ENVIRONMENTAL DETERMINANTS OF GREATER FLAMINGO FORAGING BEHAVIOUR IN AN ESTUARINE INTERTIDAL SANDFLAT

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ABSTRACT

The impact of flamingo predation on the benthic community has been well researched through the use of caging and exclusion experiments. However, there is still very little known about flamingo spatial foraging preferences and the environmental cues that determine them. The purpose of this study was to investigate the foraging distributions of non-breeding Greater Flamingos (*Phoenicopterus ruber roseus*) within one of their southern African overwintering grounds, the Heuningnes Estuary. This was achieved by comparing spatial level differences in the abundance and size of flamingo foraging pits across sites and shore positions, and by examining the effects of soil moisture content and sediment profile as environmental cues driving flamingo foraging behaviour. Pit abundance was obtained as a total count per quadrat, and pit size was measured from photographs taken in the field. Sediment cores provided soil moisture content measurements, while sediment profile was measured as the angle of elevation from each shore position to the high water mark. It was found that flamingos fed homogeneously across all four sites, but restricted their foraging to the high shore and upper mid shore regions of the intertidal. Soil moisture content was not a significant driver of flamingo foraging behaviour, but sediment profile was significant. It was proposed that flamingo foraging preference for the high shore and upper mid shore regions was because: (1) the sediment profiles were flatter, (2) the macrofaunal prey densities were greater and (3) these shore positions coincided with the required depth for stamp-feeding, which was linked to the high tide and the time of day at which foraging occurred. This study provides novel information regarding the environmental drivers of Greater Flamingo foraging behaviour and the spatial use of the intertidal sandflats of the Heuningnes Estuary. Furthermore, this knowledge could be useful for the management of flamingo foraging grounds of the De Mond Nature Reserve.

INTRODUCTION

Estuaries are important stop-over areas for overwintering shorebirds (Rosa et al. 2007; Masero & Pérez-Hurtado 2001; Sripanomyom et al. 2011). They provide temporary habitats in which shorebirds can rest and forage to sustain themselves before breeding season (Finn et al. 2008). Although intertidal sandflats offer an array of benthic invertebrate prey, they are often patchily distributed within the sediments (Summers & Kalejta-Summers 1996; Yates et al. 1993). Shorebirds are well-adapted to foraging under these conditions, whether it be in morphology or behaviour (Martin 2011; Rosa et al. 2007; Summers & Kalejta-Summers 1996; Velasquez & Hockey 1992; Finn et al. 2008; Navedo et al. 2013; Masero & Pérez-Hurtado 2001). As their prey are affected by the environmental conditions around them, environmental variables can be useful cues indicating whether particular patches make worthwhile foraging areas or not. Sediment characteristics and tidal cycles have been shown to influence benthic invertebrate activity, density and distribution (Yates et al. 1993; Velasquez & Hockey 1992; VanDusen et al. 2012; Ribeiro et al. 2004; Finn et al. 2008).

Although unrelated to shorebirds (order: Charadriiformes), flamingos also utilise estuarine intertidal sandflats as foraging grounds (Johnson & Cézilly 2007). Flamingos are an ancient bird group that debatably form their own order, the Phoenicopteriformes (Johnson & Cézilly 2007). Although progress in flamingo research has been made in terms of predator-prey interactions (for example: (Hurlbert & Chang 1983; Glassom & Branch 1997a,1997b; Rodríguez-Pérez et al. 2007; Arengo & Baldassarre 1998; Arengo & Baldassarre 1995), the feeding habits of flamingos are still not fully understood. Little is known about what drives flamingos to distribute themselves along a feeding ground, and what influences them to choose to feed in certain areas over others (Johnson & Cézilly 2007). Through their studies on the American flamingo, Arengo and Baldassarre (1995, 2002) have suggested that flamingo distribution during feeding is proportional to the density of food available, i.e. following the "ideal free" distribution model proposed by Fretwell & Lucas (1970) (Figure 1). Furthermore, Arengo and Baldassarre (2002) propose that flamingo foraging behaviour could be an indication of food quality for conspecifics.

