

Resource Partitioning between Two Species of Migratory Waders, Common Redshank *Tringa totanus* (Linnaeus, 1758) and Little Stint *Calidris minuta* (Leisler, 1812) (Scolopacidae): A Behavioural Comparison in a Wetland Ecosystem in Bakhira Tal, Uttar Pradesh, India

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Abstract: Foraging behavioural comparison and movement types were studied between the common redshank (CRS) and the little stint (LS) to find out the trend of resource partitioning in a wetland ecosystem, Bakhira Tal, Santkabir Nagar District, U.P., India. Mean frequency of each foraging behavioural activity was recorded. Scanning and pecking behavioural activities were significantly higher in CRS than LS, while significantly higher frequency of probing activity was recorded in LS. Preening activity was found to be relatively less significant in LS. We observed walking activity more frequently in LS. Running activity was more common in CRS. Moreover, sprinting and resting activities were less frequently observed. In principal component analysis (PCA), PC 1 accounted for 66.37% of total variance while PC 2 and PC 3 accounted 24.31% and 6.29%, respectively. The scatter plot of PC 1 on PC 2 indicated intermingling of different behavioural activities between CRS and LS. Foraging niche breadth of CRS and LS were (1.66 ± 0.34) and (1.44 ± 0.38) , respectively, while foraging overlap was 0.87. The most frequently used as foraging habitat type by both the species was mud, followed by hydrophytes vegetation and shallow water. The result of the present study suggests that CRS and LS possess generally narrow niches with significant overlap for the two species, due to the use of analogous resources. We could conclude that there is a significant degree of overlap not only in resource utilisation, but also in foraging behavioural activities, feeding style and movement types in the common redshank and the little stint.

Key words: Bakhira Tal, niche, pecking, probing, resource partitioning

Introduction

Waders are a group of medium-sized wading birds, which have a wide variety of bill structures, long legs and toes that enable them to live and feed in shallow water habitats. The majority of the species are carnivorous and feed on small invertebrates and vertebrates, which are picked out from mud or exposed soil. The feeding behaviour of waders has been widely studied and different feeding strategies are well established among waders (GOSS-CUSTARD 1969, PIENKOWSKI 1979). They usually catch their

prey according to the particular feeding type of the species (PIENKOWSKI 1981).

Relationships between morphology and foraging ecology are well known in birds (ECKHARDT 1979, GRANT 1986). According to THOMPSON et al. (1990), the average bill and tarsus lengths are 41.8 mm and 47.6 mm, respectively, in the common redshank (CRS), and according to CRAMP & SIMMONS (1983), the average bill length and tarsus length are 18.1 mm and 21.2 mm, respectively, in the lit-

tle stint (LS). Pecking is the most frequent feeding style for CRS but occasionally probing is also used; the species feeds on intertidal invertebrates and fishes but mostly alone or dispersed (GOSS-CUSTARD 1970, NTIAMOA-BAIDU et al. 1996). CRS feed by pecking rapidly at the surface of the substratum, the bill is rarely inserted to its full depth of about 4 cm (GOSS-CUSTARD 1966). The foraging guild status is assigned as visual surface-foraging wader for CRS and tactile surface foraging-wader for LS (NTIAMOA-BAIDU et al. 1996). Some waders prefer to forage in mixed-species groups, while others forage in solitarily. LS that use probing as the most frequent foraging behaviour and are known to occur in flocks (GOSS-CUSTARD 1970).

Waders (Charadriiformes) migrate between breeding and non-breeding grounds annually, stopping at several coastal bays or estuaries or inland wetlands during the journey (MORRISON 1984). At the stopover sites, a large number of shorebird species with similar habitat requirements come together, forming dense multi-species aggregations in comparatively uniform habitats (MACLEAN & HOLMES 1971). Trophic structure (SCHOENER 1965), food partition (DAVIS & SMITH 2001), prey availability (MCNEIL et al. 1995) and selectivity (BACKWELL et al. 1998), predation threat (CRESSWELL 1994, YDENBERG et al. 2002) and abiotic factors (BURGER 1984) are often used to explain the differences in the habitat use of coexisting shorebirds.

Resource partitioning is a central concept in community ecology and it is often invoked to explain the coexistence of species using the same limiting resources (SCHOENER 1974). It has been confirmed mostly for terrestrial vertebrates (SCHOENER 1974, MACARTHUR 1958). Foraging animals compete with one another for resources (KEDDY 2001). The presence of competing individuals may lower the success of foragers and the competition may affect their survival and reproduction. Hence, competition may be an important factor for the dynamics of animal populations (CHRISTIAN 1970, GAUTHREUX 1978).

