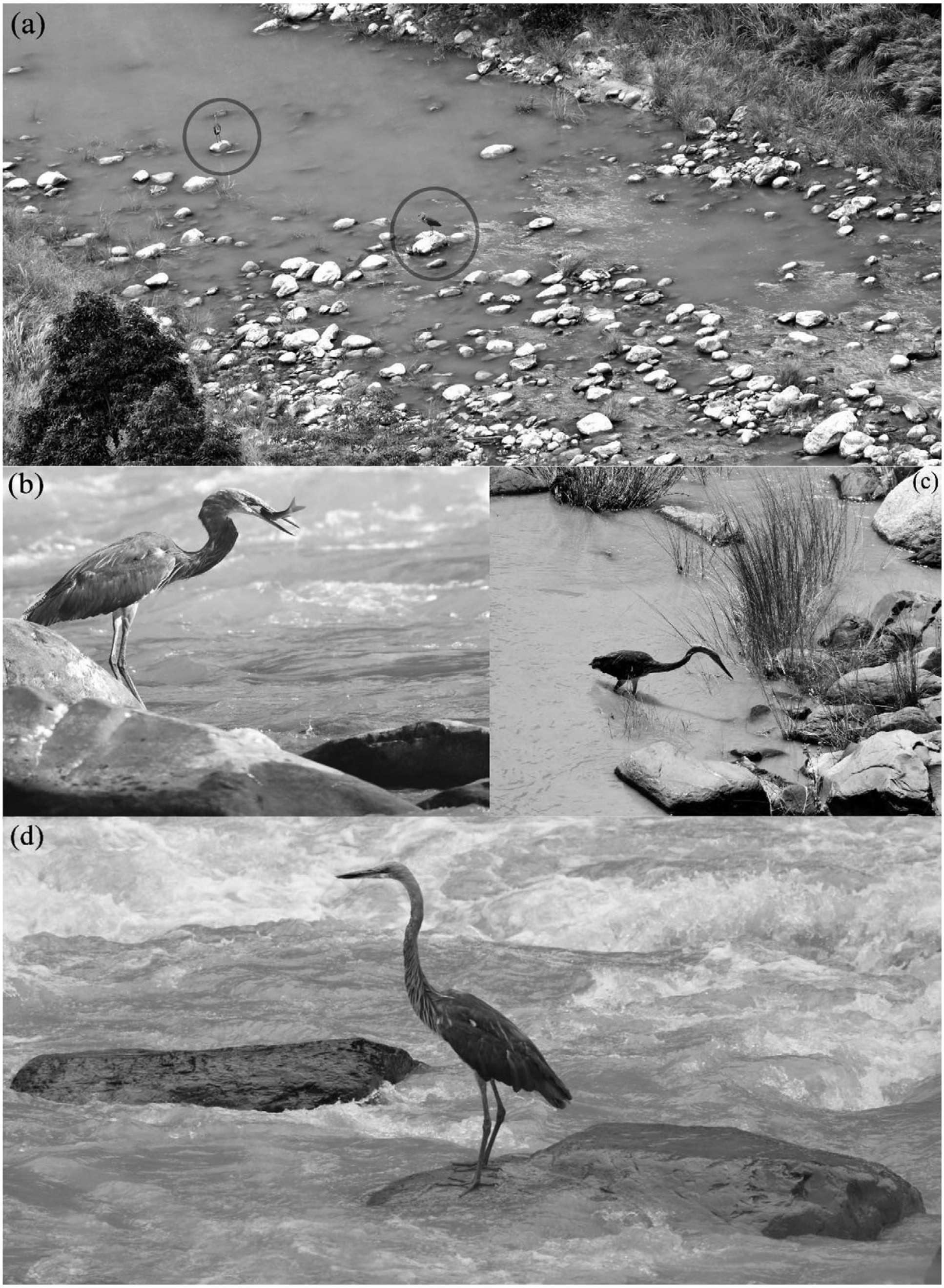

Figure 2. Four microhabitat types used by White-bellied Herons: (a) A riffle with two herons (circled) actively foraging, (b) A pool with a heron grasping a fish (*Schizothorax richardsonii*), (c) A pond with a heron's head bent forward and (d) A run with a heron standing and waiting for prey.