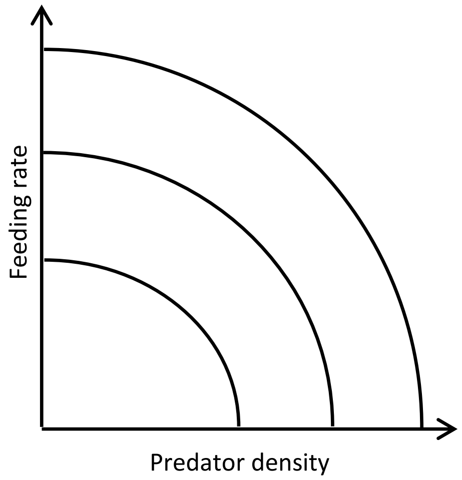

Figure 1: The ideal free distribution model proposed by Fretwell & Lucas (1970). The outer arc represents the best feeding site because it contains the highest feeding rate, whereas the inner arc represents the poorest feeding site as it as the lowest feeding rate. When predator density is low, predators should only occupy the best site. As predator density increases, interference reduces the feeding rate of the best site, so predators will spread out to the intermediate feeding sites as the feeding rate will be equivalent there. When predator abundance increases even further, the feeding rate of the intermediate site is reduced, so predators will spread out to occupy the poorest feeding site. Adapted From Sutherland (1983).

Flamingos are filter feeders and their main food items include aquatic invertebrates and their eggs and larvae (Johnson & Cézilly 2007). However, they can also forage on algae, seeds, insects or organic matter contained in mud (Johnson & Cézilly 2007). Flamingos are known to display different foraging strategies, or behaviours. This adaptation is known as foraging plasticity (Sinervo 2013). Foraging plasticity is thought to be a strategic evolutionary advantage for predators because it allows them to switch their behaviour according to environmental constraints, to allow for maximum food intake (Sinervo 2013; Gawlik 2002). The typical flamingo foraging behaviours are summarised in Figure 2.

"Stamping" is a feeding behaviour that is unique to flamingos in soft sediment habitats (Johnson & Cézilly 2007). Flamingos use their feet to dig into the sediment and gradually turn in a circle around their bills, usually forming a complete rotation (Johnson & Cézilly 2007, Brown et al. 2005). This allows them to float out buried invertebrate prey items so that they can be filtered. Stamp-feeding creates dome-like pits on the sediment surface that have been referred to as "feeding cones" by Gallet (1949) and "wheelies" by Glassom and Branch (1997a, 1997b). These pits can be up to 1 m in diameter (Glassom & Branch 1997a; 1997b). Flamingo feeding pits have been observed to be so numerous, that they transform the appearance of the sediment surface into a series of peaks and troughs (Glassom & Branch 1997a).

