

Research

Foraging Behaviour of Three Shorebird Species on Coastal Mudflats of Southwestern Sarawak

Wen Teng Ng¹, Mohamad Fizl Sidq Ramji^{1*}, Jongkar Grinang² and Andrew Alek Tuen²

1. Faculty of Resource Science and Technology, Universiti Malaysia Sarawak, 94300 Kota Samarahan, Sarawak, Malaysia
2. Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, 94300 Kota Samarahan, Sarawak, Malaysia

*Corresponding author: rmfizl@unimas.my

ABSTRAK

Many shorebirds are long-distance migrants and they congregate on intertidal mudflats for feeding throughout their non-breeding season. Despite being one of the key staging sites for migratory shorebirds, data on shorebirds foraging ecology in Sarawak is insufficient for the understanding of the interaction between shorebirds and their behaviour. This study aimed to determine the foraging behaviour of Whimbrel (*Numenius phaeopus*), Bar-tailed Godwit (*Limosa lapponica*) and Terek Sandpiper (*Xenus cinereus*) at Asajaya and Buntal mudflats. Data collection of this study was conducted at low tide, during two non-breeding seasons with a total of 12 months of sampling. Focal observations were conducted within a 50 m × 50 m quadrat. A total of 8 exclusive foraging techniques were observed for the three shorebird species, including: pecking, probing, picking, stabbing, snapping, submerging, sweeping and ingesting. Terek Sandpiper displayed all the exclusive foraging behaviours, whereas Whimbrel and Bar-tailed Godwit showed 7 and 5 behaviours, respectively. The three shorebirds also displayed non-exclusive foraging behaviours such as walking, preening and defecating. Spearman correlation test indicates a positive correlation between the foraging behaviours performed among three shorebird species. All three shorebird species adopted similar mixed foraging strategies comprising pecking and probing, with an exception on supplementary behaviours observed in Whimbrel and Terek Sandpiper. Principal Component Analysis (PCA) analysis showed a strong correlation between picking and ingesting behaviours, suggesting a high chance of foraging success with the presence of picking behaviour. The outcome of this study is crucial in understanding how shorebirds maximise their behavioural performance when foraging as well as to assist in formulating better conservation strategies for targeted migratory shorebird species and coastal mudflats.

Key words: Foraging behaviour, intertidal, migratory, Sarawak, shorebirds

Article History

Accepted: 16 February 2024

First version online: 31 March 2024

Cite This Article:

Ng, W.T., Ramji, M.F.S., Grinang, J. & Tuen, A.A. 2024. Foraging behaviour of three shorebird species on coastal mudflats of southwestern Sarawak. Malaysian Applied Biology, 53(1): 169-185. <https://doi.org/10.55230/mabjournal.v53i1.2712>

Copyright

© 2024 Malaysian Society of Applied Biology

INTRODUCTION

Most shorebirds winter in tropical regions, particularly in coastal wetlands, from their breeding area in temperate regions (Sánchez *et al.*, 2005; Turpie & Hockey, 2008). A previous study by Bamford *et al.* (2008) reported that migrating shorebirds travel more than 20,000 kilometres per year during their life span. Such long-route migration requires high energy demand from the migrants. To replenish their energy during migration, many arctic shorebirds utilize terminal spring staging areas that are strategically positioned within mid-temperate latitudes, where concentrated food resources are available (Watts *et al.*, 2017). These areas are primarily wetlands that serve as an essential staging ground to provide feeding opportunities to the migrants (Ramli & Norazlimi, 2016; Watts *et al.*, 2017). As the shorebirds experience rigorous energy demands during the long migration, sufficient feeding is therefore essential for the migrating shorebirds to sustain themselves.

Previous studies revealed that migratory birds spend most of their time feeding in the non-breeding ground to gain sufficient energy to maintain their high metabolism rate throughout the long-distance flight (Landys *et al.*, 2005;

Colwell, 2010). It is considered the most crucial activity for the migratory shorebirds during their long migration across the continents. Unlike the passerine birds that can feed nearly anywhere throughout their migration, the shorebirds only have limited access to food, and they require specialized habitats such as intertidal shores, estuaries, and wetlands to recharge themselves before continuing their journey (O'reilly & Wingfield, 1995; Stroud *et al.*, 2008). These specialized habitats play a crucial role as a refugee or stopover site for the shorebirds by providing a food source, where the distribution of shorebirds is often reflected by the presence and abundance of the food source in the stopover sites (Goss-Custard, 1977; Willems *et al.*, 2010).

Foraging refers to a series of behaviours performed by an individual animal when acquiring food, including prey detection, food acquisition, and the unique techniques being used when handling or extracting prey (Schneider, 2017). Such foraging behaviour is said to be primarily influenced by food availability (Pyke *et al.*, 1977). Nonetheless, shorebirds are a diverse bird group that possesses various kinds of foraging techniques, such as pecking and probing (Finn, 2009). Differences in foraging behaviour among shorebirds are known to be closely associated with morphological factors (Jing *et al.*, 2007; Turpie & Hockey, 2008). Generally, vision is vital for the foraging shorebirds as it aids the bird in locating prey by their tracks, disturbance of substrate or entrance of burrows. However, certain shorebirds such as Red Knots (*Calidris canutus*) and sandpipers (Scolopacidae) are highly dependent on their sensory systems on the bill when locating prey (Cunningham *et al.*, 2010).

Whimbrel (*Numenius phaeopus*), Bar-tailed Godwit (*Limosa lapponica*), and Terek Sandpiper (*Xenus cinereus*) can be found abundantly along the Sarawak coastline throughout the migrating season. Whimbrel is well-known as a non-breeding migrant to South America, Africa, and Southeast Asia as far as Australia, including Peninsular Malaysia, Sabah, Sarawak, and Singapore (Watts *et al.*, 2017). It has darker plumage, and it is physically similar to the Eurasian Curlew (*Numenius arquata*). But in terms of size, it looks smaller as compared to the Curlews. Whimbrel has a total body length ranging from 40 – 45 cm (Higgins & Davies, 1996). In addition, it possesses a long decurved bill (Finn, 2009; Myers, 2016) and an average bill length ranging from 82.0 mm to 87.1 mm (Katrínardóttir *et al.*, 2013; Norazlimi & Ramli, 2015). Adult Whimbrel has a strong pattern on its head with an eye stripe and a dark brown crown, a wingspan of 76 - 89 cm, and a weight of approximately 350 g (Higgins & Davies, 1996). Whimbrels are categorised as Least Concern (LC) in the IUCN Red List from BirdLife International (2022). It is versatile in foraging, where it often relies on visual cues and touch senses when locating prey (Finn, 2009; Norazlimi & Ramli, 2015). Whimbrel was reported to favour shelled prey, particularly on crustaceans when feeding (Dann, 1993; Zwarts & Dirksen, 1990).

Bar-tailed Godwits are known as ubiquitous species to the East Asian-Australasian Flyway (EAAF). It is a medium-sized wader distinguished from the Dowitchers by their long-upturned bill and long legs. It has a shorter yet noticeably straight yet slightly upturned bill (around 29 cm), with a prominent supercilium and curlew-like streaking upper part (Myers, 2016). Bar-tailed Godwits are long-distance migratory shorebirds that breed originally in the Arctic or Sub-arctic continents in Scandinavia, Russia, and northern and southern Alaska (Wilson *et al.*, 2007). The Bar-tailed Godwits migrate to temperate and tropical regions of basically all continents (Higgin & Davies, 1996). This bird was recorded to travel 12,000 km non-stop throughout the post-breeding migration journey (Woodley, 2022). It was also reported that Bar-tailed Godwits are found over a larger feeding area of sandy mud and sand in the outer estuaries (Greenhalgh, 1975). A study by Duijns *et al.* (2013) reported that the Bar-tailed Godwit showed a clear preference on polychaetes. A recent report by Woodley (2022) highlighted an annual decline of 2% in the Bar-tailed Godwit population, driven by the loss of habitat at one of their important staging sites – the Yellow Sea. To date, this bird is categorized as Near Threatened (NT) according to the IUCN Red List from BirdLife International (2022).

Terek Sandpiper is remarkably peculiar to the sandpipers which are easy to identify. It has a distinctive long, sharply upturned bill, with bill length ranging from 40.5 mm – 52.6 mm (Karlionova *et al.*, 2006). Terek Sandpiper possesses short bright yellow or orange legs and a uniform grey plumage overall (Karlionova *et al.*, 2006). Besides, the Terek Sandpiper is a relatively small bird with a body measurement of around 23 cm (See & Chan, 2020). They are the commonest shorebirds that can be found on the mudflats, typically in small flocks, and prefer to join the mixed flocks of waders when feeding. Similar to Whimbrel, the Terek Sandpiper was widely recognized as a crustacean specialist, feeding particularly on crabs (Piersma, 1986; Bijlsma & de Roder, 1991). This species has a vast population globally, where it is evaluated as Least Concern according to the IUCN Red List from BirdLife International (2022).