The exploitation and partitioning of resources by closely related species of birds have been previously studied (SCHOENER 1974, ECKHARDT 1979, ROTENBERRY 1985). Birds usually partition resources along habitat dimensions, followed by food, then temporal dimensions (CODY 1974). Foraging habitat use and feeding methods are important factors in resource partitioning (WELLER 1999, WIENS 1989) and can be used to assign foraging guilds of birds (LOPEZ et al. 2008, GATTO et al. 2008). Foraging theory predicts that prey availability influences feeding strategies, increasing the

trophic niche of species when food is scarce and reducing niche size when food is abundant (KREBS 1978, TODD et al. 1998, BEERENS et al. 2011, MARGALIDA et al. 2012).

Most studies attempting to reveal ecological differences between species during their migration and on their wintering grounds have been successful (RECHER 1966). However, on their northern breeding grounds, the wader species might show a greater degree of overlap in their diet and foraging behaviour. This has been suggested to be a result of limited taxonomic diversity but high density of their food resources (HOLMES & PITELKA 1968, BAKER & BAKER 1973). Although resource partition among waders has been well studied, it has not been recorded between CRS and LS. We found no available data from the study area, which imposed us to perform such observational field experiment. The aim of this paper is to study the foraging behavioural ecology of CRS and LS, particularly emphasising on feeding techniques and resource utilisation in different habitats (shallow water, mud and hydrophytes vegetation) in the study area. The study may prove successful in identifying the status of adaptability of two species of migratory waders with regards to food and feeding habitats in Bakhira Tal (wetland).

Materials and Methods

Study site

All the behavioural studies were carried out at Bakhira Tal (N 26°54' E 83°06'), a natural wetland in the Santkabir Nagar District, Uttar Pradesh (U.P.), India (Fig. 1). It has been declared a Bird Sanctuary in 1990 by the Forest and Wild life Department, Government of Uttar Pradesh, India. Bakhira Tal (wetland) is the largest natural wetland of Eastern U.P. It is a perennial wetland, where the source of water is natural rain and the Ami River, a tributary of the Rapti River. The average annual rainfall in the district is 1166 mm. During the winter, the mean minimum temperature is about 9 °C and mean maximum - 23 °C. In the post-monsoon seasons, the relative humidity is high and reaches above 70%.

Typha angustifolia, *Phragmites karka*, *Eichhornia crassipes*, *Hydrilla verticillata*, *Vallisneria spiralis*, *Potamogeton* sp. and *Lemna minor* are some of the dominant aquatic plants present in the lake. The presence of species of *Phragmites* patches inside the wetland makes it a unique habitat for migratory birds.

A large number of avian fauna, namely wader, waterfowl, migratory and other residential birds