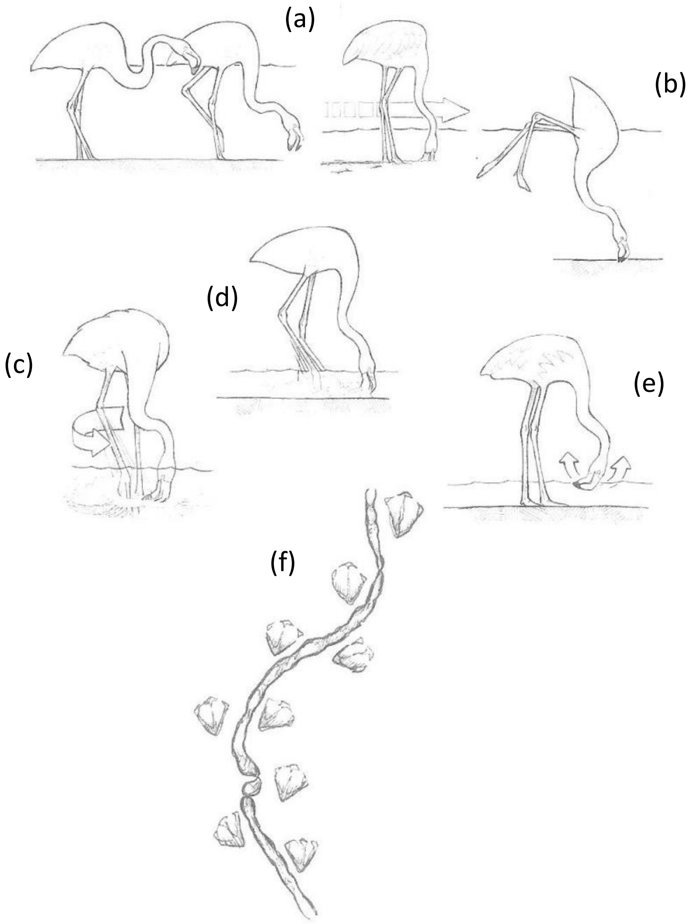

Figure 2: A summary of the various types of flamingo foraging behaviours. (a) walking and filtering or grubbing, (b) up-ending, (c) stamping, (d) stamping "marking time", (e) skimming, (f) walking "leaving tracks". Adopted from Johnson & Cézilly 2007.

Previous studies have suggested that flamingos mainly select their foraging grounds based on prey abundance and availability, which can be determined by environmental cues (Arengo & Baldassarre 1999; Arengo & Baldassarre 1995; Arengo & Baldassarre 2002; Mascitti & Castañera 2006; Velasquez & Hockey 1992; Ramesh & Ramachandran 2005). By making use of environmental cues, flamingos should be able to limit their foraging range to the most profitable patches of the intertidal sandflat. This would be advantageous for their fitness because they would not need to waste energy searching for prey in sparse patches, but maximise their prey intake in abundant patches (VanDusen et al. 2012; West et al. 2005).

Examples of environmental cues include: the tidal cycle, soil moisture content, and sediment profile. The distribution of benthic invertebrate taxa varies according to the tidal elevation of the shore, depending on their adaptations to physical and biological stresses (Peterson 1991). As flamingo foraging can only occur in water, the tide regulates the availability of the intertidal foraging ground in space and time (Velasquez & Hockey 1992). The water depth in which flamingos can forage therefore also varies with the tide. Flamingos require a water depth of up to 50 cm in order to utilise “stamping” feeding behaviour (Johnson & Cézilly 2007).

Soil moisture content, or porosity, relates to sediment grain size. Coarse sediments have poor water retention and high substrate resistance, while the opposite is true for fine sediments (Finn et al. 2008). With the exception of the immediate surface layer of the substrate, porosity decreases with depth due to sediment compaction (Herman et al. 1999). Sediments that are more porous provide more living space for infauna, and are less resistant to penetration by predators (Yates et al. 1993). Therefore, the higher prey density and lower sediment resistance of more porous sediments has been demonstrated to reduce the searching time and energy required to obtain prey (Velasquez & Hockey 1992; Dunn et al. 2013; Yates et al. 1993; Finn et al. 2008).

Shallow-sloped coastlines are expected to retain more organic matter than steeper coastlines because the rate of accretion is greater than the rate of erosion (Menn 2002). As a result, low profiled shores support large food webs of marcobenthic prey and epibenthic predators, while high profiled shores support small food webs of bacteria, protists and meiofauna (Menn 2002).

The purpose of this study was to investigate the environmental determinants Greater Flamingo (*Phoenicopterus ruber roseus*) foraging behaviour within one of their southern African overwintering grounds, the Heuningnes Estuary. This was achieved by comparing spatial level differences in pit abundance and pit size across sites and shore positions, and by examining the effects of soil moisture content and sediment profile as environmental cues driving flamingo foraging behaviour. It was hypothesised that: (1) differences in foraging pit abundance and size would be detectable on the finer-scale, i.e. the shore position spatial level rather than the site spatial level, (2) that higher soil moisture content would be preferred by flamingos because it is an indicator of higher prey density and lower sediment compaction and (3) that flatter sediment profiles would be preferred by flamingos as they are expected to be more productive.

