Effects of water level changes and wading bird abundance on the foraging behaviour of blacknecked storks *Ephippiorhynchus asiaticus* in Dudwa National Park, India

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The effect of water level changes and wading birds' abundance on the foraging behaviour of the blacknecked stork (BNS) *Ephippiorhynchus asiaticus* was studied from January 1995 to June 1997 in Dudwa National Park, Uttar Pradesh. Our observations indicate that BNS territoriality increased as food levels became depleted, resulting in increased rates of aggression towards intruders. Chasing or aggression was more intense during the early period (February and March) than the late period (April, May and June). Most of (> 50%) the aggressive encounters were observed between 0600 and 1000 h of the day. Seventeen species (including BNS) were observed interacting with BNS, throughout the study period. Most interactions were with the spoonbill, *Platalea leucorodia* (67·4%), followed by the whitenecked stork, *Ciconia episcopus* (16·6%). The distance (while foraging) between BNS and other wading birds varied significantly ($P < 0{\cdot}001$) between years indicating that BNS and other water birds foraged at different water depths and thereby explored the wetlands fully. Spoonbills were chased often; the number varied from 1 to 43 birds. BNS occasionally accepted the presence of other wading birds, including spoonbills and started foraging amidst them. This led to successful foraging of BNS (solitary feeder). Other fish-eating bird species and their numbers also limited the food consumption of foraging BNS as they had to spend time chasing away the intruders. Availability of the preferred prey fish species, *Heteropnestus fossilis*, forced BNS to stay throughout the year in their respective territories. High (> 60 cm) water levels were not suitable for BNS even though the patch had high prey abundance.

1. Introduction

The daily food requirements of birds depend on time budget, activity level, assimilation efficiency and energy content of food (Kushlan 1978). Availability of prey may vary with season i.e. wet or dry, but this depends on the fluctuation in water level conditions (Kushlan 1976, 1986). Many wading birds nest when the prey is most abundant. In most tropical areas prey is more abundant and available during the rains (Kushlan 1978). When many wading birds congregate in a particular place, competition increases between species and the chances of an individual getting food reduces. Partitioning of foraging resources is generally thought to be the result of past competition among co-occurring species with similar life history strategies (Roughgarden 1976; Pacala and Roughgarden 1982a, b). Species coexistence through resource partitioning is typical of natural systems (Pianka 1974; Wermer and Hall 1979; Mittelach 1984; Reinert 1984). However, partitioning could arise, and can be maintained by aggression or by the avoidance of aggression. An aggressively dominant species could exclude other aggressively subordinate species, forcing them into inferior habitats (Kent 1986). As a large and solitary feeder, blacknecked stork *Ephippiorhynchus asiaticus* could reveal important interspecific behaviours while foraging in mixed flocks (Stanley and Breeden 1982), especially while rearing the juveniles. This is most important in

Keywords. Blacknecked stork; *Ephippiorhynchus asiaticus*; *Heteropnestus fossilis*; inter- and intraspecies interactions; interfood interval; wading bird, water level

terms of conservation of the species as competition plays a major role since BNS are highly voracious and their population declined steeply in the Indian subcontinent (Rahmani 1989).

Models of optimal foraging behaviour often assume that individuals forage independently (Stephens and Krebs 1986). Although foraging in the presence of competitors is probably common, few studies have examined the effects of competitor presence on parameters and predictions of optimal foraging models. The conventional central place foraging (CPF) model predicts that foragers designed to maximize the net rate of prey delivery to the central place should collect increasingly large loads as distance between central place and food increases (Giraldeau *et al* 1994). Stephens and Krebs (1986), argued that central place foragers may slow their foraging in order to monitor the activities of potentially aggressive competitors. Competitor presence would therefore reduce the loading rate in a manner functionally equivalent to reducing the density of prey (Giraldeau *et al* 1994). Taking these parameters into consideration we asked the following questions:

(i) Being a solitary feeder, how do blacknecked stork (BNS) respond to the changes in water levels in its foraging territory?
(ii) When water level decreases, a number of fish-eating birds congregate. How does this affect BNS foraging patterns?
(iii) What determines the selection of feeding modes among BNS of Dudwa National Park (DNP) amidst food competitors?