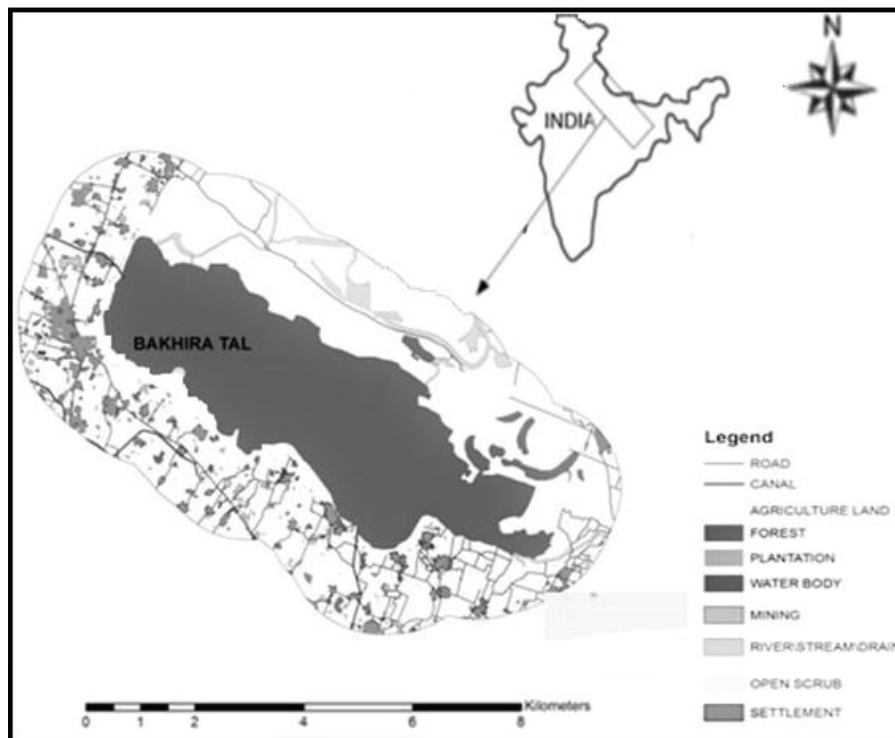


Fig.1. Map of the study area.

have been found in the study area. Also, it provides breeding and nesting ground to a large number of migratory and resident birds. The majority of the migratory birds come from Siberia, Tibet, China and Europe. Moreover, certain species of fish, amphibians, reptiles and mammals are also found dwelling in and around Bakhira Tal.

Study organisms

A total of 28 species of waders have been reported in the study area, out of which seven species are winter visitor (MISHRA et al. 2016). The most common breeding resident is the purple moorhen (*Porphyrio porphyrio*). It is also one of the most beautiful common water birds, inhabiting this wetland, locally known as “Kaima”. In the present behavioural study, the common redshank (*Tringa totanus*) and the little stint (*Calidris minuta*) were the two migratory waders under observation.

Data collection

Foraging observations were made during the winter of 2015-16 from 10th October to 24 March. Waders were easy to detect due to the lack of visual obstacles and their proximity to the observer. Random observation points were used. Individual bird movements were taken into account during switching between observation points to avoid collecting information on the same individual twice. Point count method

was applied for counting the total number of migratory species of waders.

The study site was visited randomly at 6-7-day intervals. The observation period was three times a day: morning (5:00-7:00 am), afternoon (12:00-2:00 pm) and evening (4:00-6:00 pm). Feeding behaviour of individual birds was observed in 15-minute observation sessions. Data collection consisted of a total of 46 days and 414 samples. Mean frequencies of foraging behavioural activities and movement types were recorded monthly and subsequently all data were pooled together.

Binoculars were used to observe the behavioural activities. The species identity, foraging habitats and feeding techniques of both waders were recorded using the initial observation method (i.e., only the 1st foraging observation of each individual was considered). This method is subject to conspicuousness bias, since the most active individuals are more likely to be discovered (HOLMES & ROBINSON 1988, MORSE 1990). Sequential observations (i.e., several consecutive observations of the same individual) have been avoided since they are not independent and are subject to temporal autocorrelation, i.e., each observation is usually correlated with previous ones (MORRISON 1984, HEJL et al. 1990). Three habitat types were identified as foraging habitats for migratory waders: mud, shallow water and hydrophyte vegetation.

Statistical analysis

The behavioural activity between the CRS and LS were compared using paired t-test. The probability level of 5% was used as the minimal criteria of significance. Foraging behaviour and strategy, as well as movement types were explored using principal component analysis (PCA) and MANOVA. Subsequently, data were organised in two matrices, for foraging habitat and for feeding techniques, following ALBRECHT & GOTELLI (2001). The one-dimensional matrices were used to calculate foraging niche breadth and niche overlap. The foraging niche breadth (FNB) was calculated for each species according to Levins' formula (LEVINS 1968):

$$\text{FNB} = 1 / \sum_{i=1}^n p_i^2,$$

where p_i is the proportion of observations in each category (i) within a particular niche dimension (i.e., foraging habitat and feeding technique). The values of this index range from 1 (a species uses only 1 niche category) to n (a species uses all niche categories in equal proportions). Foraging niche overlap (FO) between 2 species of migratory waders was calculated using Pianka's, formula (PIANKA 1973):

$$O_{jk} = O_{kj} = \frac{\sum_{i=1}^n p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^n p_{ij}^2 \sum_{i=1}^n p_{ik}^2}},$$

where p_{ij} and p_{ik} are the proportions of the i^{th} niche dimension used by the j^{th} and k^{th} species, respectively. This index has values from 0 (when niches are completely isolated from each other) to 1 (when niches show complete overlap). Statistical analyses were carried out using Graph Pad Prism (v. 5.01) and Paleontological software (PAST, v. 3.12).