To date, the foraging ecology of shorebirds has been widely studied in many regions under the major flyways (Bamford *et al.*, 2008). Playing a crucial role as one of the important stopover sites for the

birds migrating along the EAAF flyways, the coastline of the Yellow Sea in China has been the subject of comprehensive research. The foraging ecology of the migratory bird species, including but not limited to the Great Knots, Red Knots, and Bar-tailed Godwit, has been broadly discussed in this area (Choi, 2015; Choi, C. et al., 2017; Choi, S. et al., 2017). In Sarawak, the Bako-Buntal Bay that falls under the EAAF flyways is also one of the key stopover sites for migratory shorebirds. The foraging ecology of migratory shorebirds in this continent is, however poorly understood. The documentation of the foraging ecology of the migratory shorebirds is critical to understanding their behaviour in the non-breeding ground. Hence, the objectives of this study are to determine the foraging behaviours and strategies of the Whimbrel (*Numenius phaeopus*), Bar-tailed Godwit (*Limosa lapponica*), and Terek Sandpiper (*Xenus cinereus*) in Asajaya and Buntal mudflat located within the Bako-Buntal Bay, Sarawak, East Malaysia.

MATERIALS AND METHODS

Study area

Bako-Buntal Bay is one of the internationally recognized important sites of shorebirds in Malaysia. This bay houses several threatened shorebird species while supporting the highest number of shorebirds compared to other sites (Risidiana, 2015; Lai, 2019). Bako-Buntal Bay formed a large complex of sites, including coastal wetlands that stretch from the tip of the Santubong peninsula to the mouth of the Sadong (Bakewell et al., 2017). It is the most significant part of the entire Sarawak coastline as this bay hosts huge numbers of migratory shorebirds during the migration period.

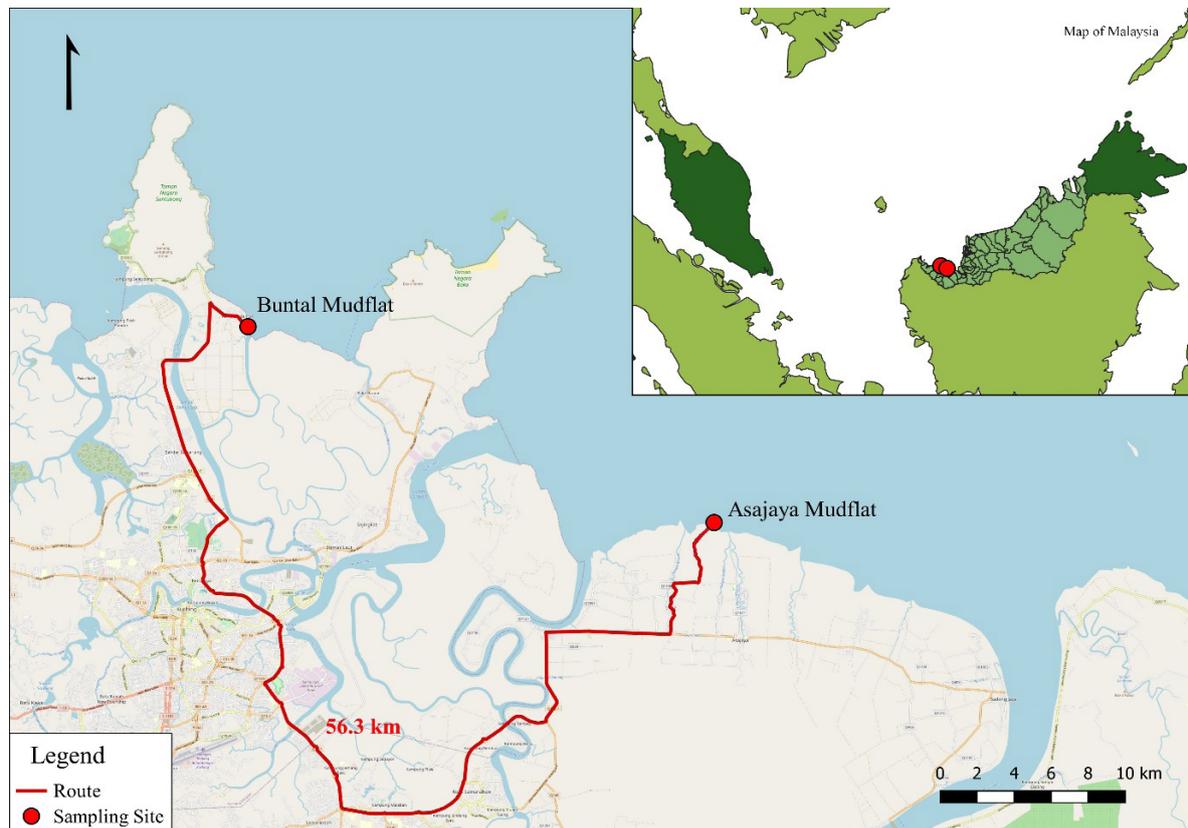


Fig. 1. Map of sampling sites showing the route between two tidal mudflats (generated from QGIS)

Asajaya mudflat (N01°36'; E110°36'; 8 m a.s.l) is located about a 40-minute drive from the UNIMAS campus in Kota Samarahan Division. Asajaya was originally known as Nonok, which was previously under the administration of Kuching Division in 1970 before Kota Samarahan took over and is popularly known as Asajaya until now. Asajaya mudflat is comprised of intertidal sandy beach and mudflat area where the locals usually collect Razor clams (*Solen* spp.) during low tide. It also has the widest mangrove stripes around the Asajaya River estuary, extending about 1.2 km out to the sea (Bakewell et al., 2017).

Meanwhile, the Buntal mudflat (N01°41.7807'; E110°22.4248'; 8 m a.s.l) is located in Kampung Buntal, Kuching, Sarawak, about 30-minute drive from Kuching. These flats are located off the Kuching-

Santubong Road, where forming a semi-circular bay bordered by the Bako National Park to the east and Gunung Santubong to the west (BirdLife International, 2020). Buntal mudflat consists of mostly sandy substrates that overlaid with the mud near the estuaries. Sandbars of the bay are constantly shifting, where almost the entire bay will be exposed during low tide (BirdLife International, 2020).



Fig. 2. Aerial view of the expansive Asajaya mudflat and Buntal mudflat

Data collection

The focal observation was conducted twice per week for 12 months from November 2017 to March 2018 and from October 2018 to March 2019. A pair of binoculars (Nikon Action EX; 10 × 50) were used to observe the targeted individuals along with a portable spotting scope (Nikon Spotting Scope 90; 20X-60X). GPS coordinates of recorded individuals or flocks were tagged using a Global Positioning System (GPS) unit (Garmin GPSMAP 78S).

The foraging behaviour of each species was recorded during low tide using a digital camera (Nikon Coolpix P900; 16 megapixels). Individuals were selected by directing the binoculars and spotting scopes within the foraging flocks. The selection of the next individual was continued by moving the scopes in one direction, from left to right or vice versa. Each individual selected was located 5 meters away from the previously observed individual to minimize the chances of observing the same individual. Following Norazlimi and Ramli (2015), focal observation was conducted within the range of thirty sec up to a maximum of five min. In this study, focal observation was modified with a minimum of ten sec and a maximum of one minute due to the gregarious behaviour of the foraging shorebirds. The focal observation begins when the individual is spotted in the frame until it is out of frame. Any individuals that left the “viewing frame” within 10 seconds during the focal observation were not included in the data analysis. The observation ended when the recording exceeded one minute. Any behaviour displayed afterwards is considered a new observation. However, the observation is still treated as one if the individual is spotted handling the prey between the first two min.

Data analysis

The foraging behaviour was measured by breaking down the behaviour into units of action patterns. These action patterns are discrete and species-specified, and where it is repeated time after time in the same manner (Brockmann, 2011). In this study, every action pattern observed from the foraging shorebirds was recorded. An ethogram was constructed along with sketches to describe and visualise the motion of each action pattern. The ethogram is an inventory of an animal’s behaviour, where any action patterns performed by the animal are listed in an ethogram along with a precise definition and detailed descriptions (Crews *et al.*, 2002; Brockmann, 2011). Description of foraging behaviour was identified based on Zweers and Gerritsen (1997), Nebel *et al.* (2005) and Nol *et al.* (2014). Additionally, the sequence of action patterns was recorded and the transition matrices – the number of transitions from one behaviour to another were also calculated. The transition frequency was then computed to determine the probability that a particular action pattern follows another. Ultimately, a kinematic diagram was constructed to show the behavioural flow that summarized the likelihood of every behavioural sequence (Brockmann, 2011). The velocity for each action pattern recorded in each studied species was also computed respectively by dividing the number of times that behaviour occurs by the total time spent. All the calculation was computed using Microsoft Excel.

Spearman correlation test was used to evaluate the association between behaviour transition

matrices among Whimbrel, Bar-tailed Godwit, and Terek Sandpiper. The statistical comparison of species transition matrices, however, requires that the matrices for each species were of the same size and contain comparable behaviours. Hence columns of zeros were included for the behaviours that were observed in one species but not another. Each species transition matrix was unfolded into a vector column whose rows represent each behavioural transition, and the comparison was made between the species vectors. The significance of the correlation coefficient was determined with the permutation test. Besides, the Spearman correlation was also used to test the relationship among the different foraging behaviours used by the studied shorebirds (i.e., techniques of capture & ingestion rate). Next, Principal Component Analysis (PCA) was performed to determine the pattern of foraging behaviour of shorebird species. This analysis was used to reduce the extensive behaviour data to a small set, comprehensive summary. PCA lies in the similarity of the foraging behaviour of the three shorebirds at two mudflats throughout the study period. The significance of variances in the foraging behaviour was tested for significance by using 1000 permutations. All statistical analyses were performed using R software 4.0 (CRAN, <http://cran.r-project.org>), with statistical packages such as *ggpubr*, *FactoMineR* and *factoextra* (R Core Team, 2022). An ethogram was illustrated to show a list of the techniques observed during the observation (Table 1).