MATERIALS AND METHODS

Study area

The Heuningnes Estuary forms part of the De Mond Nature Reserve, located 25km south of Bredasdorp and 200km east of Cape Town, Western Cape, South Africa (34°43'S, 20°07'E, (Figure 3) (BirdLife International 2014, Cape Nature 2014). Although the Heuningnes river and wetland system is approximately 9000 ha, the estuary itself is 918 ha in area (BirdLife South Africa 2014). The estuary is fed by two river systems, namely the Karsrivier and Nuwejaarsrivier (BirdLife South Africa 2014). This catchment area is 1401 km^2. The Heuningnes estuary forms an important wintering, staging and feeding habitat for breeding and migratory water birds (Ramsar 2014). Seagrasses grow in patches within the subtidal and intertidal range of the sandflat. The sand dunes that boarder the estuarine mouth have been stabilised with the exotic Marram Grass *Ammophila arenaria* (BirdLife South Africa 2014). Governmental management has kept the Heuningnes estuary mouth open artificially since 1937, to avoid flooding of neighbouring agricultural land during the wetter months of the year (BirdLife South Africa 2014). This has led to the formation of a large inner delta that has become a major feature of the lower estuary (BirdLife South Africa 2014).

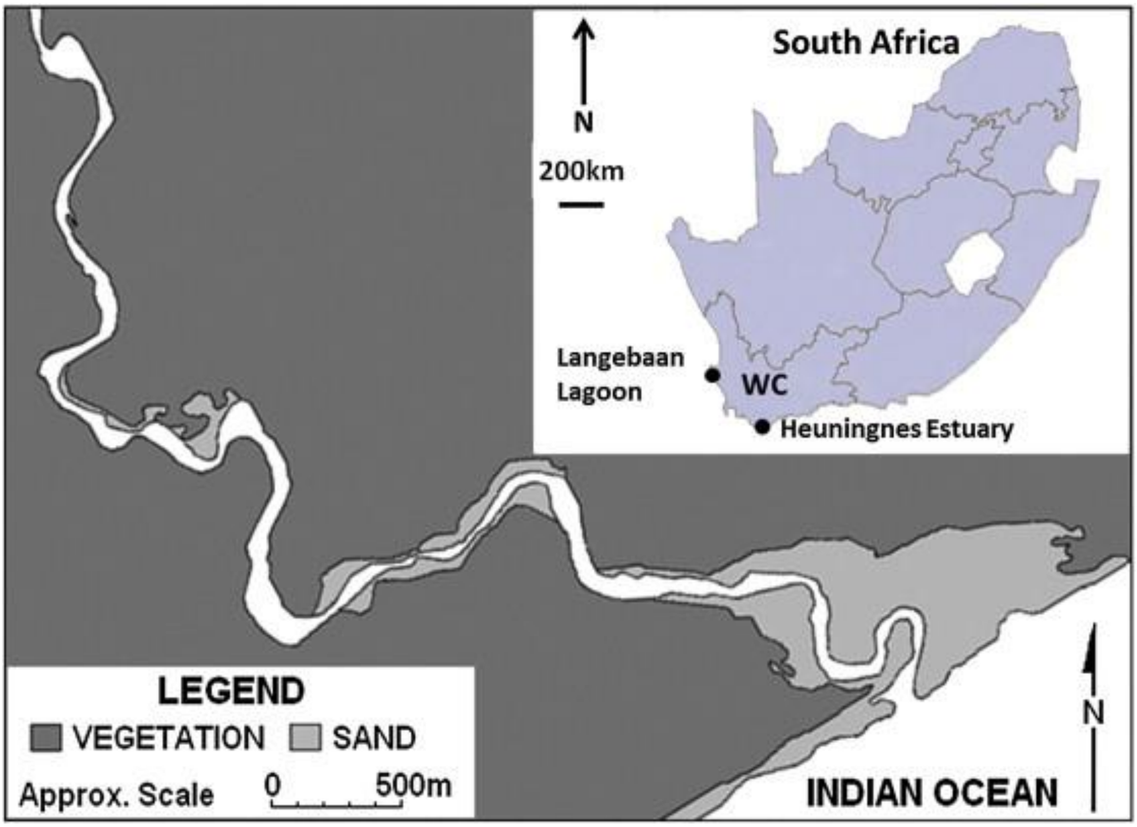

Figure 3: The geographical location of Heuningnes Estuary, Western Cape, South Africa (34°43'S, 20°07'E). Adopted from Källén et al. 2012.