Results

Mean frequency of each foraging behavioural activity was recorded (Fig. 2). Scanning activity was estimated as 55.66 ± 5.18 for CRS and 44.83 ± 7.11 for LS (Fig. 2A). Results of paired t-test indicated, that scanning was significantly higher in CRS than in LS ($t=9.286$, $p=0.0001$, $d.f.=5$, $n=414$). Mean frequency of pecking activity was 35.33 ± 8.14 and 12.66 ± 3.88 in CRS and LS, respectively (Fig. 2B). Pecking activity was highly significant ($t=11.08$, $p=0.001$, $d.f.=5$, $n=414$) in CRS than in LS. Probing activity was 45.5 ± 7.28 in LS (Fig. 2C), which was significantly higher ($t=11.83$, $p=0.0001$, $n=414$) than the one for CRS (26.47 ± 4.47). Preening activity was estimated to be 20.33 ± 3.20 and 18.33 ± 2.58 in CRS and LS, respectively (Fig. 2D). It was found to be relatively less significant ($t=3.464$, $p=0.180$, $d.f.=5$, $n=414$) in LS as compare to CRS.

Various movement types were observed and depicted (Fig. 3). Walking activity was 46.66 ± 3.88 in LS (Fig. 3A), which was significantly higher ($t=4.419$, $p=0.0069$, $d.f.=5$, $n=414$) than the one for CRS (41 ± 5.54). Running activity of CRS was 46.66 ± 3.88 , which was significantly higher ($t=5.655$, $p=0.0024$, $d.f.=5$, $n=414$) than the one for LS (33.16 ± 3.25 ; Fig. 3B). Moreover, we documented the frequency of sprinting activity to be 2.16 ± 1.16 , 2 ± 2.1 in CRS and LS, respectively (Fig. 3C), which was statistically not significant ($t=0.4152$, $p=0.6952$, $d.f.=5$, $n=414$). Resting was 35.83 ± 3.12 in CRS and 36.66 ± 4.71 in LS (Fig. 3D), which was not significantly ($t=1.185$ $d.f.=5$ $n=414$.) different in CRS and LS.

Principal component analysis (PCA) of various behavioural activities resulted into extraction of eight principal components (PCs). The first three principal components PC 1, PC 2 and PC 3 accounted for 66.37%, 24.31 % and 6.29 % of the total variance, respectively (Table 2). The PCA scatter plot of PC 1 on PC 2 indicated assortment and overlapping of behavioural activities between the two waders (Fig. 4). Percentages of resource used by CRS and LS were plotted (Fig. 5). Pecking was 53% in CRS and 42% in LS, more frequent in mud and less frequent in hydrophytes vegetation and shallow waters (Fig. 5). Probing was observed 27 %, in CRS and 48% in LS, more frequent in mud (Fig. 5). Foraging niche breadth (FNB) of CRS was 1.66 ± 0.34 and LS was 1.44 ± 0.38 , while foraging overlap (FO) between CRS and LS was 0.87 (Table 3).

Discussion

Based on descriptive statistics, we concluded there was a higher frequency of scanning in CRS than in LS. That suggested a preference for larger, more mobile prey in CRS and that they were visual surface foraging feeders. The similar pattern was reported in few water birds by NTIAMOA-BAIDU et al. (1996). Visual surface foraging feeders do not need long legs or long beaks as usually they stay out of the water and only pick up prey that is available on the surface (VAN DER GAAG 2012). While the lower frequency of scanning clearly indicated that LS is tactile surface foraging feeder because it may sense the presence of prey. GREENE (2006) has similar observations for *Tringa incana* and *Pluvialis fulva*. Tactile surface foraging waders frequently probe in mud and feed on exposed mud; while feeding, they would walk on mud to discover buried prey. This is in support of the findings of PIENKOWSKI (1979) and suggests that all waders possess two main foraging

techniques: tactile probing in the substrate and visual pecking at/ or near the substrate surface. Tactile techniques increase the chances of successful foraging, since much of the bird's time is concentrated on searching for food. The functional requirements of a tactile foraging strategy are (1) high penetration capacity and (2) high inspection capacity (BAKER & BAKER 1973, ZWEERS & GERRITSEN 1997).