2. Study area

Dudwa National Park is situated on the Indo-Nepal border in Nighasan *tehsil* of Lakhimpur-Kheri district in Uttar Pradesh. The area falls under *Terai*-bhabar biogeographic subdivision of the upper Gangetic plain (Rodgers and Panwar 1988). The park lies between 28°18′ and 28°42′ north latitude and 80°28′ and 80°57′ east longitude. The Himalayan foothills are about 30 km north of the park. Rivers Suheli and Mohana form the natural boundaries of the park. After monsoon (July through October) water levels decrease and prey become concentrated. This allows the other wading birds to forage in the area. When the summer sets in water levels decrease which in turn affects vegetation. However, as a management procedure, the Forest Department pump in water to the wetlands to maintain the water level for the benefit of endangered swamp deer *Cervus duvaceli*. This largely benefits the BNS too as they get enough water even during peak summer days to maintain their territory. Otherwise decrease of water level force most of the birds to abandon the wetlands. Regular water supply (8–10 h) for 10–15 days compensates this natural decline, facilitating birds such as BNS, egrets and herons.

3. Methodology

We conducted studies on the BNS in Dudwa National Park from December 1994 to June 1997; intensive observations on foraging BNSs were made from January 1996 to June 1997. Observations were made from a watch tower near wetlands without disturbing the birds. A digital stop watch, a hand tally counter, and a still camera were used to record the specific events of foraging activity such as the mode of prey capture (tactile/visual) and water level at each spot from where it caught a fish. Each wetland had a pair of BNS which remained throughout the study period except for a few days' temporary disappearance of either a male or a female during summer. Activity of a single individual stork was recorded continuously (from 0600 to 1800 h) from the watchtowers situated at three wetlands (Banketal, Kakrakatal and Badhital) at a height of approximately 10–15 m. One full day was spent recording the activities of either a male or a female BNS in one wetland. The sexes can be easily distinguished by the colour of the eye: the female has a yellow iris while the male has a dark brown one. Occassionally both birds were absent for a couple of days. On the next day another bird was observed continuously so that two days were spent in each of the three wetlands alternately to study both the sexes. The BNSs are highly territorial and can be seen in their respective territories. So finding a particular bird (either a male or a female) was not difficult. Sometimes having observed a male for a day, the next day if a female was not located, again the male was observed and vice versa. Focal animal sampling (Altman 1974) was used to record the behaviours of BNS. Five minute observations were made to record the following parameters: starting and ending time of each foraging bout, number of pecks/jabs, number of fish caught, fish size, handling time, water depth and the mode of food capture (tactile/visual). From the general activity pattern records, total foraging time was also calculated for each day. Whenever the BNS started foraging a timed (5 min) bout began. If it foraged for more than 5 min, another 5 min observation was started.

Number of "pecks" (attempt at catching fish) were counted with the help of a hand tally counter for each 5 min feeding bout. If a BNS caught any fish, a 5 min bout was considered as successful and if it failed to do so, the attempt was considered as a failure. As soon as it caught a prey, seconds were counted with the help of stopwatch and counting was stopped soon after it gulped the fish. This was to find out the time ("handling time") it

took to consume fishes of different size. Fish species were also recorded. Since Dudwa National Park comes under the status of India's Tiger Reserve, permission was not obtained to sample either prey abundance or vegetation profile within the BNS's feeding grounds. Therefore fish length was compared with that of BNSs' bill length by a non-invasive method. Outside the park fish were caught and their lengths (in cm) and wet weights (in g) were estimated. Water depth (at a spot where it caught a fish or foraged) was roughly estimated by comparing the leg (tarsus + tibia) length (male 60 cm; female 55 cm approx.). Apart from these, the species abundance of other wading birds was also recorded by site and date.

Midday temperatures varied from 3°C to 11°C in winter (December to April) and from 34°C to 41°C in summer (May to July). Even though data on aggressive behaviour (includes chasing and bill clattering toward intruder) of BNSs were collected from different locations, they were grouped together for statistical analyses. Observations were made on the foraging BNS to record aggressive inter- and intraspecific interactions.

Apart from foraging behaviour, chasing acts were recorded while gathering data on the activity pattern of BNS. After the monsoon, water level decreases and prey becomes concentrated; allowing other waders to forage in the area. Observations were recorded soon after either one of the two birds started chasing or showing aggressiveness towards intruders. The time of aggressiveness shown towards conspecifics and the species reacted with, along with their numbers was also recorded. Condition of the wetlands i.e. water level at which intruders were foraging, distance from the BNS, and how far the intruder flew after being chased by BNS were also noted down. The mode of interaction was also recorded, i.e. whether BNS showed aggressiveness by bill clatter or physically attacked an intruder and how successful the BNS was in this act. The number of encounters, is measured as the number of times a BNS chases an intruder irrespective of species. The activity of BNS before it chased any intruder was also recorded. The time taken to chase away an intruder, the distance chased and the distance between BNS and an intruder before engaging in the aggressive act were also noted.