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channels with depth (0.2–0.5 m) and moderate average velocity (0.25 mps) agitated by rocks. Runs were defined as faster running water with higher average velocity (0.34 mps) and greater depth (> 1 m) typically at the center of main river channels. We grouped our observations into four seasons prevalent in Bhutan: winter (December–February), spring (March–May), summer (June–August) and autumn (September–November). Time of day was divided into three periods: morning (06h00–10h00), midday (10h01–14h00), and afternoon (14h01–16h00). WBH age was grouped into adults and juveniles. Adult WBH have more extended lace-like plumes on the nape than the juveniles (BirdLife International 2018). The juveniles have shorter white scapulars than adults. The adults have a white underbelly while juveniles have a brownish underbelly. Sex determination was not possible to infer in the field due to an innate lack of dimorphism.

Microhabitat use and biomass catch per unit effort (CPUE)

The foraging habitat use was determined by direct observation of the WBH in each microhabitat from our daily surveys. Thus, the relative abundance of the WBH in each microhabitat was estimated by dividing the number of observations of WBH in each microhabitat by the total observations of WBH in all microhabitats (Jing *et al.* 2007, Gyimesi *et al.* 2012). The CPUE (g/h) of each species of fish caught during the sampling period was calculated by dividing the total catch in biomass (g), by total sampling effort (h) (Ghosh and Biswas 2017).

Prey availability

Fish prey sampling was carried out in both Mangdechhu and Punatsangchhu basins. Thirteen different 100-m thalweg lengths approximately 500 m from where the WBH was sighted foraging were randomly selected for fish sampling, following the methods of Arunachalam (2000) and Johnson and Arunachalam (2009). Fish sampling was carried out on 18 different days with the help of local fishermen and field assistants. Cast nets (10 and 20 mm mesh) and electrofishing gear (6 V) were used in different microhabitats to reduce bias arising due to the type of gear used (Ghosh and Biswas 2017). Cast nets and electrofishing gear were employed for a total of 18 days (5 hrs/day on average) equally in the four microhabitats as much as possible. Fish sampling was carried out when the herons were not using the immediate area to minimize human disturbance. The caught fish were counted, measured (total length, girth, and weight) and released after two hours to prevent double counting (Dorji 2016). Fish species identification was carried out with the help of the published checklist of fishes from the local regions (Gurung *et al.* 2013, NRCRLF 2017) and photos were taken to further validate their identification with the help of an experienced ichthyologist.

Based on our field observations, WBH exhibit foraging behaviours similar to other herons. Stand and wait is a common behaviour where the bird stands at one location typically lasting more than five minutes with its neck either retracted or fully erect. Walking slowly or stalking is also exhibited frequently by the WBH while scanning for potential prey. Hopping or foot paddling are seldom employed. WBH catch prey through both impaling as well as grasp capture. To understand the foraging activity patterns and efficiency of WBH, five variables were collected: pacing rate, striking rate, capture rate, success rate, and intake rate. For foraging details, the number of steps/min was defined as the pacing rate. The striking rate was calculated as the total number of strikes divided by total observed duration, whereas the capture rate was calculated by using the total number of captures divided by total duration of the observations. The number of prey captured per strike was defined as the success rate. Intake rate was calculated as the prey biomass consumed by the bird divided by the total observation time. A feeding attempt made to capture prey using a deliberate forward movement of the head was defined as a strike.

A volume index was adopted to calculate the relative biomass of the ingested prey by squaring the length of the prey (Sato and Maruyama 1996) since the body shape was roughly the same for almost all the fish species. Prey size was estimated in relation to the average length of the bird's bill

(16.4–19 cm) (HeronConservation 2019, RSPN 2020) and grouped into three classes small (< 10 cm), medium (10–20 cm), and large (> 20 cm), (Campos and Lekuona 1997).

Statistical Analyses

We analysed data for normality using the Shapiro-Wilk tests and found that none of the variables were normally distributed. Therefore, we chose nonparametric statistics to analyse our data. Kruskal-Wallis tests were used to analyse the feeding activity variables against their factors (microhabitat, season, and time of the day) and relative abundance with the microhabitat types. Dunn's test (with Bonferroni correction) was applied as a post-hoc test to make comparisons among the groups. For microhabitat, season and time of day, the average (± SE) values were reported following Choi and Yoo (2011). Spearman's correlation test was used to test for correlations between the relative abundance of WBH and prey biomass CPUE. Mann-Whitney U tests were used to analyse foraging activity differences between the adult and juvenile WBH. For the analysis of differences between age groups, values were reported as medians and the first and third quartiles (hereafter Q_1–Q_3) following Jakubas and Manikowska (2011). All analyses were performed using R software version 3.5.2 (R Development Core Team 2018).

