Some observations of the foraging behaviour of the Australian Painted-snipe and the Greater Painted-snipe

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Foraging behaviour of Australian Painted-snipe *Rostratula australis* was analysed using video recordings replayed at slow speed. The dominant foraging mode identified was tactile. Techniques utilised were probing of the substrate and sweeping within the water column. Sampling, using receptors in the mandibles, was used to locate prey within the water column and detect traces of prey in the substrate. The birds were stationary when probing and wading when sweeping. Visual foraging using lunging and pecking was uncommon and was restricted to the muddy surrounds of wetlands.

Comparison was made with foraging behaviour of the Greater Painted-snipe *Rostratula benghalensis,* also analysed from video recordings. The dominant foraging mode identified was tactile. Sweeping and probing were the most frequently used techniques, the former being much more common. Sampling, using receptors in the mandibles, accompanied sweeping and preceded probing. Sweeping of the water column was conducted when wading, and probing of the substrate when birds were stationary. Visual foraging, using pecking, was conducted predominantly on the muddy surrounds of wetlands.

The range of water depth used by both species for foraging was similar and ranged from 0-80 mm. The average foraging depth for Australian Painted-snipe was 31 mm and for Greater Painted-snipe was 29 mm.

The foraging techniques used by both species were the same and there was no difference between the techniques used by males and females. Water depth did not influence whether sweeping or probing was used in the water column. Water snails were the most commonly observed prey items captured. The use of surface tension transport to move captured prey from the bill tip to the oral cavity was confirmed.

The dominant foraging mode for both species was tactile. Pits that house mechanoreceptors and possibly chemoreceptors were identified in the lower mandible of Australian Painted-snipe. It is speculated that some form of Grandry-type cells, also used to detect prey, may be present in the species' tongue or bill.

INTRODUCTION

The Australian Painted-snipe *Rostratula australis* is one of Australia's least-known endemic waders (Lane & Rogers 2000, Cooper *et al*. 2016). It has a small nomadic population that is dispersed widely across eastern and northern Australia, mainly around shallow, ephemeral, freshwater and brackish wetlands (Rogers *et al.* 2005; Garnett *et al*. 2011). The bird is cryptic, calls rarely, feeds mainly at night and roosts in dense vegetation during the day (Menkhorst *et al*. 2017). It is now recognised as endemic to the Australian mainland, having previously been considered a sub-species of the Greater Painted-snipe *Rostratula benghalensis* that occurs in Africa, India and Asia (Lane & Rogers 2000; Baker *et al*. 2007, Christidis & Boles 2008).

In their review of the status of the species, Lane & Rogers (2000) demonstrated substantial differences in measurements, plumage characteristics and some behaviours, between Australian Painted-snipe and Greater Painted-snipe. Rogers *et al*. (2005) also pointed out that as a result of the traditional lumping of the two species, assumptions that behaviours of Greater Painted-snipe also applied to Australian Painted-snipe, were probably incorrect.

The Australian Painted-snipe uses its long, slender bill for foraging. The bill is slightly decurved on the distal one-third and has a slightly bulbous tip on the upper mandible. The average bill length is 43.2 mm for adult male birds and 44.8 mm for the larger females. It is most frequently observed foraging in shallow water around the margins of wetlands but is also reported to forage on mud flats and open areas such as ploughed land or grassland. It is omnivorous, feeding on vegetation, seeds, molluscs, crustaceans, insects, worms, and other invertebrates (Marchant & Higgins 1993).

There is very little published information on the foraging techniques of the Australian Painted-snipe. It is reported to glean food at the water's edge and on mud, by probing in soft ground and by scything with its bill in shallow water (del Hoyo *et al*. 2020). This description, however, is a legacy account from earlier lumping, as it is behaviour previously ascribed to the Greater Painted-snipe by Cramp & Simmons (1983). Lindsey (2009) observed a bird foraging at Hexham Swamp, near Newcastle, by dipping its bill vertically into the water to around a quarter of its length while rapidly opening and almost, but not completely, closing it. The bird continued to wade while foraging. D'Ombrain (1944) described a captive bird eating worms, meat, and insects. Hindwood & Hoskin (1954) described seeds in the stomach of a bird collected near Box Hill, Victoria. G. Stevens (pers. comm.) observed numerous holes in soft mud where birds had been foraging around an ephemeral wetland at Lenaghans Swamp, near Newcastle in 1973, and D. Rogers (pers. comm.) observed a bird capturing earthworms by probing in moist soil at Rutherglen, Victoria in February 2006.

There is also limited foraging information for its close relative, the Greater Painted-snipe. Johnsgard (1981) described birds feeding by probing in mud and ooze for worms, insects, molluscs and crustaceans, and also eating some vegetable matter such as grains and weed seeds. He described foraging as typically done by probing and by a lateral scything movement of the bill in shallow water, in a similar manner to avocets. Cramp & Simmons (1983) described Greater Painted-snipe as gleaning from the edge of water and mudflats, probing in soft ground and scything with the bill in shallow water. Kirwan (2020) described it as probing soft ground like true snipes and using a scything action of its bill and head in shallow water.