To understand why BNS chased away wading birds, the activity of the individual involved (intruder) before being chased away by a BNS was also recorded. The total number of fish-eating birds present on each day at each wetland were also recorded as a measure of the changing trend of aggressiveness. These data were collected from January 1995 till June 1997. As all the birds were unmarked, we were not sure whether the BNSs repeatedly chased the same individual (spoonbills) of a flock or different individuals of a flock. This was because of the inherent difficulties of assessing identity especially of spoonbills when they were in large numbers. Actual number of occurrences of different bird species are given in appendix 1. Total hours of observations were based on 12 h (0600 to 1800 h) of observations per day.

The Mann–Whitney *U* test was used to test the difference in the number of fish caught by males and females in different months. The same test was also used to compare the difference in peck rate in different months between the male and female BNS. One-way ANOVA (*F*-test) was used to compare the mean male and female BNS's inter-food interval recorded in different months during the study period and the same test was also applied to determine male and female BNS fish handling efficiency.

A two sample *t*-test (unpaired) was used to see whether any differences were present in the chasing or aggression activity of BNS between early and late season. Mann–Whitney *U* test was used to test whether there were any difference in chase frequencies between males and females towards intruding species. The Kruskal–Wallis test was used to test for sex differences in the distance chased by BNS in different water level conditions among the years of study. All statistical analyses were performed by STATA 5·0 (StataCorp 1997) and SPSS 6·1 (Norusis 1994) statistical packages.

4. Results

In the Dudwa National Park, BNSs are highly territorial. Our general observations indicate that their territoriality increases as food depletes. During low-water period BNSs showed more inter- and intra-specific aggressiveness. The chasing or aggression (inter- and intra-specific) was more among BNSs during the early part of the year (February and March) (± SE) (2·25 ± 0·68) (mean number of chases per day) than the later (April, May and June) period (0·62 ± 0·21) ($t = 2{\cdot}277$, $N = 203$; $P < 0{\cdot}05$).

In 1995 and 1996 BNSs spent almost equal amounts of time ($t = 1{\cdot}887$, $N = 18$, $P > 0{\cdot}26$); ($t = 0{\cdot}3984$, $N = 47$, $P > 0{\cdot}70$) on interactions with intruders both in the early and late periods, but in 1997 chasing activity differed significantly ($t = 2{\cdot}8380$, $N = 205$, $P < 0{\cdot}02$) in that they spent more time for chasing in the early period (2·98 ± 0·66) than late period (0·68 ± 0·46).

During the study period of three years, aggressive (inter- and intra-specific) behaviour was recorded on 45 days among BNS. Most (> 50%) of the aggressive encounters were observed between 0600 and 1000 h. Totally 17 species (appendix 1; the list excludes BNS itself and grey headed fishing eagle but were seen interacted with BNSs of respective wetlands) were observed interacting with BNS, of which spoonbills (*Platalea leucorodia*) interacted most (67·4%) followed by white-necked storks (*Ciconia episcopus*; 16·6%).

In the three years of study there was not much difference in the population of wading birds between months (table 1). The number of fish-eating birds was also high and this could be the reason for more chases. During summer when water level was < 60 cm in the fringes of the wetland almost all wading birds left the area and the number of interactions between BNS and intruders were also reduced.

Table 1. Monthly interactions (with BNS) of fish-eating birds and their numbers recorded in three years in Dudwa National Park.

Month	Year	n^a	No. of chases[b]	No. of species[c]
February	1995	8	9	10
	1996	–	0	–
	1997	5	90	10
March	1995	1	5	1
	1996	23	21	13
	1997	5	77	11
April	1995	16	3	15
	1996	23	22	12
	1997	10	35	14
May	1995	19	1	13
	1996	5	6	10
	1997	7	3	14
June	1995	15	–	12
	1996	7	–	12
	1997	–	–	–

[a]Number of days wading bird species counts were made.
[b]Number of chases per month on the respective days of observation.
[c]Number of species considered as wading birds and potential competitors of BNS. This includes a few species which were not actually interacted with BNS during the study period.

There was no sex difference in the number of interspecies encounters between adult BNSs. The number of pecks varied among sexes in 1996 during summer, when females jabbed water in search of food more times than males. But, the success rate (i.e. the number of fish caught) did not vary between sexes (table 2). During 1997 peck rate differed between sexes in February and May (table 3) but the number of fish caught did not vary significantly among sexes.