Results

Feeding microhabitats

A total of 3,777 min of active foraging was observed. Each feeding bout lasted for 5–58 min. We recorded the presence of 42 runs, 42 pools, 34 riffles and 20 ponds of available microhabitat. The available microhabitats were located independently from each other although along the same longitudinal path of the river as the transects. Riffles were used most commonly with 80 feeding observations, followed by pools with 62 feeding observations. Twenty-eight feeding observations were made in ponds and only 17 in the runs. The relative habitat use of the WBH was determined from a total of 187 feeding observations completed in four microhabitats (Figure 3a). The highest relative abundance was observed in riffles (43%) followed by the pools (33%), followed by ponds (15%) and runs (9%). There was a significant difference in the use of microhabitats between pools and ponds ($\chi^2 = 253$, df = 3, $P < 0.001$), between riffles and ponds ($\chi^2 = 253$, df = 3, $P < 0.001$), riffles and pools ($\chi^2 = 253$, df = 3, $P < 0.001$), runs and riffles ($\chi^2 = 253$, df = 3, $P < 0.001$) and between runs and pools ($\chi^2 = 253$, df = 3, $P < 0.001$).

Microhabitat type was associated with significantly different pacing rates and intake rates of the WBH, but not the other measures of foraging behaviour (Table 1). There was a significantly higher pacing rate of the WBH in the pools compared to the runs ($\chi^2 = 9.52$, df = 3, $P < 0.05$). For biomass intake rate, there was a significantly higher rate in the riffles compared to the ponds ($\chi^2 = 9.84$, df = 3, $P < 0.05$). Although no statistically significant difference was observed among microhabitats for success rate ($\chi^2 = 4.56$, df = 3, $P = 0.2$), it tended to be higher in the riffles, pools and runs compared to the ponds (Table 1).

Prey availability

At least 12 species of fish belonging to three families were identified in this study (Table 2). The family Cyprinidae was dominant in the heron's foraging habitats. Although *Neolissochilus hexagonolepsis* was the most commonly sampled fish species, the mean CPUE was relatively low (31 ± 8 g/h). Whereas the mean CPUE for *Salmo trutta* (407 ± 166 g/h) and *Labeo pangusia* (287 ± 49 g/h) were among the highest, their frequencies of capture were very low (six and seven). *Schizothorax richardsonii* was one of the most commonly sampled fishes with a relatively high CPUE (149 ± 50 g/h).

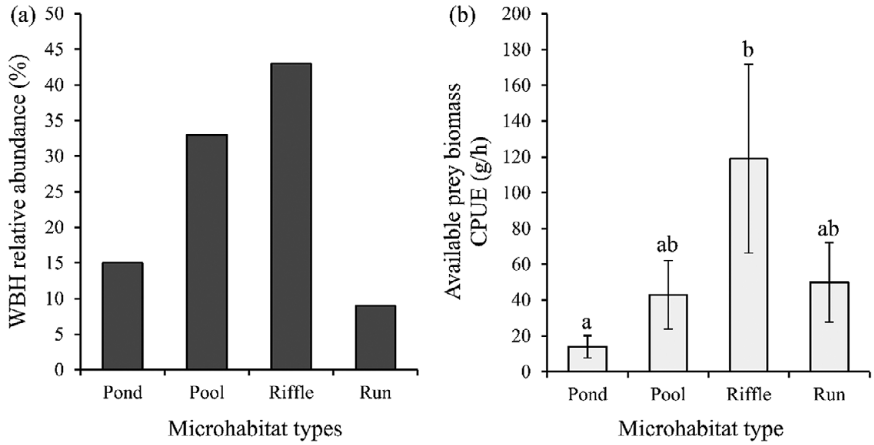

Figure 3. (a) Relative abundance of White-bellied Herons in four types of microhabitats. Values are given as a percentage. (b) Available prey biomass catch per unit effort (CPUE) (grams/hour) in the four microhabitats based on sampling with cast nets and electrofishing gear. Values are given as means (±SE). Significant differences among variables are labeled with different letters above the bars based on a Kruskal-Wallis test at $P < 0.05$.

A significant difference in the mean available prey biomass catch per unit effort (CPUE) was observed between the microhabitat types (Figure 3b). The highest biomass CPUE was observed in riffles (118 ± 5 g/h) while the lowest was found in the ponds and the difference was statistically significant (14 ± 5 g/h) ($\chi^2 = 12.50$, df = 3, $P < 0.01$). No other significant differences were found among microhabitats in relation to CPUE. A weak, but significant positive correlation was observed between the available biomass CPUE and WBH relative abundance ($r_s = 0.22$, $P < 0.01$).