Table 1. Ethogram of foraging techniques observed

Technique	Descriptions
a) Pecking (PE)	- The primary method deployed when the tip of the shorebird's bill jabbing on the ground surface. This action is repetitive and quick, where multiple pecking can be often spotted within a sec.
b) Probing (PR)	- An action when 3/4 or the entire shorebird's bill penetrates the sediments (e.g., sand flat, mudflat, or puddles) to search for prey that is burrowing under the ground.
c) Picking (PI)	- An action is when the shorebird takes and holds its prey from the ground surface using its bill.
d) Stabbing (ST)	- An action is when the bill of the shorebird is inserted into the ground and dug repeatedly into the same spot until the prey is dragged out from the burrow.
e) Snapping (SN)	- An action where the prey is being shaken and cracked into smaller pieces (i.e., detach the prey's appendages, snap off the prey's claw).
f) Submerging (SB)	- An action is observed when the shorebird dips its prey into the water puddles or by the water edges.
g) Sweeping (SW)	- An action when both the head and neck of a shorebird move side to side when thrusting into the water.
h) Ingesting (IG)	- The final step is foraging where the prey intake is successful. It is an action when the shorebird swallows the prey, with its head slightly lifted.
i) Preening (PREEN)	- Can be seen usually when the tide has risen when the shorebird starts to groom its feathers or beak. Occur randomly at times.
j) Walking (WALK)	- Action where the shorebird displays to move from one spot to another. Commonly displayed as slow walking, normal walking, and running.
k) Defecating (DF)	- An action of digestion where the shorebird's faeces are discharged through its anus.

These techniques were further categorised into two: (i) exclusive behaviour (i.e. behaviour performed restricted to foraging) and (ii) non-exclusive behaviour (i.e. series of general techniques performed throughout the focal activity). The non-exclusive behaviours refer to the actions which are not concerned with foraging, such as locomotion (e.g., walking, running, flying), comfort (e.g., stretching, preen, bath), and maintenance behaviour (i.e., defecating) (King, 2008; Gokula, 2012; Boggies, 2018). These actions were marked since they were generally displayed by the shorebirds in pre-, during, and post-foraging. Although none of the non-exclusive behaviour rates were calculated in the study, it is necessary to record these actions as they are crucial to depict the foraging behaviours of shorebirds.

RESULTS

Ethogram

A total of 717 focal observations comprising: (i) Whimbrel ($n=269$), (ii) Bar-tailed Godwit ($n=211$) and Terek Sandpiper ($n=237$) were recorded in the study. An average of 8-10 individuals per species were observed monthly. Based on the observations, a total of 11 foraging techniques were recognised. A consolidation of ethogram charts was illustrated to show the behaviours performed by each respective species. Figure 3 shows ten, eight and twelve foraging behaviours for Whimbrel, Bar-tailed Godwit

and Terek Sandpiper respectively. Seven exclusive behaviours in foraging: including pecking, probing, picking, stabbing, snapping, submerging, and ingesting were marked. Three non-exclusive behaviours such as walking, preening, and defecating were recorded as well.

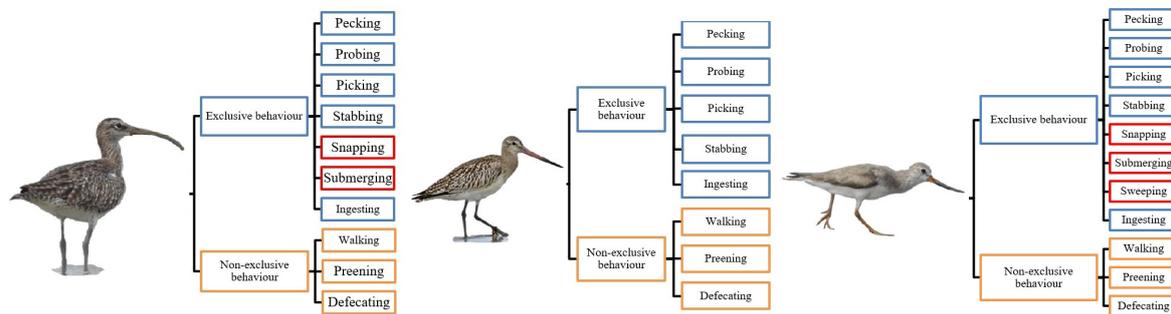


Fig. 3. An ethogram chart showing exclusive foraging behaviours (blue box) and non-exclusive behaviours (orange box) of Whimbrel, Bar-tailed Godwit and Terek Sandpiper. Behaviours in the red box indicated exclusive behaviours observed in only Whimbrel and Terek Sandpiper.

Kinematic diagram

Whimbrel

The accumulation of total recordings collected for the entire sampling was almost six hours which the selected shorebird species performed foraging for approximately 21,385 s (5 hr, 56 min & 25 s).

Whimbrel performed foraging for approximately 7,996 s (2 hr, 13 min & 15 s), with an accumulation of 269 observations recorded throughout the study. The sequence that performs the most by Whimbrel is the transition from pecking to pecking, followed by the transition from pecking to probing, probing to pecking, probing to probing, picking to ingesting, and so on. The total behavioural sequences shown by the Whimbrels were 1927 behaviour sequences, made up of a repetition of 30 behaviour sequences. A total of 197 successful foraging attempts (ended up with ingesting) were recorded from the focal observations of Whimbrel.

A kinematic diagram of Whimbrel's foraging behaviour which is composed of non-exclusive and exclusive foraging behaviours was illustrated in Figure 4. Arrows indicate the direction of transition. The transition probability of a particular behaviour sequence is indicated by different line weights and the number next to the lines. Non-exclusive behaviours are included to show the complete behavioural flow in Whimbrel's foraging.

Bar-tailed Godwit

Bar-tailed Godwit performed foraging for approximately 6,548 s (1 hr, 49 min, & 8 s), with a total of 211 observations recorded throughout the study. Results showed that Bar-tailed Godwit performed the transition from pecking to pecking the most. It was followed by the transition of probing to probing, pecking to probing, probing to pecking, picking to ingesting, probing to picking, and so on. A total of 189 successful foraging attempts (ended up with ingesting) were recorded from the focal observations of Bar-tailed Godwit.

The kinematic diagram of Bar-tailed Godwit's foraging behaviour which is composed of non-exclusive and exclusive foraging behaviours is illustrated in Figure 5. Non-exclusive behaviours are included to show the complete behavioural flow in Bar-tailed Godwit's foraging.

Terek Sandpiper

Terek Sandpiper performed foraging for approximately 8,218 s (2 hr, 16 min & 49 s), with an accumulation of 237 observations recorded throughout the study. Results showed Terek Sandpiper performed the transition of pecking to pecking the most. It was then followed by a transition of probing to probing, pecking to probing, probing to pecking, picking to ingesting, and so on. A total of 134 successful foraging attempts (ended up with ingesting) were recorded from the focal observations of Terek Sandpiper. Most of the successful attempts were made after picking, followed by submerging, snapping, probing and stabbing.

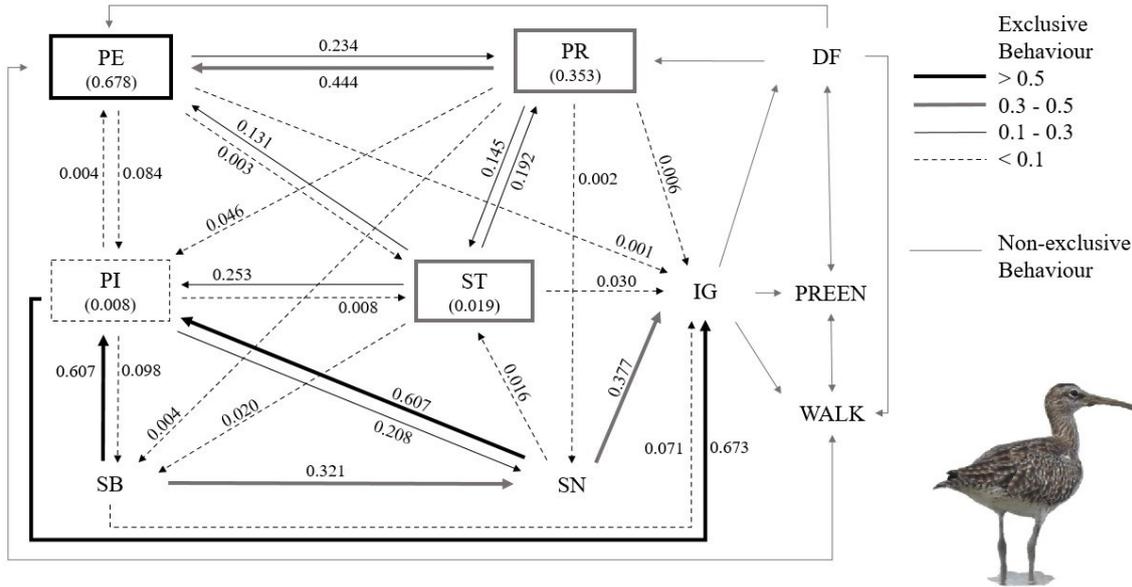


Fig. 4. Kinematic diagram of foraging behaviours displayed by Whimbrel. (Note: PE = Pecking, PR = Probing, PI = Picking, ST = Stabbing, SN = Snapping, SB = Submerging, IG = Ingesting, WALK = Walking, PREEN = Preening, DF = Defecating).