When three years' data were pooled together and analysed the distance between adult BNS and intruders varied significantly ($c^2_3 = 34{\cdot}68$, $P < 0{\cdot}0001$, $N = 270$). Whereas only in 1997 this distance varied significantly ($c^2_3 = 15{\cdot}18$, $P < 0{\cdot}001$, $N = 205$; Kruskal–Wallis test) and not in 1995 and 1996 when three years data were analysed separately. This was evident when BNS caught fishes from different water depths in both the years (table 4). BNS caught more fishes in deep watered (≥ 55 cm) areas and from the places where water level was half of its tarsus length.

Blacknecked storks were less successful in chasing away all the spoonbills from their feeding territories. As a single bird or in a pair, the BNSs could follow only 2–3 spoonbills for a minute or less while trying to chase the spoonbills. When chased by BNS, the spoonbill flock would disperse and reassemble a few metres away and start foraging quickly. Some times having failed in its attempt to chase away the spoonbill flock from a wetland, BNS too would start foraging amidst a foraging flocks of spoonbills and egrets. This tendency of BNS led to its successful foraging, but most of the fishes were 5–6 cm in size.

4.1 *Interfood interval*

We wanted to see whether there were any differences in

Table 2. Mean number of attempts (per 5 min) and the success rate of adult BNS in the presence of other fish-eating birds in 1996 in Dudwa National Park.

Month	Sex	Foraging attempt $\bar{X}$ ± SD	No. of fish caught $\bar{X}$ ± SD	No. of waders[a] $\bar{X}$ ± SD
March	Male	82·3 ± 50·9*	1·89 ± 1·69**	
	Female	56·5 ± 30·5	0·78 ± 0·85	15·0 ± 7·05
April	Male	36·7 ± 14·2*	2·05 ± 1·45*	
	Female	29·1 ± 12·3	1·33 ± 0·88	13·2 ± 7·7
May	Male	18·2 ± 11·0**	2·50 ± 1·06*	
	Female	39·8 ± 23·2	1·34 ± 1·02	3·0 ± 0·81
June	Male	19·2 ± 12·0**	1·73 ± 1·08*	
	Female	40·8 ± 26·2	3·42 ± 1·92	4·25 ± 2·37

*Non-significant (Mann–Whitney *U* test); **$P < 0{\cdot}05$.
[a]Irrespective of species which actually interacted with BNS.

the mean interfood intervals of male and female storks. In this case the sampling procedure consisted of first sampling $n1$ (male's mean interfood interval) and calculating its variance, $s1^2$; followed by sampling $n2$ (female's mean interfood interval) and calculating its variance, $s2^2$. The degrees of freedom of the two variances are $V1 = n1 - 1$ and $V2 = n2 - 1$. The sample sizes $n1$ and $n2$ may not be equal to each other but are fixed for any one sampling experiment.

The interfood interval varied among male and female BNS in different months. The mean interfood interval varied significantly ($F_{19,29} = 2{\cdot}57$, $N = 50$, $P < 0{\cdot}05$) between sexes in March 1996. The male ($26{\cdot}6 \pm 75{\cdot}8$) BNS's interfood interval was longer than the female's ($21{\cdot}5 \pm 47{\cdot}5$). In April, the female's ($46{\cdot}0 \pm 25{\cdot}8$) interfood interval was higher than the male's ($13{\cdot}6 \pm 29{\cdot}5$) ($F_{38,21} = 2{\cdot}58$, $N = 61$, $P < 0{\cdot}05$). During that period the female caught more fish often, and its foraging efficiency increased unexpectedly. She caught fish in quick succession, even though she caught fewer fish overall than the male. In May, the mean interfood interval time of the male ($7{\cdot}0 \pm 4{\cdot}86$) was shorter than that of the female ($50{\cdot}6 \pm 69{\cdot}0$) ($F_{6,15} = 201{\cdot}7$, $N = 23$, $P < 0{\cdot}05$). The total time foraged also differed significantly, the female

Table 3. Mean number of attempts (per 5 min) and the success rate of adult BNS in the presence of other fish-eating birds in 1997 in Dudwa National Park.