McNeil & Rodriguez (1996) summarized the foraging habits and strategies of shorebirds. They described the foraging pattern of *Rostratula* as largely crepuscular and partly nocturnal. The foraging strategy was partly tactile by day and partly tactile by night.

This study was prompted by the presence of a juvenile male Australian Painted-snipe at Myall Quays, Tea Gardens, NSW (32º 39' 08.22"S, 152º 09' 10.47"E) in early 2020 (Fraser 2020). The bird was present for at least 27 days from mid-January to early February 2020. The site was easily accessible, and the bird's presence was widely reported on online birding blogs and databases. Consequently, it was seen by many observers, some of whom made video recordings. These recordings and reports by observers facilitated an analysis of the bird's foraging behaviour.

The objectives of this article are to describe and compare the observed foraging behaviour of the two painted-snipe species and consider adaptations that support those modes of behaviour. The study has considerable limitations, as it is based on recordings of a small number of birds, mostly present at wetland habitats in the daytime. Moreover, the behaviour of some of the birds might have been influenced by their awareness of the videographer. However, since very little has previously been documented of the foraging behaviour of either species, particularly for the Australian Painted-snipe, it seems important to place the present observations on record.

Prey detection and capture methods used by shorebirds

Long-billed shorebirds (waders) have several unique adaptations that allow them to successfully exploit their shoreline and wetland habitats. Prey detection methods used include sound, smell, taste, sight and mechanoreception. Waders mainly exploit the latter two methods. Their eyes are large and high-set, and they have well-developed optic lobes of the brain which provide excellent vision. While most of their field of view is monocular, long-billed birds have a narrow field of binocular vision commencing slightly forward of the tip of their bills (Tyrrell & Fernández-Juricic 2017).

Included among the bird's mechanoreception senses is tactile reception, an adaptation that is well-developed in waders that forage by probing for unseen prey in soft substrates. Many long-billed shorebirds such as godwits, curlews, snipe, redshanks, knots and dunlin have Herbst corpuscles housed in small pits under the keratin layer in the tips of their bills, that can detect change in pressure gradients in the substrate (Bolze 1968). These pits vary in shape, size and number between species. The pits of Red Knot *Calidris canutus* are elliptical, 112-200 µm wide, and up to 300 µm long (Piersma *et al*. 1998). In Western Sandpiper *Calidris mauri*, pits are 22-27 µm long and 6-9 µm wide, in Dunlin *Calidris alpina* 14-22 µm long and 6-10 µm wide, and in Least Sandpiper *Calidris minutilla* 11-13 µm long and 6-8 µm wide (Nebel *et al*. 2005). Sharpe (1896) reported no pits were present in the bills of specimens of Genus Rostratula at the British Museum.

This technique of prey detection relies on pore water in the substrate to transmit pressure waves. For Red Knot, the repeated probing action of the bill produces pressure waves in the substrate. Herbst corpuscles detect changes in the pressure gradient induced by the presence of solid objects such as prey. Other species use Herbst corpuscles to detect pressure waves induced by the movement of prey in the substrate or by tamping of bird's feet on the surface (Piersma *et al*. 1998).

An additional sense which shorebirds can use to identify and differentiate prey is taste (chemo-reception). Clark *et al*. (2014) reported that birds have a well-developed system for gustation (tasting) which affects their behaviour and ecology. Taste receptors are located in taste buds throughout the oral cavity and birds use these to select nutrient-rich prey and avoid toxins. Van Heezik *et al*. (1983) demonstrated that Sanderling *Calidris alba* and Dunlin used taste to determine whether prey was present or absent in a substrate and modified their foraging behaviour accordingly.

Many shorebirds forage with a slightly open bill, indicating that receptors inside the bill are involved in prey detection. The tongues of many aquatic birds have been shown to contain numerous tactile sensory structures known as Grandry corpuscles, especially in the tip of the tongue (Grandry 1869). Toyoshima (1993) described Grandry corpuscles in the tongues of ducks as composed of two or three large, hemispherical Grandry cells 40-45 µm diameter and 16-18 µm thick. These corpuscles have both chemoreceptive and mechanoreceptive functions (Toyoshima 1989). Piersma *et al*. (1998) found complexes of large sensory cells of the Grandry type under the keratin spines on the palate of Red Knot. Grandry corpuscles of geese and ducks have been described as 'rapidly adapting mechanoreceptors' (Gottschaldt 1985).

Some long-billed shorebird species have been shown to transfer prey from the bill tip to the oral cavity via surface tension transport (Rubega & Obst 1993). This mechanism employs the surface tension between keratin in the bill and the water surrounding captured prey to transport small items along the bill without the use of suction or tongue movements. After the bird seizes a food item with its bill tips, transport along the bill is accomplished by rapid partial mandibular spreading. This motion increases the free surface area of the water drop that surrounds the food item adhering to the bird's bill and drives it up the bill and into the bird's oral cavity. According to these authors, it is likely that any bird with a needle-shaped bill, foraging in water, will be capable of some degree of surface-tension transport.

Another mechanism used by long-billed waders to assist foraging for prey buried in the substrate and unable to be seen, is distal rhynchokinesis. This process allows the upper part of the bill to flex upwards independently of the rest of the bill, thus opening the tip of the bill wide enough to seize detected prey (Estrella & Masero 2007).