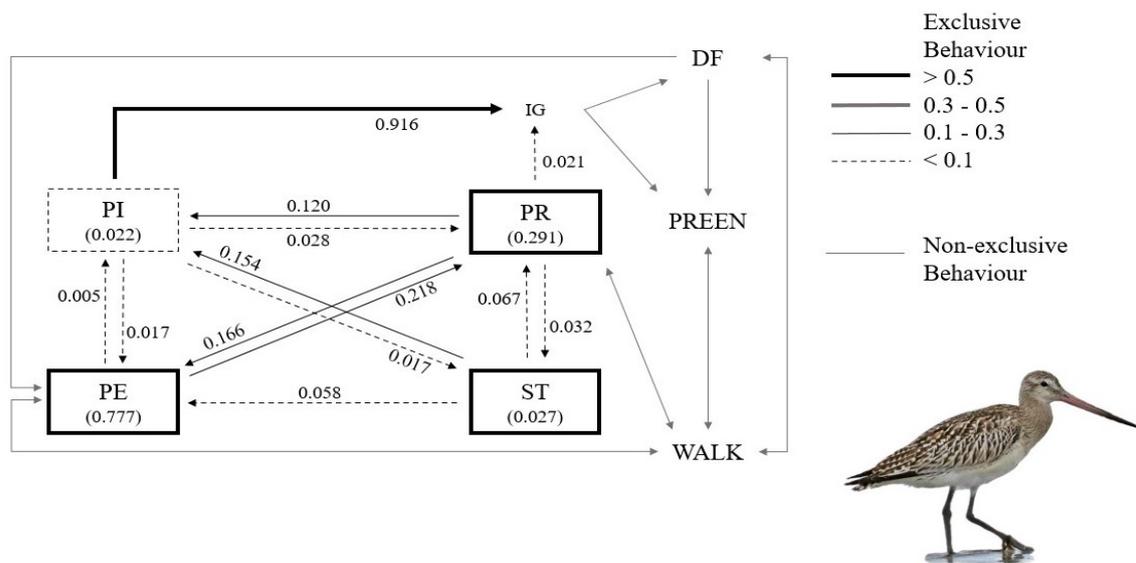


Fig. 5. Kinematic diagram of foraging behaviours displayed by Bar-tailed Godwit. (Note: PE = Pecking, PR = Probing, PI = Picking, ST = Stabbing, IG = Ingesting, WALK = Walking, PREEN = Preening, DF = Defecating).

The kinematic diagram of Terek Sandpiper's foraging behaviour which is composed of non-exclusive and exclusive foraging behaviours was illustrated in Figure 6. Non-exclusive behaviours are included to show the complete behavioural flow in Terek Sandpiper's foraging.

Total frequency of foraging behaviours

The total frequency of each exclusive foraging behaviour performed by the studied shorebirds was summed in this study. The occurrence rate of each behaviour (\pm SE) has been computed. The results are presented in Table 2.

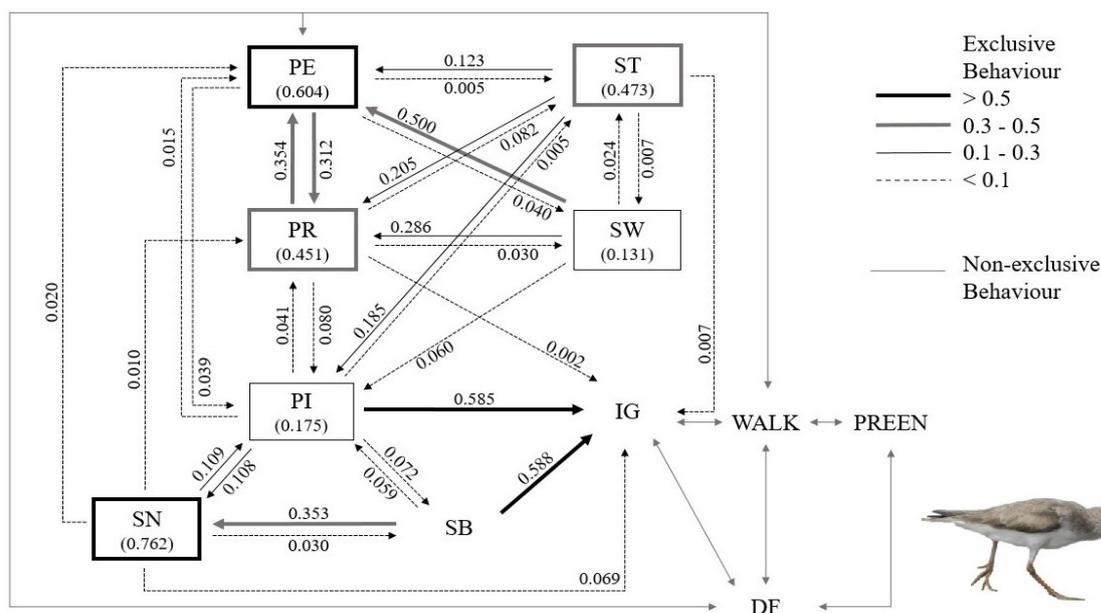


Fig. 6. Kinematic diagram of foraging behaviours displayed by Terek Sandpiper. (Note: PE = Pecking, PR = Probing, PI = Picking, ST = Stabbing, SN = Snapping, SB = Submerging, SW = Sweeping, IG = Ingesting, WALK = Walking, PREEN = Preening, DF = Defecating).

Table 2. A number of different exclusive foraging behaviours of shorebirds at Asajaya and Buntal mudflat based on the analysis of focal observation

Behaviour	Whimbrel	Bar-tailed Godwit	Terek Sandpiper
Pecking	8.63 ± 0.35	12.99 ± 0.67	8.28 ± 0.42
Probing	4.07 ± 0.20	12.11 ± 0.77	6.48 ± 0.36
Picking	1.88 ± 0.16	1.64 ± 0.18	1.43 ± 0.09
Stabbing	0.86 ± 0.10	1.08 ± 0.21	1.08 ± 0.12
Snapping	0.46 ± 0.07	Not observed	0.76 ± 0.15
Submerging	0.21 ± 0.04	Not observed	0.12 ± 0.03
Sweeping	Not observed	Not observed	0.64 ± 0.09
Ingesting	1.48 ± 0.12	1.73 ± 0.18	0.98 ± 0.05

Results are expressed as mean/min ± SE

The result above showed a considerable variation in foraging behaviour recorded among the studied shorebirds. Based on the result, three studied species recorded an ingesting rate of 1 prey min^{-1} on average. Pecking behaviour was used by all studied species in this study. This behaviour has the highest rate among the behaviours observed, with an average rate of approximately 10 pecks min^{-1} . Meanwhile, probing behaviour was also commonly adopted by the studied species, but at a distinctive rate, ranging from the highest of 12 probes min^{-1} in Bar-tailed Godwit to 6 probes min^{-1} in Terek Sandpiper and the least, 4 probes min^{-1} in the foraging Whimbrel. Other behaviours such as picking and stabbing were generally seen in the studied species, each with an average of 1 pick min^{-1} and 1 stab min^{-1} . Apart from that, behaviour such as snapping and submerging was recorded in all species except for the Bar-tailed Godwit, while sweeping behaviour was recorded only in Terek Sandpiper. All these behaviours (i.e., snapping, submerging & sweeping) recorded a relatively low rate, each with an average of not exceeding 1 action per min.

Assemblages of foraging behaviour among studied species

Based on the transition matrices recorded from the foraging shorebirds, the Spearman correlation test revealed a significant relationship among the behavioural transition frequencies for all comparisons between species (Table 3). Based on the result, the studied species yielded a moderate strength of relationship in their behavioural transitions when foraging ($r_s=0.60-0.68$; $p_{perm}<0.001$). Overall,

the transition of the shorebirds foraging behaviours in this study has yielded a positive monotonic relationship in this study.

Table 3. Result of Spearman correlation test between unfolded behavioural transition matrices for each species

	Rho, r_s	P_{perm}
Whimbrel: Bar-tailed Godwit	0.68	1.81e-08
Whimbrel: Terek Sandpiper	0.60	8.44e-07
Bar-tailed Godwit: Terek Sandpiper	0.66	5.38e-08

Significance (p -value) was determined via permutation test

Spearman correlation further revealed the relationship of different foraging behaviours recorded among the studied species in this study (Table 4).

Table 4. Result of the Spearman correlation test applied to the studied behavioural parameters of the studied species.

	PE	PR	PI	ST	SN	SB	SW	IG
PE	1.00							
PR	0.29	1						
PI	-0.05	0.19	1					
ST	-0.07	0.20	0.22	1				
SN	-0.03	0.00	0.39	0.12	1			
SB	-0.01	0.01	0.25	0.15	0.34	1		
SW	0.15	0.04	-0.04	-0.02	0.11	-0.03	1	
IG	-0.03	0.25	*0.91	0.21	0.31	0.22	-0.08	1

*Note: PE = Pecking; PR = Probing; PI = Picking; ST = Stabbing; SN= Snapping; SB= Stabbing; SW = Sweeping; IG = Ingesting

Significant correlation (*) at p -value<0.001

Based on Table 4, prey capture rate (ingesting) showed a highly significant correlation with picking techniques ($r_s=0.91$, $p<0.001$), while other techniques showed weak correlations with each other. Both picking and ingesting techniques show a positive monotonic relationship, suggesting that frequent picking attempts result in a high ingestion rate. Contrastingly, there is no correlation between snapping and probing, indicating no relationship between these techniques. In other words, both snapping and probing techniques do not vary together at all.