Month	Sex	Foraging attempt $\bar{X} \pm$ SD	No. of fish caught $\bar{X} \pm$ SD	No. of waders[a] $\bar{X} \pm$ SD
January	Male	80·7 ± 47·8*	3·31 ± 2·12*	
	Female	59·0 ± 31·6	1·40 ± 0·89	–
February	Male	97·5 ± 34·8***	4·13 ± 0·61*	
	Female	56·5 ± 12·6	2·60 ± 1·17	3·3 ± 1·63
March	Male	79·3 ± 41·7*	4·26 ± 0·61*	
	Female	67·2 ± 20·4	2·81 ± 1·94	3·8 ± 1·60
April	Male	45·3 ± 24·3*	3·02 ± 2·44*	
	Female	41·5 ± 34·6	2·33 ± 3·23	4·5 ± 3·15
May	Male	36·3 ± 25·0**	4·42 ± 2·71*	
	Female	41·9 ± 20.6	3.60 ± 1.65	2.71 ± 2.26

*Non-significant (Mann–Whitney U test); **$P < 0.05$; ***$P < 0.001$.
[a]Irrespective of species which actually interacted with BNS.

Table 4. Number (n) per 5 min and percentage of fishes in relation to their size taken by adult female and male BNS at each water level in two year (1996 and 1997).

	Female						Male				
	Water level* (cm)						Water level (cm)				
Fish size	15[a]	30[b]	40[c]	55[d]	Total		15	30	40	55	Total
< 5 cm											
n	7	31	14	67	119	*n*	11	127	34	135	307
%	6	26	12	56	100	%	4	41	11	44	100
5–10 cm											
n	7	41	13	142	203	*n*	10	66	18	281	375
%	4	20	6	70	100	%	3	18	5	74	100
> 10 cm											
n	–	–	2	3	5	*n*	1	2	–	5	8
%	–	–	40	60	100	%	13	25	–	62	100
Total	14	72	29	212	327		22	195	52	421	690

*Based on the tarsal length of the female and male BNS and not the general water level.
[a] ¼ of foraging BNS's tarsus length; [b] ½ of foraging BNS's tarsus length; [c] ¾ of foraging BNS's tarsus length; [d] water lever at full tarsus length.

(39·8 ± 27·7) having spent more time than the male (18·3 ± 2·89) ($F_{3,2}$ = 91·9, N = 7, P < 0·05). All these differences were because of changes in the number of interactions between BNSs and intruders (table 1).

In 1997, interfood interval of male and female BNS differed significantly in all four months [e.g. in March interfood interval of female (127·6 ± 152·4) was greater than male (67·6 ± 102·6) ($F_{18,4}$ = 2·20, N = 24, P < 0·05)]. The total time foraged did not vary between sexes in different months except February. In February even though the total time (in min) foraged was apparently not much different between male (79·0 ± 54·0) and female (70·5 ± 10·6) it varied statistically ($F_{2,1}$ = 25·9, N = 5, P < 0·05).

Usually BNSs avoided foraging amidst other flock foraging species and in turn it showed aggressiveness and tried to chase away the conspecifics. Almost all wetlands in Dudwa are shallow and dry up quickly in summer and attract birds like spoonbills in large numbers. The majority of the intruders were chased by BNS when they were actively engaged in foraging. Only a few resting birds were disturbed by BNS and they were of their own family (Ciconiidae) such as whitenecked stork *Ciconia episcopus*, lesser adjutant stork *Leptoptilos javanicus*, painted stork *Mycteria leucocephala* and openbill stork *Anastomus oscitans*.

We had rarely seen a BNS physically attacking any intruder, instead it gives a strong threat signal by clattering its bill loudly, thereby intimidating an intruder. In case an intruder fails to respond to the high profile threat display, then the BNS would start chasing the same until the opponent disappears from the territory fully or settles somewhere far away from the BNS's foraging territory.

When the spoonbills were present in high concentration (> 40 birds), the main attention of the BNS was diverted towards them mainly because they were the major food competitors of the BNS. After the monsoon rains, the wetlands of Dudwa are filled with water and aquatic vegetation. Till mid-February their foraging is hampered by thick aquatic vegetation. During this period the BNS slowly jab the water in search of prey. Therefore the number of attempts increase and the rate of fish catch decreases (tables 2 and 3).

5. Discussion

Blacknecked storks in the Dudwa National Park, are highly territorial and their territoriality (aggression) increased as food was depleted. This was evident from the presence of other piscivorous birds particularly in the early season when these birds start congregating in the wetlands of the Dudwa National Park and start consuming prey available in a wetland. The reason why chasing was more during the early period might be due to BNS's tendency to protect its feeding territory from intruders, because immediately after monsoon, the water level starts decreasing in all the wetlands. When more and more water birds start coming to the water bodies that were already occupied by the BNS, confrontations occur when the latter tries to chase away the intruders.