The present study clearly showed a significant difference in feeding behaviour between CRS and LS. The two main foraging behavioural activities of these migratory waders were pecking and probing. Our field experiment revealed that pecking was the most frequent feeding style in CRS but probing technique was also adapted occasionally: they fed on intertidal invertebrates at or near the sediment surface (epifaunal prey) and fishes. We found that LS also preferred pecking but probing was the principal mode of foraging technique. Pecking and probing are thought to be the main methods for visual and tactile foraging, respectively (BAKER & BAKER 1973).

Shorebirds make their foraging decisions based on a substitution between rewards and costs (MOURITSEN & JENSEN 1992). Pecking consisted of superficial peck (a single touch of the bill tip to the sediment surface) or medium peck (insertion of half of their beak into the sediment). Shorebirds may be using visual cues to detect epifauna and take out them by either pecking (BURTON 1974) or using surface-tension transport (RUBEGA 1997). During the observation session, we have recorded quick pecking motions directed forward and towards the ground in both species. This presumably aims at bring invertebrates to the surface of the substrate (MEYERRIECKS 1959 & GOSS-CUSTARD 1969).

Probing involves insertion of the bill into the sediment, allowing the capture of invertebrates that live below the sediment surface (infaunal prey). Probing is expected to facilitate the capture of larger prey (DURELL 2000) but also obstructs the field of vision more than pecking and may reduce the ability to detect predators during feeding (BARBOSA & MORENO 1999). Probing may appear more rewarding in terms of success rate on advantageous prey than pecking because of the higher prey availability potential within the extended search depths (MOURITSEN & JENSEN 1992). However, probing can cost more than pecking in terms of time and energy (GERRITSEN & VAN HEEZIK 1985) or potential risk of bill wear due to friction with sediment particles (DURELL 2000).

The underlying food preferences of these species can be inferred from their behavioural dif-

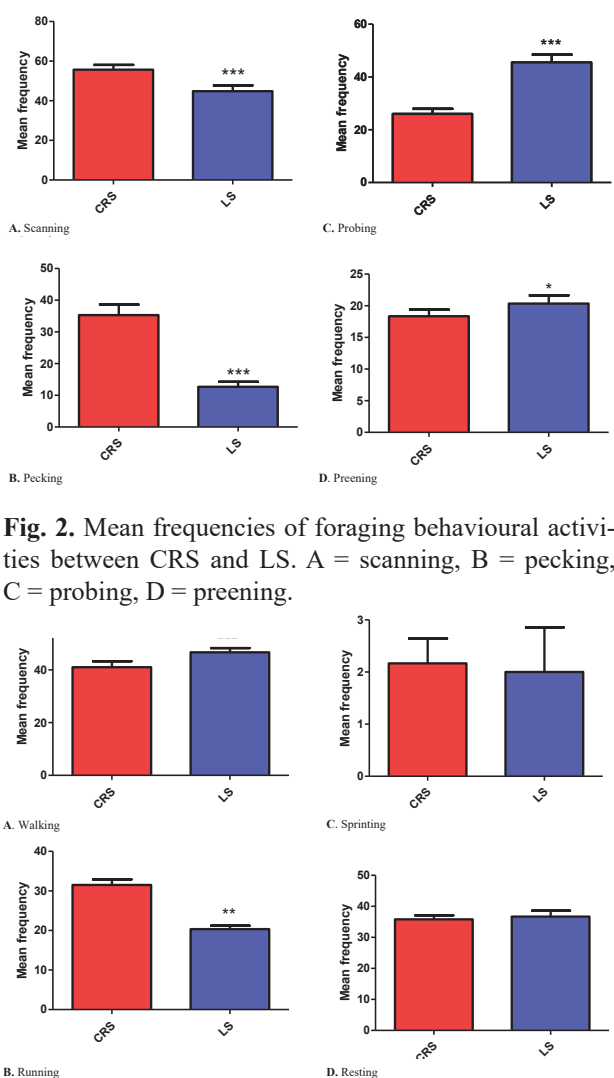


Fig. 2. Mean frequencies of foraging behavioural activities between CRS and LS. A = scanning, B = pecking, C = probing, D = preening.

Fig. 3. Mean frequencies of movement types for CRS and LS. A = walking, B = running, C = sprinting and D = resting).

ferences. An evolutionary pathway from pecking to probing has been proposed by many authors (ZWEERS 1991a, ZWEERS et al. 1995, ZWEERS & GERRITSEN 1997), using deductive methodology. This hypothesis considers pecking be the “historical initial condition for avian feeding mechanisms” (ZWEER 1991a, 1991b, ZWEERS et al. 1994).