Besides, PCA showed that all principal components (PCs) contain information that can be regarded as significant above random chance. The selected principal components (PC1 and PC2) accounted for 47% of the information in the data set (Table 5). These principal components explained the major variance of 28.19% and 18.90% respectively. The first principal component (PC1) significantly loaded highly on two variables, which are picking ($r=0.908$, $p<0.01$) and ingesting ($r=0.887$, $p<0.01$) (Table 5, Figure 7). Other variables were also significantly loaded onto PC1, but with |loadings| ~ 0.3 , suggesting their contribution in the first principal component is less important. Besides, the variables with high positive loadings in the second principal component (PC2) were related to pecking ($r=0.758$, $p<0.01$) and probing ($r=0.682$, $p<0.01$), while a moderate loading of snapping and submerging (with |loadings| ~ 0.3) were recorded at the opposite.

The first axis (PC1, Table 5 & Figure 7) emphasised the positive correlation between picking and ingesting, which allowed one to compare the species in terms of the picking attempt and ingestion rate. Meanwhile, the second axis showed the behavioural gradient related to the adoption of common foraging techniques which comprised of probing and pecking, to the use of additional prey handling techniques of snapping and submerging. Lower scores of submerging and snapping suggested that these techniques are occasionally adopted by the foraging individual to handle the captured prey before consumption. Contrarily, significant values in pecking and probing indicate dynamic hunting of the studied species throughout their foraging events. The distribution of three selected shorebird species, Whimbrel, Bar-tailed Godwit and Terek Sandpiper on the factorial map PC1-PC2 depicted the foraging strategy adopted by three studied shorebird species, in response to the foraging techniques they used.

Differences between foraging strategies were identified according to the parameters mentioned. The first group is positioned towards the positive side of PC1, which is the Bar-tailed Godwit (Figure 6). Based on the result, Bar-tailed Godwit adopted a mixed hunting strategy exclusively in foraging, where it hunts predominantly with pecking and probing techniques. Also, it was observed directly picking its

prey upon detection at high efficacy, thus resulting in a high prey capture rate in this study. Based on the results, Terek Sandpiper was observed to engage in all kinds of techniques throughout its foraging process. Meanwhile, Whimbrel was separated from the formers on the first PC, where its coordination on the second principal component seemed to be weakly associated with submerging and snapping techniques. Both Whimbrel and Terek Sandpiper that utilised additional foraging techniques, however, did not seem to contribute much to their respective prey capture rate.

Table 5. Result of the principal component analysis (PCA) performed on foraging behaviour of shorebirds

Eigenvalues	PC 1	PC 2
Variance	2.255	1.512
% of variance	28.191	18.897
Cumulative % of variance	28.191	47.088
Correlation with variables		
Pecking	0.176	0.758
Probing	0.437	0.682
Picking	0.908	-0.185
Stabbing	0.364	-0.012
Snapping	0.398	-0.340
Submerging	0.363	-0.316
Sweeping	0.027	0.471
Ingesting	0.887	-0.024

Eigenvalues of the first two principal components (PC1 & PC2) and their correlations with studied variables

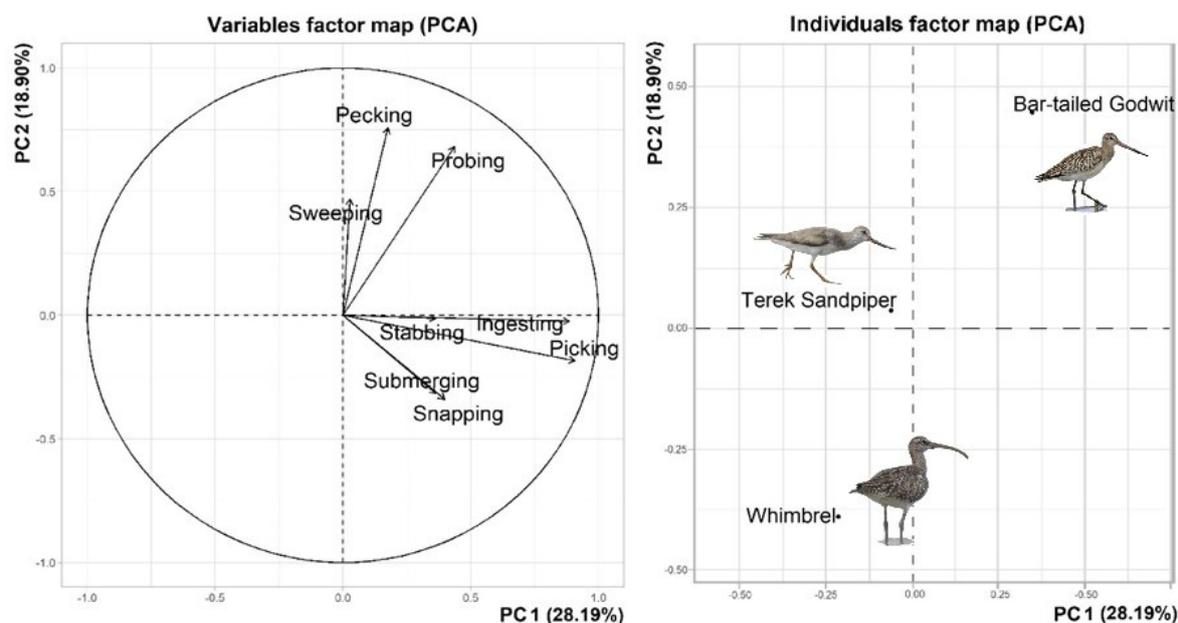


Fig. 7. Result of Principal Component Analysis (PCA). (a) Factorial maps PC1 and PC2 at left represent the correlation circle of studied variables (Pecking, Probing, Picking, Stabbing, Snapping, Submerging, Sweeping & Ingesting). (b) Distribution of shorebird species at right depicted on the individual factorial map (PC1-PC2) according to foraging behaviours used.

DISCUSSION

Foraging strategy of shorebirds

Based on the results, Whimbrel, Bar-tailed Godwit, and Terek Sandpiper exhibit different numbers of foraging techniques. Our findings reported a moderate correlation of the behavioural transitions displayed by the studied species, suggesting the use of a similar foraging strategy among the birds. Previous studies categorised the shorebird's foraging strategies into tactile, visual, and pause-travel, each represented by the key behaviours of pecking, probing, and scanning-pecking (Barbosa, 1995; Norazlimi & Ramli, 2015). Both Whimbrel and Bar-tailed Godwit are recorded as tactile foragers, while Terek Sandpiper was reported to hunt visually (Jing *et al.*, 2007; Norazlimi & Ramli, 2015; Touhami *et al.*, 2020). In contrast with previous reports, our results showed that Whimbrel, Bar-tailed Godwit, and

Terek Sandpiper adopted mixed foraging strategies comprising both pecking and probing techniques, probably indicating that these species are versatile foragers.

Pecking is the most common foraging technique adopted by most shorebirds, regardless of any particular food acquisition behaviours they might deploy while foraging (Zweers & Gerritsen, 1997). It was an ancestral behaviour in shorebirds foraging, where it further specialized into various kinds of foraging techniques to fulfil different functional requirements (Zweers, 1991; Baguette *et al.*, 2023). Although pecking was highly associated with visual (Zweers & Gerritsen, 1997; Nebel *et al.*, 2005), it was performed with a relatively high speed by the Whimbrel, Bar-tailed Godwit, and Terek Sandpiper in this study, with ranges between 8 pecks to 12 pecks per min. Such results thus suggest that the pecking technique was a partially tactile hunting mechanism. This is because birds that used rapid pecking seemed to depend less on visual cues and more on tactile cues (Baker & Baker, 1973, Kumar *et al.*, 2021). These rapid pecks may help the foraging birds to find suitable locations in which to probe and also allow them to catch prey at random (Pienkowski, 1983; Davidson *et al.*, 1986).

Meanwhile, probing is an adaptation of tactile feeding driven by the evolution of the longer bill, along with the increased number of mechanoreceptors in the shorebird's bill tip (Baker & Baker, 1973; Zweers, 1991; Cunningham *et al.*, 2010). The presence of mechanoreceptors in shorebird's bill tip aids in detecting the seismic reactions of the benthic invertebrates that hide beneath the foraging substrates (Zweers & Gerritsen, 1997; Durell, 2000; Cunningham *et al.*, 2010). Previous studies reported that probing could be more rewarding compared to pecking, as the birds can feed on greater yet profitable prey in return (Zweers, 1991; Mouritsen & Jensen, 1992; Ntiamoa-Baidu *et al.*, 1998; Norazlimi & Ramli, 2015; Touhami *et al.*, 2020). Our results revealed that Whimbrel, Bar-tailed Godwit, and Terek Sandpiper often performed probing when locating prey, with an average of 7 probes per min. Nevertheless, these species exhibited slightly lower probing rates compared to the pecking in their foraging. This might probably be because probing was costly in terms of energy, and time spent and possesses a potential risk of bill wear due to the friction exerted when the birds penetrate their bill into sediments to hunt (Gerritsen & Heezik, 1985; Durell, 2000).

A significant number of pecking and probing were recorded among three shorebird species in this study, suggesting that these two techniques dominate the other foraging techniques. Such dominance is because shorebirds mainly rely on visual cues and touching senses to initiate their foraging. Results in the study also suggested that the dominance of pecking and probing in foraging observed among the shorebirds is attributed to the versatility. This is because both pecking and probing techniques can be adopted across various ecological niches, in which the shorebirds are capable of exploiting different prey types in different habitats. The versatility of both foraging techniques can be observed from the kinematic diagram, where the behavioural transition from pecking to pecking, probing to probing, pecking to probing or vice versa was greatly recorded in Whimbrel, Bar-tailed Godwit and Terek Sandpiper in this study.