In 1997 all the three study pairs were seen with 1–3 juveniles on their foraging grounds. These juveniles were totally dependent on their parents for food. This compelled the parents to forage for a longer time, and this was the period when other fish-eating birds started coming to these water bodies. Therefore, the BNS were actively engaged in chasing away food competitor more in the early season. This considerably decreased their time spent in foraging. Intruders in turn started consuming food in large amounts. The BNS showed more aggressiveness towards the Threskiornithid and Ciconiid species than others.

The reason why spoonbills were chased or interacted more with BNS might be due to their presence in almost all the wetlands in high numbers. Number of spoonbills interacted with BNS varied from a single bird to 43 birds (appendix 1). Whenever spoonbills were targeted by BNS they were actively foraging. The spoonbills were generally high in numbers and had a tendency to forage almost throughout the day (personal observation). This stimulated BNS to react in an aggressive manner towards them.

Spoonbills exploited the foraging niche of BNS more effectively as they were in flocks. This results in their being chased more often by the highly aggressive BNS. Birds that had realized relatively poor capture success chased conspecifics more often than did successful foragers (Wiggins 1991). Foraging attempts and capture successes were significantly higher for birds foraging in groups, than for those foraging in group break-ups or individually (Wiggins 1991). Consequently the energy expended in chasing conspecifics was higher than for solitary foragers (Wiggins 1991). An aggression among wintering black-capped chickades *Parus atricapillus* is also higher among those birds foraging solitarily (Barash 1974). On a few occasions it was observed that BNS accepted the presence of spoonbills, ibises and other fish-eating birds. This was only when they (BNS) were actively foraging and had no time to chase other birds.

It was not only the spoonbills which were chased by BNS, but also the other waders by either male or female or by both BNS. It has also been observed that presence of spoonbills in large numbers attracted other wading birds. Studies have shown that white

birds or models are more attractive to other waders than dark birds (Kushlan 1977), but some dark species also have been shown to be "attracters" (Krebs 1974).

Many of the studies show that group-foraging species may increase foraging intake rate by flocking (Rand 1954; Murton *et al* 1966; Krebs 1973, 1974; Pulliam 1973; Morse 1978). Solitary foragers like BNS too enhanced their foraging success while foraging amidst group foragers like spoonbills.

Other fish-eating bird species and their numbers also affect the food consumption of foraging BNS. Most of the wetlands inside Dudwa National Park were occupied by other fish-eating species and this varied greatly depending upon the food abundance. When the food was abundant the variety of wading birds species and their numbers too increased. It has been observed that egrets, herons and cormorants (cormorants are not included as wading bird in this study) fed mostly on fish even though BNS foraged from the same wetland.

The duration between two successive (interfood interval) food catching bouts varied significantly in all four months in 1997. This may have been due to a complete change in the water level when compared with the previous year. In 1996 water level was high in all wetland studied so the BNSs completely avoided visiting them till February. In 1997, BNS were foraging in their respective territories from January onwards and this was possible for them due to the optimum water level, and hence the ease in foraging.

In 1996, BNS were seen without any juveniles and whatever they consumed was for themselves. In 1997 all study pairs were maintaining 1–3 juveniles in their respective foraging grounds. Generally it was been observed that the males fed the juveniles more often and this may be the reason why the males interfood intervals were greater than females.

The phenomenon of BNS enhanced foraging success when foraging along with group foragers like spoonbills, egrets and herons is unusual. If solitary foragers like BNS forage with group foragers, they (BNS) stand to gain but this again will be short-term as there was a quick depletion of prey.

In 1995, the chase distance was greatest when water level was highest (> 50 cm, in March) and there were a large number of spoonbills. In 1996 also the chase distance was high when spoonbills were seen in large numbers. However in 1997 the chase distance was highest when water levels were lower (< 40 cm, in May). This was due to the presence of grey herons *Ardea cinerea* which were chased for a long distance in the absence of spoonbills. This might be due to less water levels, and this was highly unsuitable for probing spoonbills. When water level was more (in March), 31 interactions involved spoonbills.