Diet composition

From the 97 prey items caught by WBH, 95% were fish, of which 71% could be identified to the genus level (Table 3). The remainder (5%) could not be identified because the species was too small or the observer too far away to allow identification. The most commonly consumed food by the WBH belonged to the genus *Schizothorax* (64%). Snow trout *Schizothorax richardsonii* constituted 28% of the observed prey, while unidentified *Schizothorax* spp. accounted for 36% of the total diet. Because of the prey's often distinctive morphology, observations made in proximity (≤ 100 m) often enabled us to make identification at the species level. Fish belonging to genus *Garra* contributed only 3% of the total consumed fish. *Schizothorax* spp. were the only fish prey exploited during all months of the year by the WBH.

Season

The foraging activity of the WBH differed significantly among the seasons (Table 4). There was a significantly higher pacing rate in autumn than the spring ($\chi^2 = 7.9$, df = 3, $P < 0.05$), while no significant differences were observed among the other seasons. The striking rate was significantly higher during the spring than the others ($\chi^2 = 37.9$, df = 3, $P < 0.001$). However, the capture rate was significantly higher during the summer than the spring ($\chi^2 = 10.1$, df = 3, $P < 0.05$). The success rate did not differ between the seasons ($\chi^2 = 5.4$, df = 3, $P = 0.14$) and there was no significant difference in biomass intake rate across all seasons ($\chi^2 = 5.9$, df = 3, $P = 0.11$) (Table 4).

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Table 1. Effect of microhabitat types on the foraging activities of White-bellied Herons expressed as means (±SE). Superscripts with the same letter indicates no significant difference using Dunn's post-hoc test with Bonferroni correction ($P > 0.05$). Numbers in the parenthesis are sample sizes of the behaviors in the given habitat type, NS, not significant; Kruskal-Wallis test results for the effect of microhabitat on the given foraging behavior are listed at the bottom of each column.

Microhabitat type (n)	Pacing Rate (steps min $^{-1}$)	Striking Rate (strikes min $^{-1}$)	Capture Rate (captures min $^{-1}$)	Success Rate (captures strike $^{-1}$)	Intake Rate (Biomass (g) min $^{-1}$)	Number of Successful Captures	Total Observation Time (min)
Pond (28)	23 ± 4^{ab}	0.3 ± 0.20	0.03 ± 0.01	0.2 ± 0.1	2 ± 1^{a}	17	456
Riffle (80)	20 ± 3^{ab}	0.2 ± 0.04	0.10 ± 0.02	0.4 ± 0.1	32 ± 8^{b}	40	1262
Pool (62)	29 ± 4^{a}	0.4 ± 0.10	0.10 ± 0.02	0.4 ± 0.1	18 ± 4^{ab}	37	1717
Run (17)	11 ± 1^{b}	0.1 ± 0.02	0.02 ± 0.01	0.4 ± 0.1	21 ± 6^{ab}	3	342
	$P < 0.05$	NS	NS	NS	$P < 0.05$		

Table 2. Summary of the available fish species sampled from the three rivers where the White-bellied Herons were found foraging most frequently. Catch per unit effort (CPUE) (grams/hour) values are given as means (±SE).

Family	Species	n	Total length (cm) Mean (min-max)	Total weight (g) Mean (min-max)	CPUE (g/h) Mean (±SE)	River
Balitoridae	Gadera, *Schistura cf. savona*	3	5 (5–5)	3 (3–3)	1.3 ± .01	PC
Cyprinidae	Gardee, *Labeo pangusia*	7	34 (30–41)	419 (230–640)	287 ± 49	PC
Cyprinidae	Alwan Snow Trout, *Schizothorax richardsonii*	52	19 (7–32)	167 (6–950)	149 ± 50	PC, MC
Cyprinidae	*Garra* spp.	17	13 (9–19)	51 (5–90)	66 ± 15	PC
Cyprinidae	Copper Mahseer, *Neolissochilus hexagonolepsis*	113	11 (5–26)	32 (3–450)	31 ± 8	PC, MC
Cyprinidae	Barna Beril, *Barilius barna*	2	11 (11–11)	49 (7–90)	35 ± 24	PC
Cyprinidae	*Schizothorax* spp.	6	14 (5–24)	53 (7–130)	25 ± 15	PC, MC
Cyprinidae	Hamilton's Barila, *Barilius bendelisis*	21	6 (4–12)	6 (3–9)	20 ± 7	PC
Cyprinidae	Bhitti, *Devario assamensis*	11	8 (7–11)	19 (4–110)	12 ± 7	PC
Cyprinidae	Annandale Garra, *Garra annandalei*	11	10 (5–14)	19 (4–80)	10 ± 3	PC
Cyprinidae	Golden Mahseer, *Tor putitora*	5	10 (10–10)	5 (5–5)	2 ± 0.1	PC
Salmonidae	Brown Trout, *Salmo trutta*	6	30 (25–34)	497 (120–1200)	407 ± 166	PC

River codes: PC Punatsangchhu, MC Mangdechhu.