Despite the predominance of using pecking and probing when foraging, other techniques such as picking and stabbing were also observed in all three species. Picking was performed by the studied species before the prey ingestion, suggesting that these techniques are attributed to the process of foraging. This technique was observed when the prey was clutched by the shorebirds and was held in between the mandibles to prevent the prey from escaping before consumption. Meanwhile, stabbing observed among the studied species is often preceded by probing. After the prey was located by probing, the birds vigorously stabbed their bill into the substrate to disturb the buried prey. Stabbing can help improve the prey activities and substrates' penetrability (Granadeiro *et al.*, 2006; Kuwae *et al.*, 2010), thus facilitating and increasing the prey capture rates in shorebird's foraging (Dierschke *et al.*, 1999; Navedo *et al.*, 2012).

Although the studied species showed similarities in the foraging techniques used, they only shared about 50% of the behavioural variation, which can be observed in the kinematic diagrams (Figure 4-6). For instance, both snapping and submerging were recorded in Whimbrel and Terek Sandpiper, but Bar-tailed Godwit never used these techniques to forage. The presence of a particular foraging technique – sweeping in this study further segregated Terek Sandpiper with Whimbrel. The presence of snapping and submerging techniques is often associated with the feeding of large shelled prey (Zwarts, 1985; Piersma, 1986; Carneiro *et al.*, 2017). Previous studies reported that Whimbrel and Terek Sandpiper tend to feed on shelled prey when such prey types are available at the feeding site (Bijlsma & de Roder, 1991; Turpie & Hockey, 2008; Navedo *et al.*, 2012). More than half of the benthic prey inhabit the study sites – Asajaya and Buntal mudflat were comprised of shelled prey (i.e., crustaceans & molluscs) (Zakirah *et al.*, 2019). Compared to submerging, high snapping rates were recorded in these species suggesting that snapping is essential. These species often dismembered the shelled prey

before ingesting, while rinsing the prey before swallowing was spotted occasionally (Piersma, 1986; Dann, 1993). Using snapping and submerging techniques when foraging is a way to test the prey toxin concentration, regardless of whether the birds might end up partially ingesting or rejecting the prey (Kvitek & Bretz., 2004).

Durell (2000) mentioned that shorebirds' foraging specialisations are mostly constrained to their bill morphology. Sweeping was commonly adopted by birds with an up-curved bill such as avocets and stilts (Hamilton, 1975; Moreira, 1995; Barbosa & Moreno, 1999; Zusi, 2020). Terek Sandpiper possesses an up-turned bill that is morphologically adapted to this technique. Findings in this study showed that Terek Sandpiper often performed sweeping along with pecking. This is because sweeping can be rewarding if pecking is made to inspect the water column at first (Barbosa & Moreno, 1999). During sweeping, sideways movement made by the birds under the water's surface allowed them to scan for prey that assembled at the interface between soft mud and water (Hamilton, 1975; Owens, 1984). However, Terek Sandpiper was observed occasionally sweeping throughout its foraging in this study (< 1 sweep/min). It is hence suggested that the number of prey taken by sweeping was unpredictable, and probably less profitable as the bird also swallowed water when sweeping their bill across the water edges.

Unlike the Bar-tailed Godwit, the Terek Sandpiper in this study was observed to utilise various kinds of foraging techniques, suggesting that these birds are probably flexible foragers. Meanwhile, the weak association towards submerging and snapping technique throughout the focal observation further suggests the opportunistic foraging behaviour found in Whimbrel. Regardless of the slight differences in foraging techniques used, a weak partitioning among Whimbrel, Bar-tailed Godwit and Terek Sandpiper was documented throughout this study. High niche overlap among the studied species, particularly the Whimbrel and Terek Sandpiper has indicated an interspecific competition between them as these species were sharing the same food resources (i.e. crustaceans) when foraging at Asajaya and Buntal mudflats. In addition, Whimbrel, Bar-tailed Godwit and Terek Sandpiper in this study were observed sharing the same foraging sites and often foraged in a mixed flock. Previous studies reported that the spatial separation among shorebirds was prominent and mainly driven by diverse habitats and the low densities of forage individuals (Davis & Smith, 2001; Granadeiro *et al.*, 2007). Limited foraging habitats used and the presence of high densities of shorebirds in this study have therefore documented a high level of spatial overlap among the shorebirds.

Factors Influence Foraging Behaviour

A study by Davidson *et al.* (1986) reported that straight bill was morphologically adapted to thrusting actions (i.e., probing & stabbing), as by Bar-tailed Godwit. In contrast, a curved bill (i.e., Whimbrel & Terek Sandpiper) was structurally weaker compared to a straight bill (Owens, 1984). The risk for a curved bill to break is significant when a rapid thrusting action is performed (Davidson *et al.*, 1986). Nevertheless, a curved bill was more flexible and easier to manipulate, yet able to exhibit different foraging strategies and abilities (Davidson *et al.*, 1986; Higgins & Davies, 1996). These can be observed among three shorebirds in this study, where the curved-billed shorebirds (i.e. Whimbrel & Terek Sandpiper) employed various techniques to facilitate their foraging compared to the straight-billed Bar-tailed Godwit. Additionally, the foraging strategies of shorebirds are highly influenced by their capability to hunt for desired prey types (Jing *et al.*, 2007). Although shorebirds were reported to feed primarily on any benthic invertebrates inhabiting the tidal mudflats, only a small fraction of the prey was harvestable (Zwarts & Wanink, 1993). With their distinctive bill morphology, shorebirds can utilise different foraging techniques to exploit the entire mudflats and locate various kinds of prey. The diversity of shorebirds' bills, thus makes them a versatile yet opportunistic forager.

Apart from bill morphology, the difference in substrate types at the foraging site might also influence the foraging strategies taken by the shorebirds. Ramli and Norazlimi (2016) mentioned that low tide peak was the most favourable condition for shorebirds foraging as the water level does not hinder shorebirds' movements. However, a decrease in the penetrability of sediment with time after emersion has reduced the mode choice flexibility in shorebirds, as their bill use when foraging was restricted by the presence of dry substrates at the foraging site (Myers *et al.*, 1980; Wilson, 2002; Kuwae *et al.*, 2010). This could probably explain why pecking is more often observed in Whimbrel, Bar-tailed Godwit and Terek Sandpipers throughout the focal observation in Asajaya and Buntal mudflats. This is because pecking allowed the shorebirds to continue foraging at dry mudflats during low tide, without exposing themselves to the risk of bill fracture caused by probing their bill into the dry substrates. A study by Kuwae *et al.* (2010) also highlighted those shorebirds that favoured probing often chose to peck when feeding on dried substrates and shifted back to probing when they were fed at the wet substrates. The versatility of shorebirds under such circumstances suggests that the shift of foraging mode by the

shorebirds is an alternative approach to maximize their intake rate as a response to the changes in the environmental condition (Nebel & Thompson, 2005; Kuwae *et al.*, 2010).

CONCLUSION

In conclusion, a total of eight foraging techniques including pecking, probing, picking, stabbing, snapping, submerging, sweeping, and ingesting, were recorded in this study. Among the techniques recorded, snapping, submerging and sweeping were recorded only in Whimbrel and Terek Sandpiper. Meanwhile, the use of sweeping techniques has further segregated Whimbrel from Terek Sandpiper. Although not all the behaviours recorded were adopted by all species, these behaviours are still part of the behavioural mechanism exhibited by the shorebirds when foraging. Three studied species in this study – Whimbrel, Bar-tailed Godwit, and Terek Sandpiper showed a moderate similarity in the transition of the foraging behaviour. From the data shown, probing, pecking, and picking are the most important behaviours in obtaining prey. This has resulted in a close frequency of successful foraging attempts among the studied species, with an average of one prey taken per min. Adoption of the mixed foraging strategy comprising pecking and probing techniques suggests that the studied species in this study are versatile foragers.

Overall, findings in this study highlighted that bill morphology plays a vital role in determining their foraging behaviour. Difference in bill morphology among the shorebirds is greatly associated with their specialization in foraging behaviour. Based on the findings, specialised foraging behaviours recorded among the studied species did not seem to have much impact on their foraging outcome. It is hard to conclude which bill types (i.e., straight bill & curved bill) are more profitable as different foraging specialisations are associated with different benefits and risks. Besides, shifting in foraging techniques used by shorebirds during foraging, particularly between pecking and probing, is mainly due to environmental constraints (e.g., substrate penetrability). Habitat conservation, particularly of sediments in Asajaya and Buntal is therefore essential to protect the available staging sites for the shorebirds.

ACKNOWLEDGEMENTS

The authors thank the support of the UNIMAS Special MyRA Grant Scheme [F07/SpMYRA/1710/2018] for funding the project. The authors would also like to express the greatest gratitude to Sarawak Forestry Corporation and Sarawak Forestry Department for granting the research permit number (141) JHS/NCCD/600-7/2/107 to conduct the research.