Whereas in the case of BNS they foraged throughout the day and success rate was higher (57·9%) in early morning period in the case of male BNS in 1996 and 1997, and more during early morning period (57·5%) in the case of female. According to the accepted hypothesis, most of the fish-eating wading birds maximize their food intake at dawn or at dusk and are less active during mid-day. As a solitary feeder BNS used the period of time when other wading birds become less active to improve foraging success. This was further evident from the fact that more interactions between BNS and intruders occurred in the early period (0600–1000 h) than mid-day period. And whatever the interactions that occurred in the mid-day period were all because of other solitary feeders such as large egret *Ardea alba*, grey herons and the white-necked stork which opted to forage during that period of the day, or when new members of intruders arrived from other locations.

The reason why foraging attempt rate of BNS was high during certain periods of the year, especially when they decided to forage together with group foragers such as spoonbills, large egrets, and grey herons might be due to the other wading bird which serve as beaters. The success rate of feeding does not necessarily increase because of commensal feeding (Siegfried 1971).

Ultimately the success of an individual strike depends on the prey species and nature of the habitat (Kushlan 1977), and this appears to be the case in Dudwa National Park, *H. fossilis* prefer muddy areas for hiding and chances of BNS catching them by means of visual technique are not possible. BNS forage by tactile and visual method depending on the prey and habitat, and 90% of the foraging was by tactile mode at Dudwa National Park. However when a large number of fish-eating bird gather in a wetland, the fish are disturbed and the fleeing fish are caught by BNS after short chases.

As swamp deer are present in all wetlands of Dudwa, the Forest Department had to pump in water with the help of pumps and water level was maintained at optimum level. During summer, evaporation is high and that is compensated by pumped out ground water. So there is a steady increase in the water level which keeps the BNS in its territory. The tendency of *H. fossilis* to hide in the muddy areas of a wetland allow them to survive for long time without being preyed upon by fish-eating birds. Other fish species which are not mud dwelling types are easily preyed upon by birds especially when water level decreases. The birds with small bills unsuited to explore the bottom of the wetlands leave the area.

BNS were more efficient when tactile foraging was employed. A wading bird can select the most appropriate foraging behaviour for its needs, and the choice of a

successful foraging behaviour should reinforce repeated use (Kushlan 1978). So, selection of a particular foraging technique among fish-eating birds depends on the condition of wetlands, prey behaviour and the quality of the wetland.

The wetland condition determines whether foraging birds should remain as a specialist, or a generalist. BNS of Dudwa National Park opt to forage by tactile techniques since most of the wetlands are shallow and water level changed rapidly. When water level decreased the turbidity increased especially in the summer. In the rainy season, water was less turbid and aquatic vegetation was more dense and fish were available. BNS usually go for larger fish ignoring *H. fossilis* even though they are present in large numbers. Thus BNS tend to be opportunists rather than specialists or generalists – opportunistic in terms of selection of a particular fish species with respect to changes in wetland condition. This is contradictory to Kushlan's (1978) hypothesis that, in case of prey selection, birds that mostly search for prey should be generalists, while birds that actively pursue prey and those that wait for prey to approach them should have more restricted diets. The non-visual predator, being a searcher should have a generalized diet, specialized in prey it can most easily catch. If the condition of the waterbody is calm and clear BNS use both tactile and visual mode of feeding. This depends on the type of various fish species, such as surface feeders, bottom dwellers or mud-dwellers like *H. fossilis*. If the water is murky BNS go for tactile mode of feeding. Since it has a long, broad bill it could easily procure *H. fossilis* as well as other fish.

Most work on predation ecology has concerned visually foraging predators. However, many predators, such as the white ibis, are tactile, non-visual foragers (Kushlan 1978) and are limited in their ability to choose among potential prey. The reason why BNS selected other prey species (other than *H. fossilis*) in bigger wetlands might be due to the competition. As a major predator of fish and a dominant competitor among other fish-eating birds, BNS may deliberately feed on the same prey species, most other piscivorous birds of the region preferred to feed upon. This was mainly to finish the common prey species when they were plentiful and easily accessible, leaving the *H. fossilis* (mostly inaccessible to other fish-eating birds because of its habits of hiding in mud) to feed on latter. Because of the decrease in common prey species, other fish-eating birds left the area. This was another reason why BNS were less aggressive and allowed intruders including lesser adjutant stork in bigger wetlands where diversity of prey species was greater. Interaction between BNS and intruders was greater in Banketal where only a few prey species were (based on number of times BNS came up with different species of fish) available during the study period.

Gonzalez (1997) found a seasonal difference in water depth and vegetation height selected by wood storks *Mycteria americana* at their foraging sites. Wood storks showed a clear preference for open waters without vegetation during the dry season, whereas they chose areas with abundant emergent vegetation during the rainy season.