Time of day

The foraging activity of the WBH differed with time of day (Table 5). The capture rate was significantly higher in the morning compared to midday periods (χ^2 = 12.05, df = 2, P < 0.01), with WBH capturing five times more fish in the morning than midday. There was no significant differences in capture rates observed among other times. The success rate was significantly higher in the morning compared to midday (at least three times more efficient in catching fish) (χ^2 = 13.53, df = 2, P < 0.001). Therefore, the intake rate was significantly higher during the morning than the midday period (χ^2 = 9.64, df = 2, P < 0.01). Consequently, the biomass consumption per unit time was more than two-fold higher in the morning than the midday period. No other differences were observed in the biomass consumption. There was no significant difference in pacing (χ^2 = 0.3, df = 2, P = 0.86) and striking rates (χ^2 = 2.6, df = 2, P = 0.27) with the time of the day.

Age

A total of 163 feeding bouts for adults and 24 for juvenile WBH were analysed to compare their feeding activities. There was no statistically significant difference between the pacing rates (Mann-Whitney U test, Z = 0.5, P = 0.65) of adults (median = 23 steps/min, Q_1–Q_3 = 0–35) and juveniles (median 22 steps/min, Q_1–Q_3 = 0–37) (Figure 4a). There was a statistically significant difference in

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Table 3. Summary of monthly observations of the prey species consumed by White-bellied Herons.

	2018											2019		
Prey types	Feb.*	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Total	Composition (%)
Schizothorax spp.		7	3	2	1	1	1	3	6	3	4	4	35	36
Schizothorax richardsonii		2	1		1	1	1	3	6	5	5	2	27	28
Fish Unknown		2	10	2	5		3				1		23	24
Salmo trutta			1	3									4	4
Garra spp.						2	1						3	3
Undetermined		1			3		1						5	5
Total observations	0	12	15	7	10	4	7	6	12	8	10	6	97	100

Table 4. Differences between seasons in the foraging activity of White-bellied Heron expressed as means (±SE). Superscripts with the same letters indicates no significant difference using Dunn's post-hoc test with Bonferroni correction ($P > 0.05$). Numbers in the parenthesis are sample sizes for the birds observed in each season, NS, indicates not significant. Kruskal-Wallis test results for the effect of seasons on the given foraging behavior are listed at the bottom of each column.

Season (n)	Pacing Rate (steps min $^{-1}$)	Striking Rate (strikes min $^{-1}$)	Capture Rate (captures min $^{-1}$)	Success Rate (captures strike $^{-1}$)	Intake Rate (Biomass min $^{-1}$)
Winter Dec.–Feb. (31)	22 ± 4^{ab}	0.2 ± 0.03^{a}	0.03 ± 0.01^{ab}	0.4 ± 0.1	16 ± 05
Spring Mar.–May (57)	19 ± 3^{a}	0.6 ± 0.10^{b}	0.06 ± 0.01^{a}	0.4 ± 0.1	15 ± 04
Summer Jun.–Aug. (62)	27 ± 4^{ab}	0.2 ± 0.04^{a}	0.10 ± 0.03^{b}	0.3 ± 0.1	19 ± 07
Autumn Sept.–Nov. (35)	34 ± 4^{b}	0.1 ± 0.02^{a}	0.05 ± 0.01^{ab}	0.4 ± 0.1	44 ± 10
	$P < 0.05$	$P < 0.001$	$P < 0.05$	NS	NS

Table 5. Effect of time of day on the foraging activity of the White-bellied Herons expressed as means (± SE). Superscripts with the same letter indicates no significant difference after Dunn's post-hoc test with Bonferroni correction ($P > 0.05$). Numbers in the parenthesis are sample sizes, NS, not significant. Kruskal-Wallis test results for the effect of time of day on the given foraging behavior are listed at the bottom of each column.