ETHICAL STATEMENT

Not applicable.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

REFERENCES

- Baguette, M., Hannier, L., Kirchhoff, F., Le Floch, G., Schtickzelle, N., Stevens, V. & Bels, V. 2023. Repertoire of food acquisition behaviors in shorebirds (Aves, Charadriiforme). Preprints, 2023: 2023101737. <https://doi.org/10.20944/preprints202310.1737.v1>
- Baker, M.C. & Baker, A.E.M. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. *Ecological Monographs*, 43(2): 193-212. <https://doi.org/10.2307/1942194>
- Bakewell, D., Wong, A., Kong, D. & Rose, A. 2017. *Waterbird Surveys of the Sarawak Coast (2010-2012)*. Malaysian Nature Society, Kuala Lumpur. 271 pp.
- Bamford, M., Watkins, D., Bancroft, W., Tischler, G. & Wahl, J. 2008. *Migratory Shorebirds of The East Asian-Australasian Flyway: Population Estimates and Internationally Important Sites*. Wetlands International - Oceania, Canberra. 24 pp.
- Barbosa, A. & Moreno, E. 1999. Evolution of foraging strategies in shorebirds: An ecomorphological approach. *The Auk*, 116(3): 712-725. <https://doi.org/10.2307/4089332>
- Barbosa, A. 1995. Foraging strategies and their influence on scanning and flocking behaviour of waders. *Journal of Avian Biology*, 26(3): 182-186. <https://doi.org/10.2307/3677317>
- Bijlsma, R.G. & de Roder, F.E. 1991. Foraging behaviour of Terek Sandpipers *Xenus cinereus* in Thailand. *Wader Study Group Bulletin*, 61: 22-26.
- Birdlife International. 2020. Important bird areas factsheet: Bako-Buntal Bay [WWW Document]. BirdLife International. URL <http://datazone.birdlife.org/site/factsheet/bako-buntal-bay-iba-malaysia/>

- refs (assessed 11.03.20).
- BirdLife International. 2022. IUCN red list for birds [WWW Document]. BirdLife International. URL datazone.birdlife.org/species/factsheet (assessed 01.12.22).
- Boggies, M.A. 2018. Linking Diet, Behaviour, and Bioenergetics of A Migratory Waterbird to Evaluate Response to Wintering Ground Conditions (Ph.D). New Mexico State University.
- Brockmann, H.J. 2011. Measuring behavior: Ethograms, kinematic diagrams, and time budgets [WWW Document]. College of the Holy Cross. URL https://college.holycross.edu/faculty/kprestwi/behavior/e&be_notes/E&BE_ethograms.pdf (assessed 01.12.22).
- Carneiro, C., Gunnarsson, T.G. & Alves, J.A. 2017. Bloody cockles: A novel and important food item for whimbrels in the Banc d'Arguin. *Wader Study*, 124(2): 161-162. <https://doi.org/10.18194/ws.00072>
- Choi, C.Y. 2015. The Northward Migration Stopover Ecology of Bar-Tailed Godwits and Great Knots in The Yalu Jiang Estuary National Nature Reserve, China (Ph.D). Massey University.
- Choi, C., Battley, P.F., Potter, M.A., Ma, Z., Melville, D.S. & Sukkaewmanee, P. 2017. How migratory shorebirds selectively exploit prey at a staging site dominated by a single prey species. *The Auk*, 134(1): 76-91. <https://doi.org/10.1642/AUK-16-58.1>
- Choi, S., Kang, S., Lee, S., Min, J. & Kim, B. 2017. Foraging behavior and diet of northward migrating Bar-Tailed Godwits (*Limosa lapponica*) and Great Knots (*Calidris tenuirostris*) at a key stopover site. *International Journal of Sciences: Basic and Applied Research (IJSBAR)*, 36(6): 276-286.
- Colwell, M.A. 2010. *Shorebird Ecology, Conservation, and Management*. University of California Press, California. 344 pp. <https://doi.org/10.1525/9780520947962>
- Crews, J., Braude, S., Stephenson, C. & Clardy, T. 2002. *The Ethogram and Animal Behaviour Research*. Washington University, St. Louis. 122 pp.
- Cunningham, S.J., Alley, M.R., Castro, I., Potter, M.A., Cunningham, M. & Pyne, M.J. 2010. Bill morphology of ibises suggests a remote-tactile sensory system for prey detection. *Auk*, 127(2): 308-316. <https://doi.org/10.1525/auk.2009.09117>
- Dann, P. 1993. Abundance, diet and feeding behaviour of the Whimbrel, *Numenius phaeopus variegatus* in Rhyll Inlet, Victoria. *Corella*, 17(2): 52-57.
- Davidson, N.C., Townsend, D.J., Pienkowski, M.W. & Speakman, J.R. 1986. Why do curlews *Numenius* have decurved bills? *Bird Study*, 33: 61-69. <https://doi.org/10.1080/00063658609476896>
- Davis, C.A. & Smith, L.M. 2001. Foraging strategies and niche dynamics of coexisting shorebirds at stopover sites in the Southern Great Plains. *Auk*, 118: 484-495. <https://doi.org/10.1093/auk/118.2.484>
- Dierschke, V., Kube, J., Probst, S. & Brenning, U. 1999. Feeding ecology of dunlins *Calidris alpina* staging in the southern Baltic Sea, I. Habitat use and food selection. *Journal of Sea Research*, 42(1999): 49-64. [https://doi.org/10.1016/S1385-1101\(99\)00013-1](https://doi.org/10.1016/S1385-1101(99)00013-1)
- Duijns, S., Hidayati, N.A. & Piersma, T. 2013. Bar-tailed Godwits *Limosa l. lapponica* eat polychaete worms whenever they winter in Europe. *Bird Study*, 60: 509-517. <https://doi.org/10.1080/00063657.2013.836153>
- Durell, S. 2000. Individual feeding specialisation in shorebirds: Population consequences and conservation implications. *Biological Reviews*, 75(4): 503-518. <https://doi.org/10.1111/j.1469-185X.2000.tb00053.x>
- Finn, P. 2009. *Habitat Selection, Foraging Ecology and Conservation of Eastern Curlews on Their Non-Breeding Grounds* (Ph.D). Griffith University.
- Gerritsen, A.F.C. & Heezrik, Y.M. 1985. Substrate preference and substrate related foraging behaviour in three calidris species. *Netherlands Journal of Zoology*, 35(4): 671-692. <https://doi.org/10.1163/002829685X00235>
- Gokula, V. 2012. An ethogram of Spot-billed Pelican (*Pelecanus philippensis*). *Chinese Birds*, 2(4): 183-192. <https://doi.org/10.5122/cbirds.2011.0030>
- Goss-Custard, J.D. 1977. The ecology of the wash. I. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). *The Journal of Applied Ecology*, 14(3): 721-739. <https://doi.org/10.2307/2402805>
- Granadeiro, J.P., Dias, M.P., Martins, R.C. & Palmeirim, J.M. 2006. Variation in numbers and behaviour of waders during the tidal cycle: Implications for the use of estuarine sediment flats. *Acta Oecologica*, 29(2006): 293-300. <https://doi.org/10.1016/j.actao.2005.11.008>
- Granadeiro, J.P., Santos, C.D. & Dias, M.P. 2007. Environmental factors drive habitats partitioning in birds feeding in intertidal flats; implication for conservation. *Hydrobiologia*, 587: 291-302. <https://doi.org/10.1007/s10750-007-0692-8>
- Greenhalgh, M.E. 1975. *Study of the Food and Feeding Ecology of the Wading Birds* (Ph.D). Liverpool Polytechnic.