METHODS

Video recordings of foraging activity by Australian Painted-snipe and Greater Painted-snipe were obtained using internet-based searches and by specific requests to the birdwatching community. Only higher quality recordings that allowed accurate discrimination of foraging details were used. Recording duration varied from a few seconds to several minutes. The amount of foraging behaviour on each recording varied greatly.

Video recordings from YouTube (https://www.youtube.com/) and the Macaulay Library at the Cornell Lab of Ornithology eBird portal (https://ebird.org/) were viewed online at one-quarter speed and high definition mode while supplied recordings were viewed at one-quarter speed using VLC Media Player software. Windows Media Player software was used for frame-by-frame viewing when required. Details recorded where possible were: sex of the bird, time of day, foraging substrate, estimated depth of water, foraging mode, foraging technique, depth of probe, duration of probe, head movement, prey captured, bill movement, swallowing and eye movement.

The terminology used to describe foraging mode and technique is defined as follows:

Visual foraging: Use of visual information for guidance of the bill position when capturing prey.
Tactile foraging: Foraging guided primarily by tactile information derived from receptors located within sensory pits in the bone around the bill tips.
Lunging: Rapid forward striking motion to catch moving prey on water or in the air.
Pecking: Striking motion with the bill to capture prey on water surface or muddy substrate.
Sampling: Rapid, partial opening and closing of the mandibles when inserted into the water column. This most commonly precedes probing and accompanies sweeping.
Probing: Inserting the bill into the substrate to search for and capture prey.
Vertical Sweeping: Side-to-side movement of bill introduced vertically into water column.
Substrate Sweeping: Near-horizontal back-and-forth movement of bill over substrate at base of water column.

The sweeping technique described here is likely to be the same as the scything action of painted-snipe described elsewhere (Johnsgard 1981, del Hoyo *et al*. 2020). However, the term scything was originally used by Hamilton (1975) to describe a tactile foraging technique used by American Avocet *Recurvirostra americana* with the recurved tip of the bill placed flat on the substrate while the head was moved from side to side. The word implies a cutting action which does not occur, and consequently the term sweeping is used here. Martin & Piersma (2009) described the vertical sweeping technique as blind trawling.

Time of day could only be estimated in broad terms, except where it was specified by the videographer. Water depth was estimated by comparing the submerged length of the bird's leg while standing, with the total length of the leg. Total leg length (metatarsus + tibia) was estimated to be 65 mm, taking into account the angular presentation of the tibia in most circumstances. Depth of probe was estimated by comparing the submerged length of the bird's bill with the reported average bill length of 44 mm (Marchant & Higgins 1993).

Skin specimens of Australian Painted-snipe and Greater Painted-snipe at the Australian Museum, Sydney were examined for the presence of corpuscular pits in the mandibles.

RESULTS

Analyses of recordings revealed both species of painted-snipe to be opportunistic feeders using a variety of foraging techniques, and adapting their methods to best suit the prevailing conditions of the habitat. Both visual and tactile foraging modes were used, at times in conjunction. Visual foraging was used to capture prey that could be observed in the air, on the water surface or on the muddy surrounds. Tactile techniques were used to locate unseen prey and included sampling of the water column, probing in the substrate, vertical sweeping through the water column or near-horizontal sweeping across the wetland substrate. The recordings analysed for Australian Painted-snipe (10) are summarized in **Table 1** and those analysed for Greater Painted-snipe (55) are summarized in **Table 2**. Sixty-three recordings were of daytime foraging and two were of foraging at night. An analysis of mean water depth while foraging is presented in **Figure 1**.

Table 1. Video recordings analysed for foraging mode and technique of Australian Painted-snipe.

Foraging Mode	Dominant Foraging Technique	Sex	Water Depth (mm)	Location	Time of Day	Reference
Visual	Lunging	M	60-65	Wanganella, NSW	Night	Maher (2011a)
Visual	Pecking	M & F	0-5	Wanganella, NSW	Day	Maher (2011b)
Tactile	Probing	M	15	Lake Eda, WA	Day	Jarvis (2016)
Tactile	Probing	M	10-15	Kooralbyn, Qld	Day	Siggs (2015)
Tactile	Probing	M	20-30	Pitt Town, NSW	Evening	BIBY TV (2017)
Tactile	Probing	F	40-50	Palerang, NSW	Day	Wallace (2017)
	Sweeping		80			
Tactile	Probing	M	10-65	Tea Gardens, NSW	0639-0735	Hosken (2020)
Tactile	Probing	M	10-30	Tea Gardens, NSW	900	Kinsey (2020)
Tactile	Sweeping	M	20	Kooralbyn, Qld	Day	Laven (2009)
Tactile	Sweeping	M	10-40	Tea Gardens, NSW	1740	Parashou (2020)

Table 2. Video recordings analysed for foraging mode and technique of Greater Painted-snipe.