Period (n)	Time (hr.)	Pacing Rate (steps min $^{-1}$)	Striking Rate (strikes min $^{-1}$)	Capture Rate (captures min $^{-1}$)	Success Rate (captures strike $^{-1}$)	Intake Rate (biomass min $^{-1}$)
Morning (78)	06h01-10h00	26 ± 3	0.7 ± 0.1	0.10 ± 0.03^{b}	0.4 ± 0.1^{b}	29 ± 7^{b}
Midday (51)	10h01-14h00	23 ± 3	0.5 ± 0.1	0.02 ± 0.01^{a}	0.1 ± 0.1^{a}	10 ± 3^{a}
Afternoon (61)	14h01-18h00	25 ± 4	0.4 ± 0.1	0.05 ± 0.01^{ab}	0.2 ± 0.1^{ab}	21 ± 7^{ab}
		NS	NS	$P < 0.001$	$P < 0.001$	$P < 0.05$

the striking rate (Mann-Whitney U test, $Z = -3.4$, $P < 0.001$) between adults (median = 0.13 strikes/min, Q_1–Q_3 = 0.04–0.43) and juveniles (median = 0.6 strikes/min, Q_1–Q_3 = 0.3–1.2) (Figure 4b), with the striking rate of juvenile herons being four times higher than the adults. However, the capture rate (Mann-Whitney U test, $Z = 1.7$, $P = 0.24$) did not differ between adults (median = 0.04 captures/min, Q_1–Q_3 = 0–0.07) and juveniles WBH (median = 0 captures/min, Q_1–Q_3 = 0–0.06) (Figure 4c). The success rate (Mann-Whitney U test, $Z = 2.6$, $P < 0.05$) was significantly higher for the adults (median = 0.1 success/strike, Q_1–Q_3 = 0–1) compared to the juveniles (median = 0 success/strike, Q_1–Q_3 = 0–0.05) with the adults acquiring more than thrice as many fish as juveniles (Fig 4d). Consequently, the biomass intake rate of adults (median = 2 g/min, Q_1–Q_3 = 0–20) was significantly higher (Mann-Whitney U test, $Z = 0.5$, $P < 0.05$) than juveniles (median = 0 g/min, Q_1–Q_3 = 0–2.5) (Figure 4e).

Discussion

Overall, we found some notable differences in the use of the four principal microhabitats by WBH as well some clear differences regarding season, time of day, and age. The higher relative abundance of the WBH in riffles and pools may be attributed to a number of factors, but primarily higher prey biomass CPUE in these microhabitats as well as the likelihood of foraging success. The prey availability, distribution, and abundance influence the microhabitat use and selection in wading birds including most ardeid species (Kersten *et al.* 1991). The higher capture and success rates in

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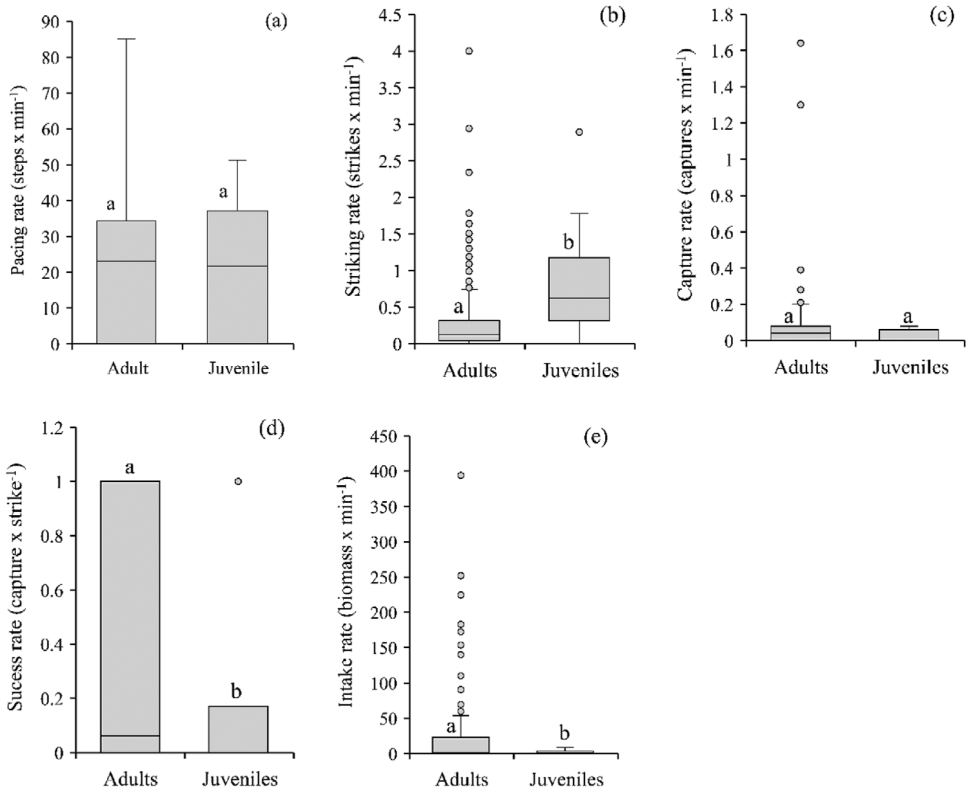