We found that preening was higher in LS. In preening, we observed the use of the bill to position feathers, interlock feather barbules that have become separated and clean plumage. Preening seemed to occur periodically between intensive foraging. Similar observation was reported by TJØRVE et al. (2007) in the little stint.

Walking behaviour was more frequently observed in LS than in CRS, which suggested that LS preferred for mobile prey. Similar were the observations of GREENE (2006) on *Tringa incana* and

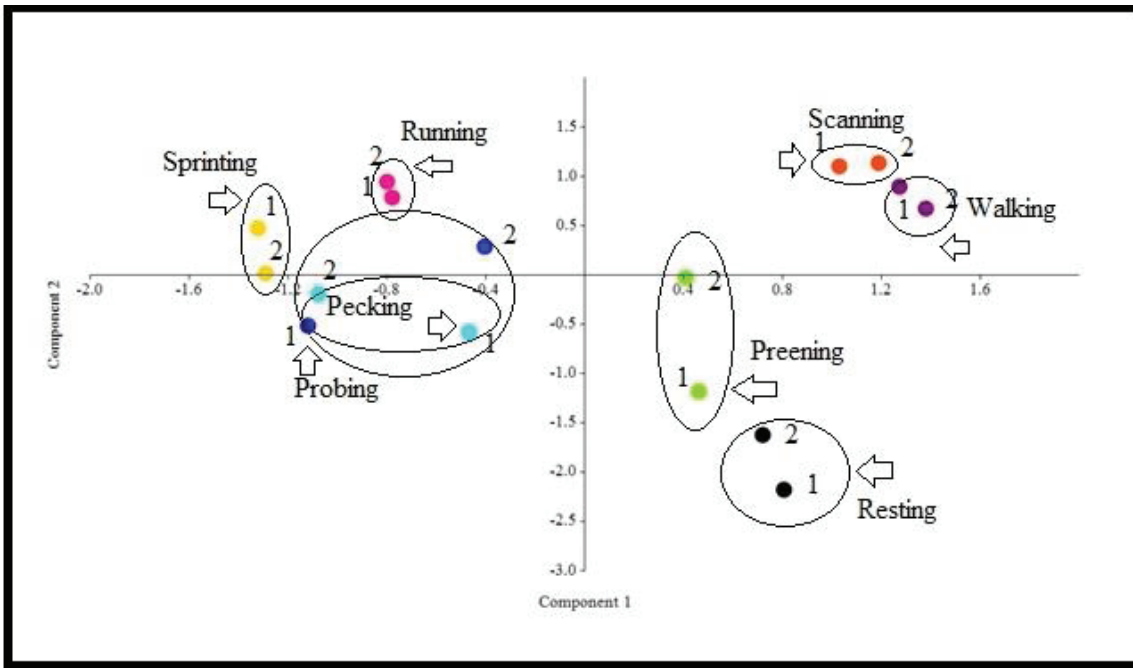
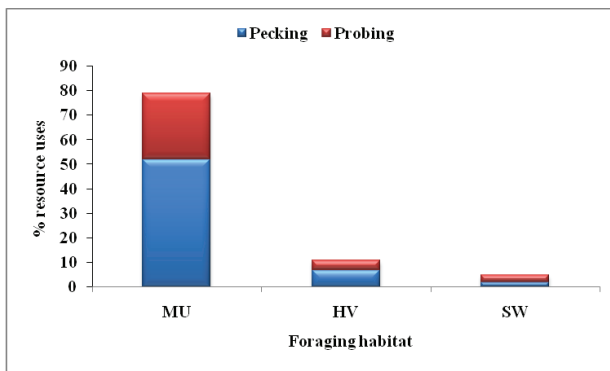
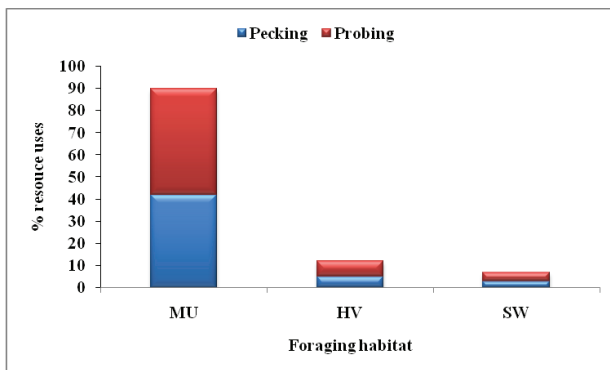


Fig. 4. Scatter plot of PC1 on PC2 of different foraging behavioural activities and movement types between the common redshank (1) and the little stint (2).