Foraging Mode	Dominant Foraging Technique	Sex	Water Depth (mm)	Location	Time of Day	Reference
Visual	Lunging	F	0	Western, Uganda	Day	del Hoyo (2006)
Visual	Pecking	M&F	0	Japan	Day	Birdlover.jp (2017)
Visual	Pecking	M&F	0	Tamil Nadu, India	Day	Thillainayagam (2021)
Visual	Pecking	M	10	Tamil Nadu, India	Day	Thillainayagam (2021)
Visual	Pecking	M	0	Maharashtra, India	Day	Bhagwat (2022a)
Visual	Pecking	F	0-5	Madhya Pradesh, India	Day	Tigers & Birds of India (2022)
Visual	Pecking	M&F	0-5	Perak, Malaysia	0730-0900	Amar-Singh (2020)
Tactile	Sweeping		10-55			
Tactile	Probing	F	0	Western, Uganda	Evening	Kennewell, (2004)

Tactile	Probing	M	70	Thiés, Senegal	Day	Sanabria (2007a)
Tactile	Probing	F	20-30	Nagpur, India	Day	Aditya Wildlife (2010)
Tactile	Probing	M	45	Gujarat, India	Day	del Hoyo (2011a)
Tactile	Probing	M	40-45	Gujarat, India	Day	del Hoyo (2011b)
Tactile	Probing	M	20	Central River, Gambia	Day	Jimenez (2011a)
Tactile	Probing	M	20-40	Eswatini, Swaziland	Night	Coker (2020)
Tactile	Probing	M&F	10-40	Perak, Malaysia	Day	Blake (2022a)
Tactile	Probing	M&F	20-50	Perak, Malaysia	Day	Blake (2022b)
Tactile	Probing	M&F	30-40	Rift Valley, Kenya	Day	Clibbon (2022)
Tactile	Probing	M&F	20	Rift Valley, Kenya	Day	Clibbon (2022)
Tactile	Probing	M	20	Karnataka, India	Day	Desai (2022a)
Tactile	Probing	M&F	0	Karnataka, India	Day	Lakshmi (2022)
Tactile	Probing	M	10-20	Singapore	Day	13seaeagle (2014)
	Sweeping	M	30-50			
Tactile	Probing	M&F chicks	10-30	Mai Po, Hong Kong	Day	Hilldog (2010)
	Sweeping					
Tactile	Sweeping	M	70	Thiés, Senegal	Day	Sanabria (2007b)
Tactile	Sweeping	M	70	Thiés, Senegal	Day	Sanabria (2007c)
Tactile	Sweeping	F	20-40	Central River, Gambia	Day	Jimenez (2011b)
Tactile	Sweeping	M&F	10	Japan	Day	HelloAoba5541 (2013)
Tactile	Sweeping	Juv	30-40	Rajasthan, India	Day	del Hoyo (2014a)
Tactile	Sweeping	Juv	40-60	Rajasthan, India	Day	del Hoyo (2014b)
Tactile	Sweeping	Juv	20-40	Rajasthan, India	Day	del Hoyo (2014c)
Tactile	Sweeping	M	20-40	Okavango, Botswana	Day	Sun Destinations (2016)
Tactile	Sweeping	M	30-40	Rajasthan, India	Evening	Tewari (2017)
Tactile	Sweeping	F	10-30	Naledi, South Africa	Day	Beech (2019)
Tactile	Sweeping	M&F	30-70	Karnataka, India	Day	Prince (2020)
Tactile	Sweeping	M&F	10-55	Madhya Pradesh, India	Day	Sahana (2020a)
Tactile	Sweeping	M	40-45	Karnataka, India	Day	Sahana (2020b)
Tactile	Sweeping	M&F	25-30	Karnataka, India	Day	Sahana (2020c)
Tactile	Sweeping	M&F	25-30	Karnataka, India	Day	Sahana (2020d)
Tactile	Sweeping	M	20-30	Leste, Guinea-Bissau	Day	Xeira (2020)
Tactile	Sweeping	F	20-30	Rajasthan, India	Day	Birding GuRu (2021)
Tactile	Sweeping	M&F	10-20	Kerala, India	Day	Puravankara (2021)
Tactile	Sweeping	M	40	Maharashtra, India	Day	Bhagwat (2022b)
Tactile	Sweeping	M	5-10	Maharashtra, India	Day	Bhagwat (2022c)
Tactile	Sweeping	M	0	Maharashtra, India	Day	Bhagwat (2022d)
Tactile	Sweeping	M	45-50	Maharashtra, India	Day	Bhagwat (2022e)
Tactile	Sweeping	M	40	Maharashtra, India	Day	Bhagwat (2022f)
Tactile	Sweeping	M	10-20	Maharashtra, India	Day	Bhagwat (2022g)
Tactile	Sweeping	M	30-65	Karnataka, India	Day	Desai (2022b)
Tactile	Sweeping	M	45	Karnataka, India	Day	Desai (2022c)
Tactile	Sweeping	M	40-60	Karnataka, India	Day	Desai (2022d)
Tactile	Sweeping	M	60-65	Karnataka, India	Day	Desai (2022e)
Tactile	Sweeping	M	60-65	Karnataka, India	Day	Desai (2022f)
Tactile	Sweeping	M	60-65	Karnataka, India	Day	Desai (2022g)
Tactile	Sweeping	M	10	Karnataka, India	Day	Desai (2022h)
Tactile	Sweeping	M	15	Kerala, India	Day	Karingamadathil (2022)
Tactile	Sweeping	M	45	Maharashtra, India	Day	Shenai (2022)