Figure 4. Effect of age on the foraging activities of the White-bellied Herons expressed as medians (Q_1–Q_3). Significant differences among variables are labeled with different letters based on Mann-Whitney tests at $P < 0.05$.

riffles and pools suggests that these are likely the most suitable microhabitats for the WBH. Riffles were used more commonly by the WBH than other microhabitats despite the lower availability of these habitats compared to runs and pools. The shallow water in the riffles may have also increased prey visibility and vulnerability (Gawlik 2002). Similar studies carried out on other waders found that most wading birds showed microhabitat use and selection in relation to water levels (Bancroft *et al.* 2002, Maccarone and Brzorad 2005, Baschuk *et al.* 2012, Renken *et al.* 2016). Overall, the WBH has relatively long legs with tibio-tarsus measuring 25–30 cm and bill (18–20 cm) (RSPN 2020) which probably makes the bird a versatile forager in habitats with varying water depths (Grant 1968, Baker 1979).

The WBH in the pools, riffles and the ponds had higher pacing rates compared to the runs probably because these habitats were mostly surrounded by open areas of sand and gravel bars which likely enabled them to scan through more foraging points in a relatively shorter period of time compared to the runs. However, the WBH in runs were found standing on rocks while waiting for prey to appear. Their movements were also limited to the exposed surface area of the rocks. Thus, the WBH took more time to catch fish in runs when compared to other microhabitats based on the comparatively lower observed capture rates. Overall, although herons in the pools had the highest pacing rates and tended to have the higher intake rates, there was not a clear relationship between pacing rate and intake rate as in other studies (Papakostas *et al.* 2005).

The genus *Schizothorax* was the most important prey item in the diet of the WBH; it was the dominant prey consumed in all the seasons of the year, indicating that *Schizothorax* spp. were available to the WBH year-round. RSPN (2011) carried out prey sampling using cast nets and suggested that snow trout *Schizothorax richardsonii* and brown trout *Salmo trutta* were the only two species large enough to be captured by the WBH. During our prey sampling we also recorded larger sized fish most commonly from the genus *Schizothorax*, thus the size of the fish and their availability likely explain the dominance of *Schizothorax* spp. in the diet. The dominance of these species in the WBH diet, suggests that this might be a target for restocking, if it is needed (see below) and also an important food source for captive-bred birds.

Pradhan *et al.* (2007) showed that nesting took place in March to early June, while the summer (June–August) and autumn (September–November) seasons coincide with feeding of fledglings (RSPN 2011, Acharja 2020) when the parents need to provide food to the juveniles and themselves, as seen with other ardeids (Fasola 1984, Moreno 1984, McGuire 1986, Martin 1987). We observed that adults continue to feed the juveniles that had fledged perhaps until as late as October. This may be the reason for their higher biomass intake rates during the summer and autumn seasons compared to winter and spring. In contrast, our field observations indicated that WBH mostly avoided the swollen and muddy mainstream river and foraged in pools and temporary ponds near the riverbanks which might have resulted in lower success rates in the summer.

While there is no concrete evidence of predation on adult WBH, there are likely several competitors. Great Cormorants *Phalacrocorax carbo* are possibly the main competitors during the winter-spring seasons when large migrant flocks of these birds are present in WBH habitats. Otters are also perhaps one of the principal mammalian competitors throughout the season. However, the type of interaction between these species and the WBH is yet to be ascertained.

WBH, like many ardeids had varying feeding intensity in relation to time of day (Lo and Fordham 1986) with foraging peaks during the morning and afternoon, and reduced feeding around midday (Kushlan 1976). This study found that WBH was more efficient in foraging during the morning and afternoon with comparatively higher capture and success rates relative to midday hours, although some other ardeids have shown no significant difference in their foraging efficiency in relation to time of day (Papakostas *et al.* 2005, Choi and Yoo 2011). The glare of the sunlight may have impeded their foraging success during the midday as is the case with birds that hunt for food over water (Krebs and Partridge 1973). WBH was also observed to avoid the hotter midday hours by shading itself on a nearby perch, thus reducing their foraging time.