Common redshank



Little stint

Fig. 5. Foraging habitat types and feeding techniques of the common redshank and the little stint. Habitats code: MU-mud, HV-hydrophytes vegetation and SW-shallow water.

Pluvialis fulva. CRS preferred non- mobile prey as we have observed less frequency of walking behaviour. The similar pattern was recorded in few waders by DIAS et al. (2009).

Our results demonstrated that running behaviour was more frequent in CRS than LS, which also suggested that CRS was visual surface forager. Visual surface foraging waders are the small waders that would intermittently run, pause and watch and then take another run, sometimes to catch surface-living benthic invertebrates or fish by visually detecting the prey items. SPEAKMAN & BRYANT (1993) reported a similar pattern of movement in the common redshank.

In the present study, sprinting activity was rare in both CRS and LS. Moreover, we recorded that there were no significant difference in resting activity in CRS and LS.

The PCA scatter plot of the foraging behavioural activities and movement types between CRS and LS depicted the intermingling of different behavioural activities between the two waders. The small niche breadth and significant niche overlap suggested huge overlapping in resources utilisation was in disagreement with the findings LIORDOS(2010). Based on the use of two foraging niche dimensions, '1' horizontal (foraging habitat) and '2' vertical (feeding technique), which were recorded in order to assist in understanding the spatial distribution of CRS and LS at Bakhira Tal, we can

Table 1. Different foraging behavioural types and their description.

S.N.	Behaviour Type	Description
1	Scanning	Visually searching for prey
2	Pecking	Taking food bit by bit
3	Probing	Probing in mud or shallow water
4	Preening	Grooming of feathers

Table 2. First three principal components extracted from the principal component analysis of different foraging behavioural activities and movement types between CRS and LS in Bakhira Tal.

S.N	Behavioural activities	PC 1	PC 2	PC 3
1	Scanning	0.01657	-0.01955	0.10445
2	Pecking	0.02239	-0.06454	0.17643
3	Probing	0.32504	0.53767	-0.58891
4	Preening	0.15566	0.77172	0.39065
5	Walking	0.52883	-0.09038	0.62211
6	Running	0.75978	-0.31937	-0.26404
7	Sprinting	-0.08363	0.01237	0.04252
8	Resting	-0.07367	0.02223	-0.00157
	Eigen value	1.00390	0.51341	0.18994
	Total variance (%)	66.373	24.309	6.2914

Table 3. Foraging niche breadth (FNB) and foraging overlap (FO) of migratory waders wintering at Bakhira Tal.

Species	FNB (Habitat)	FNB (Technique)	Mean FNB	Foraging Overlap (FO)
CRS	1.91	1.42	1.66±0.34	0.87
LS	1.72	1.17	1.44±0.38	

infer that knowledge of the ecological requirements of these waders can be used for their conservation and monitoring at Bakhira Tal.

A variety of foraging habitat types and feeding techniques were used by these species of waders during the wintering season. During the field observation, we have seen that the most frequently utilised habitat types were mud and hydrophytes vegetation.

Variations in the proportions of resource use also occurred depending either on habitat or on feeding technique. The presence of other birds, usually conspecifics, may have a great effect on foraging behaviour (GOSS CUSTARD 1984, PUTTICK 1984). Some individuals of birds switch between techniques in response to changes in prey availability and feeding habitat (HARRINGTON 1982, WHITFIELD 1990).

Despite these differences, CRS and LS have generally narrow niches and significant niche overlap between them, due to the use of similar resources. The use of similar foraging habitats and feeding techniques suggested that the two birds utilised similar food types (WIENS 1989) and should, therefore, differ in some other niche dimensions.

Initially, guild structure was considered to be generated through intense interspecific competition (PIANKA 1980, JAKSIC & MEDEL 1990). However, it was found that the opportunistic use of temporarily superabundant resources may give similar results (WIENS 1989).

Conclusion

CRS and LS have generally narrow niches and significant niche overlap between them, due to the use of similar resources and the relatively rich feeding habitat they share. The current foraging observational experiments concluded that also the degree of foraging behavioural activities, feeding style and movement types of the two species of migratory waders is significant.

Conflict of interest: The authors do not have any conflict of interest to declare.

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