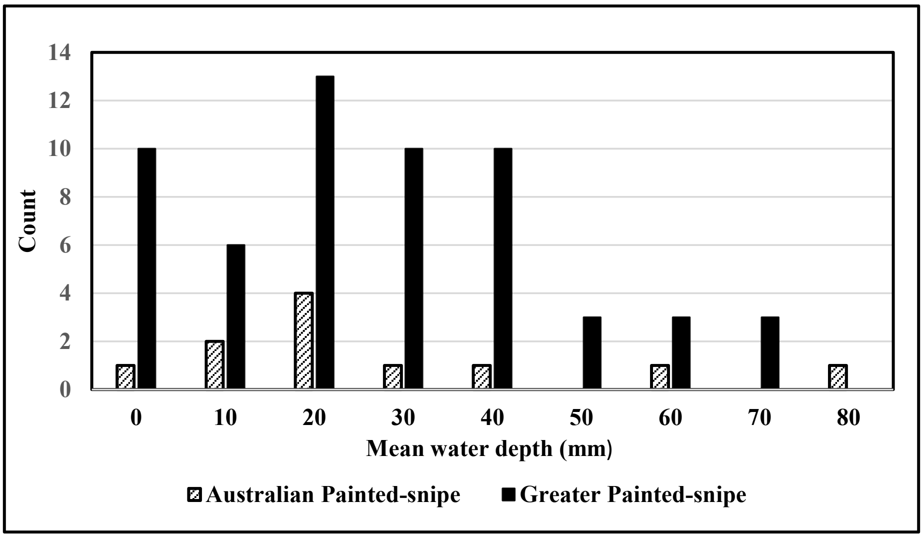

Figure 1. Mean water depth for Australian Painted-snipe and Greater Painted-snipe when foraging.

Australian Painted-snipe

Ten recordings from New South Wales, Queensland and Western Australia were analysed for foraging behaviour as summarized in **Table 1**. Both visual and tactile foraging modes were recorded. The dominant techniques used were probing and sweeping. The most common technique was probing.

Probing was observed in the soft substrate around the margins and within the shallower, near-shore parts of wetlands. Six recordings exhibited this technique (Siggs 2015; Jarvis 2016; BIBY TV 2017; Wallace 2017; Hosken 2020; Kinsey pers. comm.). The most extensive records were for the bird at Tea Gardens (Hosken 2020; Kinsey pers. comm.) This bird was wading slowly through relatively clear water 10-65 mm deep. Probing commenced with the bill thrust into the water, near vertically to a depth of 40-65 mm. In some probes, the bird's eyes and part of the head were immersed. The probing action was preceded initially by a period of sampling with side-to-side and more irregular movements of the bill, and in some instances, up-and-down movements. The bird usually remained stationary during the probe although on a few occasions it took one small step forward. The duration of the probe was generally 2-3 seconds. When the bill entered the water, the mandibles were initially slightly open, and then rapidly opened and closed while sampling the water column. The extent of mandible opening in the water column could not be estimated.

When prey were caught, the bill was withdrawn from the water and the mandibles were opened and closed rapidly five or six times as the prey was transferred to the oral cavity. This process took around 0.5 seconds. The width of mandible opening was estimated to be 1-2 mm. When no food item was captured, the bill when withdrawn from the water was closed. The bird's eyes were closed as the bill entered the water and then gradually opened as the probe continued. They were fully open as the bill was withdrawn. When the head and eyes were thrust underwater, the eyes remained closed until the bill was withdrawn. Although the water was clear, there were no indications the bird was using visual cues to locate prey or locations for probing. The bird's selection of probing sites appeared to be random. The other recordings (Siggs 2015; Jarvis 2016; BIBY TV 2017) are of birds probing in generally shallower water (10-30 mm). All other recorded details were generally similar to the above.

A recording of a female bird (Wallace 2017) initially showed probing of the substrate in water 40 mm deep, with head immersed 40-50 mm and eyes closed. The bird was subsequently probing in water 80 mm deep, with head fully immersed and eyes closed. This was accompanied by apparent side-to-side head movements which were interpreted to be a sweeping action across the substrate

Two recordings show birds using a sweeping technique to search for prey (Laven 2009; Parashou 2020). The bird at Tea Gardens (Parashou 2020) was wading slowly in relatively clear water 10-40 mm deep along the edge of a pond. The bill was held near-vertical and was swept side-to-side through the water as the bird moved steadily forward while sampling the water column. At times the bird stopped and used an up-and-down action with its bill, possibly when attempting to capture prey. The mandibles were slightly open as they entered the water and were then rapidly opened and closed as the bird advanced. The extent of mandible opening could not be estimated. When the bird's bill was withdrawn from the water it was closed indicating no prey had been captured. The eyes were closed when the bill entered the water and were partially opened towards the end of each set of actions. The depth of the bill in the water was 5-35 mm and the duration of each sweeping action was 0.5-1.0 seconds. No mandible movements with associated swallowing were observed following the sweeps. The selection of sweeping locations appeared random and there were no indications the bird was using visual cues to identify prey or foraging locations. The depth to which the bill entered the water and the lack of probing indicates the bird was using the sweeping action to search for prey, possibly larvae, within the water column. The sampling action could also have been used to detect the chemical signature of prey in the substrate.