Whitfield and Blaber (1978) found that the fishing behaviour of birds was related to the depth at which the birds were able to forage and the presence or absence of aquatic macrophytes. In our study area, the water level in some wetlands was highest in the middle of the sites. Such areas were avoided by the BNS as they could not wade through. Foraging success of a particular wading bird species also may rely on specific aspects of water level fluctuations, such as depth (Kushlan 1978; Powell 1987) or concentration and entrapment of prey through water level recession. When BNS foraged at the wetland fringes, foraging attempt rate decreased. In clearer water, as we mentioned earlier, BNS could forage both by means of tactile or by vision. Higher water levels (> 60 cm) is not suitable to wading birds including the BNS even though the patch is free from aquatic vegetation and has more prey species. The tarsometatarsal length of the different species determined the depth at which the bird fished. This spatial segregation of the foraging area result in resource segregation because small fish congregated in shallow areas, whereas larger fish were restricted to deeper waters (Whitfield and Balber 1978).

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Appendix 1. Number of occurrences of fish-eating bird species[a] recorded in Dudwa National Park during the study period.

Species*	BI	SB	LC	LE	GH	WNS	PH	ME	LRE	CE	LAS	OBS	PRH	DTR	ISH	Average
1995 (n = 708 h)[b]																
February	6	7	6	4	6	7	6	2	3	2	–	–	–	–	–	3·3 ± 2·9
March	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	0·06 ± 0·03
April	15	3	1	2	3	7	7	1	6	1	3	8	7	5	2	4·7 ± 3·8
May	12	1	–	3	2	8	15	7	1	–	6	15	3	2	8	5·5 ± 5·2
June	9	1	–	3	–	9	8	2	–	2	1	14	3	3	4	3·9 ± 4·2
	8·4 ± 5·8	2·4 ± 2·8	1·4 ± 2·6	2·4 ± 1·5	2·2 ± 2·5	6·4 ± 3·1	7·2 ± 5·4	2·4 ± 2·7	2·0 ± 2·5	1·0 ± 1·0	2·0 ± 2·5	7·4 ± 7·3	7·4 ± 7·2	2·0 ± 2·1	2·8 ± 3·3	
1996 (n = 698 h)																
February	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
March	22	43	8	19	13	22	17	21	23	3	2	–	14	13	–	14·6 ± 11·4
April	21	18	3	16	16	22	5	21	18	–	2	3	14	–	–	10·6 ± 8·8
May	2	2	–	3	2	4	3	4	3	–	–	3	4	–	–	2·0 ± 1·6
June	7	6	–	2	4	5	2	3	7	6	1	7	1	–	–	3·4 ± 2·7
	13·0 ± 10·0	17·2 ± 18·4	2·7 ± 3·7	10·0 ± 8·7	8·7 ± 6·8	13·2 ± 10·1	6·7 ± 6·9	12·2 ± 10·1	12·7 ± 9·3	2·3 ± 2·8	1·2 ± 0·9	3·2 ± 2·8	8·2 ± 6·6	3·2 ± 6·5	0·0 ± 0·0	
1997 (n = 324 h)																
February	1	–	4	3	3	4	1	5	6	–	–	–	4	2	–	2·2 ± 2·1
March	2	4	4	5	5	5	3	5	6	–	–	–	2	1	–	2·8 ± 2·2
April	3	6	1	2	5	10	2	6	12	–	3	4	2	4	3	4·2 ± 3·3
May	1	1	–	1	6	7	2	2	5	1	1	3	1	1	6	2·5 ± 2·3
June	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	1·7 ± 0·91	2·7 ± 2·7	2·3 ± 2·0	2·8 ± 1·7	4·7 ± 1·2	6·5 ± 2·6	2·0 ± 0·8	4·5 ± 1·7	7·2 ± 3·2	0·2 ± 0·5	1·0 ± 1·4	1·7 ± 2·0	2·2 ± 1·2	2·0 ± 1·4	2·2 ± 2·8	

*BI, black ibis; SB, spoonbill; LC, little cormorant; LE, little egret; GH, grey heron; WNS, whitenecked stork; PH, pond heron; ME, median egret; LRE, large egret; CE, cattle egret; LAS, lesser adjutant stork; OBS, openbill stork; PRH, purple heron; DTR, oriental darter; ISH, Indian shag.

[a]Number of species considered as wading birds and potential competitors of BNS. This includes a few species which were not actually interacted with BNS during the study period.

[b]Hours of observations are all months combined together for each year; this varied from one month to another.

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