Juvenile WBH chiefly foraged in pond and pool microhabitats. While they were occasionally seen exploring riffles, they were never seen using the run microhabitat in the entire study period. This suggests that either juveniles were inefficient in exploiting the fish from the runs or habitat conditions were not favourable for the less experienced juveniles. It is likely that herons may adopt varying foraging techniques to maximize their foraging efficiency with regard to habitat conditions and prey characteristics (Dimalexis *et al.* 1997, Gwiazda and Amirowicz 2006). Although the striking rate was significantly higher in juvenile WBH than the adults, capture, success, and biomass intake rates were comparatively lower in juveniles. This suggests that juvenile herons are less efficient foragers than adults, likely due to less experience in catching and handling prey (Draulans and Van Vessem 1985, Marchetti and Price 1989) which is also associated with less developed sensorimotor faculties (Cezilly and Boy 1988).

Overall, our results imply that WBH exhibit both habitat and food specialist foraging behaviour in contrast to the generalist feeding behaviours of other species in this genus. For instance, Purple Heron *Ardea purpurea*, which is the most closely related species to the WBH (Xi *et al.* 2018, Klinsawat *et al.* 2019) was found using agricultural lands and rivers for foraging and their diet comprised numerous prey species including insects, reptiles, amphibians and crustaceans (Campos and Lekuona 1997, 2001). Hancock and Kushlan (1984) assumed that besides fish, WBH might also consume amphibians, reptiles, or small mammals. However, WBH were observed to forage only in freshwater bodies and their sole diet is probably fish in these basins. Therefore, it is particularly important to protect their existing riverine habitats from further degradation and loss and enhance their food resources to increase the carrying capacity of the current habitats of WBH for their long-term survival. Thus, it is also reasonable to assess whether supplementary diet provisioning through the creation of few artificial weirs and ponds restocked with the native fish species would be beneficial to WBH and their river ecosystems.

Apart from dams and exposed power lines, we have also encountered numerous locations where dredging of sand and gravel from the riverbanks is carried out for commercial as well household consumption in our study area. Uncontrolled sand and gravel mining in the river systems is a serious threat not only to globally threatened species (Menzies *et al*. 2020) but also native fish and biotic communities (Kanehl and Lyons 1992, Koehnken *et al.* 2020). Also, construction of access roads and storage sites for sand mining leads to further fragmentation and loss of the riverine vegetation (Kondolf *et al.* 2007, Kumar and Kumar, 2014), which is crucial for the nesting and roosting of WBH (Khandu *et al.* 2020a, 2020b). Thus, it is imperative that the daily operation of the sand and gravel mining activities is monitored on a regular basis by the relevant agencies and proper restorative and mitigation measures are put in place (Kondolf *et al.* 2007). Crushed stone sand should be encouraged for use as an alternative to dredged sand from the rivers. In our study sites, we have also recorded numerous instances of illegal fishing using a variety of gear including cast nets, hook-and-line, gillnets and snare traps which are likely depleting fish communities (Österblom and Bodin 2012, Agnew *et al.* 2009, Beddington *et al.* 2007) and potentially endangering WBH near these fishing sites. Therefore, better surveillance of illegal fishing with occasional night patrolling by the foresters, and suspension of permitted fish harvesting, especially during their breeding seasons in core habitats (Puntsangchhu and Mangdechhu) is warranted. Establishing fishponds for interested members of the community is supported by the Royal Society for the Protection of Nature (RSPN) to curb illegal fishing and habitat disturbance. Simultaneously, periodic community awareness and social networking especially targeting local fishermen should be carried out by appropriate NGOs and agencies to enhance compliance with regulations (Scholz and Wang 2006) and to help shift the local people's attitudes towards conservation interventions (Williams *et al.* 2019).

Through our personal observations, we also noticed that WBH tend to explore small streams (25–35 m wet width) near (mean distance 74 m) their nest sites (Acharja 2020), especially during the summer seasons when the monsoonal rain floods their usual foraging habitat. These small streams also need protection as they provide valuable foraging habitat when the foraging conditions in their usual habitats along the larger rivers become unfavourable.

Conclusion

Further study is required to understand how the WBH responds to seasonal changes in river microhabitat parameters such as velocity, turbidity, and temperature caused by monsoonal dynamics as well as human disturbance. This study could not account for the seasonal variations and abundance of its prey species, which might affect their daily foraging activity and success. It is also vital that the fish abundance and density in the WBH habitats are monitored periodically to ensure that the WBH are not deprived of their daily dietary needs. A thorough study is also warranted in Punatsangchhu and Mangdechhu basins to assess the direct impacts of dams and sand and gravel mining to WBH and the fish community so that appropriate mitigation measures can be proposed and implemented.

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