There were no differences observed in the probing and sweeping techniques of male and female birds.

Visual foraging was observed in two recordings (Maher 2011a; Maher 2011b). Lunging was observed in a recording of a bird attempting to capture small flying insects at night (Maher 2011a). The bird was wading slowly through water about 60-65 mm deep, and was closely watching insects alighting on and moving across the surface of the water. An initial lunge with opened mandibles in the direction of an insect was followed by a period of rapid irregular head movements in the water. This was accompanied by rapid opening and closing of the mandibles as the bird attempted to secure its prey. The mandibles were opened 5-10 mm at their distal end. The bird's eyes were closed when the lunge commenced and gradually opened towards the end of the action. The bill was inserted into the water about 10 mm and each capture attempt was 0.25-0.75 seconds. One unsuccessful attempt was made to snatch an insect on the wing. These foraging attempts appeared to be unsuccessful.

The other recording (Maher 2011b) shows a male and female bird walking around the sandy edge of a wetland and pecking at prey on the surface as they advanced. This was the only recording which showed birds foraging on a substrate surrounding a wetland.

An analysis of mean foraging depth is shown in **Figure 1**. It varied from 0-80 mm and the average depth was 31 mm.

Captured prey was identified in one recording (Wallace 2017) where the bird was using probing and substrate-sweeping techniques to capture small snails. The snails were held at the distal end of the bill as it was withdrawn from the water, and were moved rapidly to the oral cavity by surface tension transport. The bird at Tea Gardens was also observed foraging briefly on the leaves of Brahmi *Bacopa monnieri* growing at the water's edge (Hosken 2020).

Greater Painted-snipe

Fifty-five recordings from Africa, India, Hong Kong, Malaysia, Singapore and Japan were analysed for foraging behaviour as summarized in **Table 2**. Both visual and tactile foraging modes were recorded. The dominant techniques used were lunging, pecking, probing and sweeping. The most common technique was sweeping.

A bird in Western Uganda, was recorded lunging unsuccessfully at flying insects (del Hoyo 2006). During the lunge which was 0.1-0.2 seconds duration, the eyes remained open and the mandibles were widely extended. The bird was foraging on partially vegetated mud.

Pecking was observed in six (10%) of the recordings. In all instances it occurred on the muddy surrounds of a wetland or the surface of shallow water. It was best illustrated at the start and at the end of a recording from Perak, Malaysia (Amar-Singh 2020). The bird was capturing snails in shallow water at the edge of a wetland by pecking with open eyes. The bill was open around 5-8 mm at the commencement of the peck. It remained open during the peck, although several rapid partial closures of 1-2 mm accompanied the action. The bill was rarely inserted more than 10 mm into the water. When snails were captured, the bill was withdrawn and the snails transported to the oral cavity. In some instances, the bill was not withdrawn from the water while the transport process occurred. The bird used surface tension transport to transport the snail from the distal tip of the bill to the oral cavity. This is illustrated in **Figure 2** which shows the transport process taking around 0.6 seconds. A female bird was recorded capturing prey by pecking with open eyes on partially vegetated dry mud, but the type of prey could not be determined (Birdlover.jp 2017). Surface tension transport was used to move the prey from the distal bill tip to the oral cavity.

Figure 2. Female Greater Painted-snipe using surface tension transport to transfer captured snail from distal tip of bill to the oral cavity. Frame sequence total 0.6 seconds. Note incremental increasing separation of mandibles between frames. Filmed at Ipoh, Perak, Malaysia, by Amar-Singh HSS, 7 May 2020

Probing was observed in 15 (27%) recordings. The most extensive record was from an artificial wetland in Singapore with a muddy substrate and a rocky shoreline (13seaeagle 2014). Probing and sweeping were the dominant techniques used, plus a short period of pecking. Probing was mostly in the deeper sections where the water depth was 10-50 mm. At the commencement of each probe, the bill was thrust near vertically to a depth of 40-55 mm, at times immersing the eyes. Probing mainly involved short side-to-side movements of the bill with occasional more irregular movements. The bird usually remained stationary during the probe but on a few occasions took a small step forward. The duration of each probe was 2-3 seconds. The mandibles were slightly open as the bill entered the water and they were rapidly opened and closed as the probing continued and the water column was sampled. The extent of mandible opening in the water could not be estimated. The bird was not observed to swallow any prey and when the bill was withdrawn from the water it was already closed. The eyes were closed when the probing action commenced and were opened gradually as it continued. The bird's eyes were fully open when the bill was withdrawn. The eyes remained closed when thrust underwater.