- Hamilton, R.B. 1975. Comparative behaviour of the American Avocet and the Black-necked Stilt (Recurvirostridae). Ornithological Monographs, 47(2): 177. <https://doi.org/10.2307/4512224>
- Higgins, P.J. & Davies, S.J.J.F. 1996. Handbook of Australian, New Zealand and Antarctic Birds Snipe to Pigeons, Volume 3. Oxford University Press, Melbourne. 815 pp.
- Jing, K., Ma, Z., Li, B., Li, J. & Chen, J. 2007. Foraging strategies involved in habitat use of shorebirds at the intertidal area of Chongming Dongtan, China. Ecological Research, 22(4): 559-570. <https://doi.org/10.1007/s11284-006-0302-7>
- Karlionova, N., Remisiewicz, M. & Pinchuk, P. 2006. Biometrics and breeding phenology of Terek Sandpipers in the Pripyat' Valley, S. Belarus. Wader Study Group Bulletin, 110: 54-58.
- Katrínardóttir, B., Pálsson, S., Gunnarsson, T.G. & Sigurjónsdóttir, H. 2013. Sexing Icelandic Whimbrels *Numerius phaeopus islandicus* with DNA and biometrics. Ringing and Migration, 28(1): 43-46. <https://doi.org/10.1080/03078698.2013.811160>
- King, K.A. 2008. Behaviour Patterns and Habitat Use of the Brolga (*Grus rubicundus*) at Two Flocking Sites in South-West Victoria (BSc). Deakin University.
- Kumar, V., Mishra, H. & Kumar, A. 2021. Foraging behaviour in river lapwing, *Vanellus duvaucelii* (Lesson, 1826) (Charadriiformes: Charadriidae): differences in technique, prey and habitat. Journal of Asia-Pacific Biodiversity, 14(1): 33-39. <https://doi.org/10.1016/j.japb.2020.09.011>
- Kuwa, T., Miyoshi, E., Sassa, S. & Watabe, Y. 2010. Foraging mode shift in varying environmental conditions by dunlin *Calidris alpina*. Marine Ecology Progress Series, 406(May 2010): 281-289. <https://doi.org/10.3354/meps08519>
- Kvitek, R.G. & Bretz, C.K. 2004. Harmful algal bloom toxins protect bivalve populations from sea otter predation. Marine Ecology Progress Series, 271: 233-243. <https://doi.org/10.3354/meps271233>
- Lai, C. 2019. Preserving the wintering sites of migratory birds. The Borneo Post, October 6, p. 1.
- Landys, M.M., Piersma, T., Guglielmo, C.G., Jukema, J., Ramenofsky, M. & Wingfield, J.C. 2005. Metabolic profile of long-distance migratory flight and stopover in a shorebird. In: Proceedings of the Royal Society B: Biological Sciences. The Royal Society, London. pp. 295-302. <https://doi.org/10.1098/rspb.2004.2952>
- Moreira, F. 1995. The winter-feeding ecology of Avocets *Recurvirostra avosetta* on intertidal areas. I. Feeding strategies. Ibis, 137: 92-98. <https://doi.org/10.1111/j.1474-919X.1995.tb03224.x>
- Mouritsen, K.N. & Jensen, K.T. 1992. Choice of microhabitat in tactile foraging dunlins *Calidris alpina*: The importance of sediment penetrability. Marine Ecology Progress Series, 85(1): 1-8. <https://doi.org/10.3354/meps085001>
- Myers, J.P., Williams, S.L. & Pitelka, F.A. 1980. An experimental analysis of prey availability for sanderlings (Aves: Scolopacidae) feeding on sandy beach crustaceans. Canadian Journal of Zoology, 25: 1564-1574. <https://doi.org/10.1139/z80-216>
- Myers, S. 2016. Birds of Borneo. 2nd Ed. Bloomsbury Publishing PLC, London. 272 pp.
- Navedo, J.G., Sauma-Castillo, L. & Fernández, G. 2012. Foraging activity and capture rate of large Nearctic shorebirds wintering at a tropical coastal lagoon. Waterbirds, 35(2): 301-311. <https://doi.org/10.1675/063.035.0211>
- Nebel, S. & Thompson, G.J. 2005. Foraging behaviour of western sandpiper changes with sediment temperature: implications for their hemispheric distribution. Ecological Research, 20(4): 503-507. <https://doi.org/10.1007/s11284-005-0061-x>
- Nebel, S., Jackson, D.L. & Elner, R.W. 2005. Functional association of bill morphology and foraging behaviour in calidrid sandpipers. Animal Biology, 55(3): 235-243. <https://doi.org/10.1163/1570756054472818>
- Nol, E., Mac Culloch, K., Pollock, L. & McKinnon, L. 2014. Foraging ecology and time budgets of non-breeding shorebirds in coastal Cuba. Journal of Tropical Ecology, 30(4): 347-357. <https://doi.org/10.1017/S0266467414000182>
- Norazlimi, N.A. & Ramli, R. 2015. The relationships between morphological characteristics and foraging behavior in four selected species of shorebirds and water birds utilizing tropical mudflats. Scientific World Journal, 2015: 105296. <https://doi.org/10.1155/2015/105296>
- Ntiamoa-Baidu, Y., Piersma, T., Wiersma, P., Poot, M., Battley, P. & Gordon, C. 1998. Water depth selection, daily feeding routines and diets of waterbirds in coastal lagoons in Ghana. Ibis, 140(1): 89-103. <https://doi.org/10.1111/j.1474-919X.1998.tb04545.x>
- O'reilly, K.M. & Wingfield, J.C. 1995. Spring and autumn migration in arctic shorebirds: Same distance, different strategies. Integrative and Comparative Biology, 35(3): 222-233. <https://doi.org/10.1093/icb/35.3.222>
- Owens, N. 1984. Why do curlews have curved beaks? Bird Study, 31(3): 230-231. <https://doi.org/10.1093/birdstud/31.3.230>

- [org/10.1080/00063658409476846](https://doi.org/10.1080/00063658409476846)
- Pienkowski, M.W. 1983. Changes in the foraging pattern of plovers in relation to environmental factors. *Animal Behaviour*, 31(1): 244-264. [https://doi.org/10.1016/S0003-3472\(83\)80195-X](https://doi.org/10.1016/S0003-3472(83)80195-X)
- Piersma, T. 1986. Foraging behaviour of Terek Sandpipers *Xenus cinereus* feeding on Sand-Bubbling Crabs *Scopimera globosa*. *Journal of Ornithology*, 127(4): 475-486. <https://doi.org/10.1007/BF01640262>
- Pyke, G.H., Pulliam, H.R. & Charnov, E.L. 1977. Optimal foraging: A selective review of theory and tests. *The Quarterly Review of Biology*, 52(2): 137-154. <https://doi.org/10.1086/409852>
- R Core Team. 2022. R: A language and environment for statistical computing [Computer software]. The R Project for Statistical Computing. URL <http://www.R-project.org/> (assessed 10.10.21)
- Ramli, R. & Norazlimi, N.A. 2016. Effects of tidal states and time of day on the abundance and behavior of shorebirds utilizing tropical intertidal environment. *Journal of Animal and Plant Sciences*, 26(4): 1164-1171.
- Risdiana, R. 2015. Maintaining habitat for birds in Bako Buntal Bay [WWW Document]. EAAFP. URL <https://www.eaaflyway.net/maintaining-habitat-for-birds-in-bako-buntal-bay-eaaf112-malaysia/> (assessed 12.12.21).
- Sánchez, M.I., Green, A.J. & Castellanos, E.M. 2005. Seasonal variation in the diet of Redshank *Tringa totanus* in the Odiel Marshes, Southwest Spain: A comparison of faecal and pellet analysis. *Bird Study*, 52(2): 210-216. <https://doi.org/10.1080/00063650509461393>
- Schneider, D. C. 2017. The food and feeding of migratory shorebirds. *Oceanus*, 26(1): 38-43.
- See, C.M. & Chan, K.S. 2020. Coastal Mangrove Birds of Bagan Datuk, Perak. Malaysian Nature Society, Kuala Lumpur. 70 pp.
- Stroud, D.A.A., Baker, D.E., Blanco, N.C., Davidson, S., Delany, B., Ganter, R., Gill, R., Gonzalez, P., Haanstra, L., Morrison, R.I.G., Piersma, T., Scott, D.A., Thorup, O., West, R., Wilson, J. & Zockler, C. 2008. The conservation and population status of the world's waders at the turn of the millennium. In: *Conference of Waterbirds around the world*, Edinburgh, pp. 643-648.
- Touhami, F., Idrissi, H.R. & Benhoussa, A. 2020. Foraging behaviour of wintering shorebirds at Merja Zerga lagoon (Atlantic coast, Morocco). *Ostrich*, 91(3): 244-251. <https://doi.org/10.2989/00306525.2020.1774439>
- Turpie, J.K. & Hockey, P.A.R. 2008. Adaptive variation in the foraging behaviour of Grey Plover *Pluvialis squatarola* and Whimbrel *Numenius phaeopus*. *Ibis*, 139(2): 289-298. <https://doi.org/10.1111/j.1474-919X.1997.tb04627.x>
- Watts, B.D., Smith, F.M. & Truitt, B.R. 2017. Departure patterns of whimbrels using a terminal spring staging area. *Wader Study*, 124(2): 141-146. <https://doi.org/10.18194/ws.00075>
- Willems, T., Rabaut, M., Stienen, E. & Degraer, S. 2010. Feeding ecology of shorebirds: Habitat preference and tidal constraints (MSc.). Ghent University.
- Wilson, J.R., Nebel, S. & Minton, C.D.T. 2007. Migration ecology and morphometrics of two Bar-tailed Godwit populations in Australia. *Emu*, 107(4): 262-274. <https://doi.org/10.1071/MU07026>
- Wilson, K. 2002. A survey of coastal and marine birds at Bako National Park and Samunsam Wildlife Sanctuary, Sarawak. Wildlife Management Report Number 28. The Sarawak Biodiversity Centre, Kuching.
- Woodley, K. 2022. Bar-tailed Godwit [WWW Document]. New Zealand Birds Online. URL www.nzbirdsonline.org.nz (assessed 20.12.23)
- Zakirah, M.T., Shabdin, M.L., Khairul-Adha, A.R. & Fatimah-A'tirah, M. 2019. Distribution of intertidal flat macrobenthos in Buntal Bay, Sarawak, Borneo. *Songklanakarin Journal of Science and Technology*, 41(5): 1048-1058.
- Zusi, R. L. 2020. Charadriiform. [WWW Document]. Britannica. URL <https://www.britannica.com/animal/charadriiform> (accessed 12.10.20).
- Zwarts L. & Dirksen, S. 1990. Digestive bottleneck limits the increase in food intake of Whimbrels preparing for spring migration from the Banc d'Arguin, Mauritania. *Ardea*, 78:257-258.
- Zwarts, L. & Wanink, J. H. 1993. How the food supply harvestable by waders in the wadden sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Netherlands Journal of Sea Research*, 31(4): 441-476. [https://doi.org/10.1016/0077-7579\(93\)90059-2](https://doi.org/10.1016/0077-7579(93)90059-2)
- Zwarts, L. 1985. The winter exploitation of fiddler crabs *Uca tangeri* by waders in Guinea-Bissau. *Ardea*, 73(1985): 3-12.
- Zweers, G. & Gerritsen, A.F.C. 1997. Transition from pecking to probing mechanisms in waders. *Netherlands Journal of Zoology*, 47(2): 161-208. <https://doi.org/10.1163/156854297X00166>

Zweers, G.A. 1991. Transformation of avian feeding mechanisms: a deductive method. *Acta Biotheoretica*, 29: 15-36. <https://doi.org/10.1007/BF00046405>