A male and female bird were recorded probing on wet, algae-covered mud at Karnataka, India (Lakshmi 2022). The open bill was inserted into the wet substrate between 10 and 40 mm and 2-6 rapid up-and-down vertical probes were made over 0.5-1.0 seconds. Eyes were closed initially and were opened as the probe proceeded. The bird remained stationary during the probe. Some probe sites were explored again or one or two rapid steps were made before commencing another probe. Prey was observed being swallowed but capture could not be observed.

Sweeping was present in 36 (65%) recordings. This technique was best illustrated in recordings from Singapore (13seaeagle 2014) and Perak, Malaysia (Amah-Singh HSS 2020). Birds were foraging in water 30-55 mm deep. During the sweeping action, the bill was held near-vertical and swept from side to side with accompanying head-tilting while the bird moved slowly forward. The mandibles were already slightly open when the bill entered the water and were then rapidly opened and near-closed as the bird advanced while sampling the water column. The extent of mandible opening was around 5 mm at the distal end. The bill was closed when it was withdrawn from the water after each sweep. The eyes were closed as the bill entered the water and partially opened towards the end of each sweep. The depth that the bill was inserted in the water was 10-45 mm and the duration of each sweeping action was 0.25-3 seconds. When snails were captured, the bill was withdrawn with slightly-open mandibles, which were then rapidly opened and closed as the prey was transferred to the oral cavity and swallowed.

A recording at Rajasthan, India (Birding GuRu 2021) shows a bird using vertical sweeping accompanied by rapid opening and closing of the mandibles and capturing snails. In other instances, surface tension transport action was observed followed by swallowing, but prey could not be observed in the bill. This occurred following a period of sampling of the water column. Some translucent prey, thought to be larvae, were observed falling from the bill. The bird's tongue appeared to have been involved in the transfer process.

In a number of the recordings, insects could be seen moving around the shores of the wetlands (del Hoyo 2014a & 2014c; Bhagwat 2022b; Desai 2022d). The birds must have been aware of the presence of these insects which occasionally walked immediately in front of them. However, the birds displayed no interest. This indicates the birds have specific prey preferences that do not include these readily-observable and easily-captured terrestrial invertebrates.

A recording of birds at Mai Po, Hong Kong, shows foraging by probing and sweeping (Hilldog 2010). A male bird was using its bill to remove dead vegetation from mud in search of underlying prey. Another male bird, accompanied by four chicks, was foraging by probing in shallow water. On capturing prey, the adult allowed a chick to take the prey from its bill. Subsequent recordings of the young birds as chicks and as juveniles, show them capturing snails by probing and pecking, but being unable to transport them up the bill to the oral cavity.

Eight recordings show birds foraging on other substrates. In all instances the locations were mud, or partially vegetated muddy surrounds of wetlands, or possibly unplanted rice fields. The birds were using pecking or probing.

One recording shows a bird foraging at night at Eswatini, Swaziland (Coker 2020). Although the habitat was difficult to observe, the bird appeared to be probing in water 20-40 mm deep. The probing action, with bill open, was preceded by an initial closing of the eyes, followed by opening. The bird made a single unsuccessful lunge at a flying insect with eyes closed.

The birds were observed capturing prey in the majority of recordings but in many instances the prey item could not be seen and only swallowing was noted. Birds were observed capturing small snails (1-2 mm) in 16 recordings. Worms were observed being captured in two recordings (Sanabria 2007a; Blake 2022b). An analysis of mean foraging depth is shown in **Figure 1**. It varied from 0-70 mm and the average depth was 29 mm.

Examination of specimens

Specimens of male and female Australian Painted-snipe were examined at the Australian Museum, Sydney in May 2022. The upper and lower mandibles of most specimens were covered by a layer of dark-brown keratin and the underlying bone structure could not be observed. However, some specimens had very pale and/or thin keratin or small areas where the keratin was absent, allowing partial examination of the underlying bone. Hundreds of small, roughly circular structures were observed in the lower mandible of three Australian Painted-snipe specimens. The structures were restricted to the distal 5-8 mm of the mandible and were more densely clustered towards the distal end. The structures were observed with a binocular microscope at x50 magnification and were estimated to be 10-20 µm in diameter. Structures could not be observed in the upper mandibles of these specimens due to the thick layer of dark brown keratin.

The specimens examined were prepared skins. Although labelled Australian Painted-snipe and Greater Painted-snipe, all specimens had been taken within Australia. Skeletal specimens may have provided an unobstructed view of the bones of both mandibles but were unavailable at the time of the visit.

DISCUSSION

The data set used here was uncontrolled and cannot be considered to be a representative sample of the behaviour of either species. The recordings are of variable duration and some had been edited or were a series of compiled clips. Less than one half of the recordings reviewed featured foraging behaviour. The exact time of recording and details of locations and prevailing conditions generally were not available. The slowest playback speed of some recordings that could be achieved was one-quarter normal which was insufficient to fully view some actions and accurately determine their duration. However, the consistency of behaviour that the birds demonstrated was considered to provide a sufficiently-sound basis for analysing their foraging techniques.

The influence of the presence of a videographer on the bird's foraging behaviour could not be assessed. In some instances, the bird's behaviour indicated they were aware of the videographer – for example, they ceased foraging and exhibited threat displays and/or made alarm calls. There are many other factors that could potentially influence foraging behaviour. These could include the type of substrate, its physical properties and the availability and type of prey. Data on these topics could not be obtained from the recordings and could not be assessed as part of this study. There are insufficient records to make any meaningful assessment of night-time foraging techniques although both visual and tactile modes were briefly observed.

Most of the recordings were of Greater Painted-snipe due to its more widespread occurrence, greater abundance and somewhat less-elusive nature. Tactile foraging was used more frequently than visual. No differences were identified in the probing and sweeping foraging behaviour of the two species in wetland habitats. The recordings of the Greater Painted-snipe showed it made more extensive use of the sweeping technique, but this possibly reflects the limited nature of the Australian data set. Lunging to capture flying insects was uncommon, although the few recorded instances may reflect the limitations of the data set. Lunging does not appear to be a very successful foraging technique. This was probably due to the bird's limited field of binocular vision. Habitat was observed to influence foraging technique with pecking being most common on muddy substrates and sweeping and probing occurring mainly in water-covered wetland habitats.

The range of water depth used for foraging was similar for both species and the average foraging depth was only marginally different. There were more recordings of Greater Painted-snipe foraging on muddy substrates, but again, this may reflect the larger data set for the species.

Although both species are reported to be largely crepuscular (Marchant & Higgins 1993; McNeil & Rodriguez 1996), all but two of the foraging recordings, and all of the non-foraging recordings, show birds active during the day. While this may reflect the unrepresentative data set, crepuscular behaviour may be an oversimplification of the temporal foraging behaviour of both species.

The presence of small pits in the distal section of the bill of the Australian Painted-snipe that probably house Herbst-type corpuscles, indicates that mechanoreception and possibly chemoreception were being used to assist tactile foraging. The sampling process of rapid opening and closing of the mandibles when probing and sweeping utilizes these receptors to detect prey. The receptors could be used to physically detect the presence of prey in the sampled water column or substrate, or to detect its chemical signature indicating its presence. The presence of Grandry-type cells in the tongue may also assist in the physical detection of prey in the sampled water column.

This study confirmed the birds' use of the surface tension transport mechanism described by Rubega & Obst (1993) to move captured prey from the distal tip of the bill to the oral cavity. A video frame sequence provided by Amar-Singh HSS (2020) illustrated a female Greater Painted-snipe transferring a snail to the oral cavity in 0.6 seconds (**Figure 2**). A recording by Hilldog (2010) of birds at Mai Po, Hong Kong, shows chicks, about two months old, capturing snails but unable to transport them up the bill to the oral cavity. This suggests that surface tension transport in this species was a learned skill acquired at a later age when the bill is fully developed. This video also showed a chick taking captured prey from the bill of a male bird. This may indicate chicks are not entirely precocial as stated in Marchant & Higgins (1993). There was no evidence in the recordings that indicated that Greater Painted-snipe used distal rhynchokinesis to capture its prey.

CONCLUSIONS

This study should be considered preliminary as it involved an unrepresentative data set of relatively short periods of observation. It has, however, yielded new information about the behaviour of one of Australia's least known endemic waders and of the closely-related Greater Painted-snipe.

Australian Painted-snipe use both visual and tactile foraging modes, with tactile foraging being dominant. The species uses probing and sweeping techniques to search for prey. There were insufficient records to determine a preferred technique or the factors driving their use.

Greater Painted-snipe also use both visual and tactile foraging modes. Visual foraging, using lunging and pecking was used dominantly on the muddy surrounds of wetlands. Tactile foraging used both probing and sweeping techniques, with sweeping being dominant. Probing was performed when the bird was stationary while sweeping was usually used when moving. Water depth did not appear to influence whether probing or sweeping was used, although sweeping was more common.

There were no observed differences between the sweeping or probing techniques as used by Australian Painted-snipe and Greater Painted-snipe.

Small water snails were the most commonly observed prey captured. Both visual and tactile techniques were used in their capture. Worms were captured by probing. Insect larvae in the water column may also have been captured by sweeping and sampling.

The presence of small pits under the keratin layer, clustered near the distal tip of the mandible indicates that Herbst-type corpuscles are probably present in Australian Painted-snipe. The sampling action of rapidly opening and partially closing the mandibles during sweeping and probing is probably part of the prey detection process using mechanoreception and possibly chemoreception.

Several directions for future research were identified. Detailed examination of specimens with keratin removed from upper and lower mandibles is required to accurately determine the distribution, number, size and shape of the structures observed in this study. Examination of confirmed Greater Painted-snipe specimens is also recommended to check for the presence of receptor pits in the mandibles. Investigations of the anatomy of the tongue is recommended to confirm the presence of Grandry-type receptors.

The use of frame-by-frame analysis of videography to obtain a more detailed and temporally accurate analysis of foraging techniques, prey captured and the prey-transfer mechanisms is recommended. The behaviour of birds foraging on other types of habitat and for other food items, such as plants and seeds, should be recorded and analysed. Infra-red video recording may provide more detailed information for analysis of nocturnal foraging.

The availability of thousands of hours of videography of most avian species on on-line platforms constitutes a relatively underutilised resource for the detailed study of avian behaviour.

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