Sampling methodology and data extraction

Sampling took place in winter 2014 from 26 July - 30 July. Four sites (A-D) were sampled over this study period in an intertidal sandflat in the Heuninges Estuary that was observed to be frequented by flamingos for foraging. Each site was divided into three transects that ran perpendicular from the high- to low-shore and positioned roughly 2 m apart. Each transect was divided into four quadrats (5 m x 5 m) that were representative of shore position (Figure 4). In each quadrat, the number and size of flamingo pits were quantified. In total, 12 data samples were obtained per site (4 quadrats x 3 transects), with a total of 48 samples for this study.

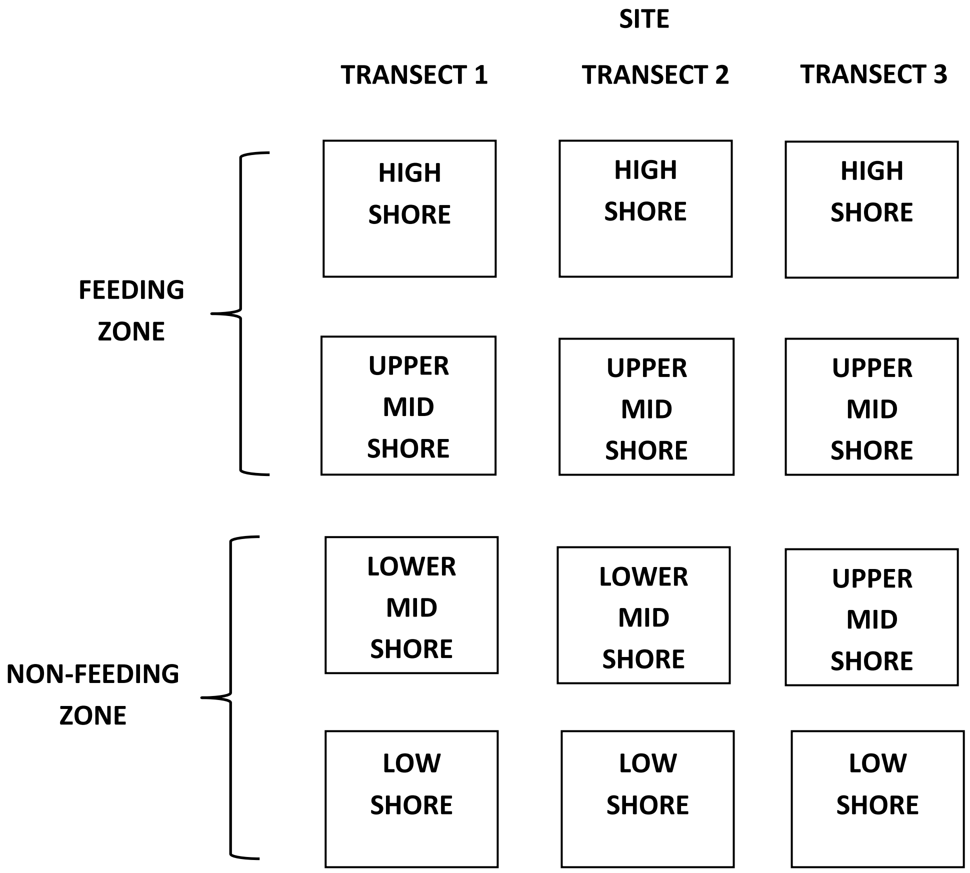

Figure 4: The sampling design used to test the foraging behaviour of Greater Flamingos for the four sites sampled within Heuningnes estuary. Each site was divided into three transects that ran perpendicular to the shore, and each transect consisted of four quadrats representative of shore position.

In order to measure pit abundance per quadrat, every pit observed within a quadrat was photographed using a waterproof point-and-shoot digital camera. To aid in estimating pit sizes per quadrat, a spirit level was attached on the camera in order to maintain a consistent depth of field for every photograph, while a 30 cm ruler was included next to pits in the shot to be used as a reference scale bar (Figure 4). ImageJ (version 1.48, 2014) was used to estimate pit areas from photographs of pits. Firstly, the “Straight” selection tool was used to select the length of the ruler, so that the scale could be set. Thereafter, the “Freehand” selection tool was used to estimate the area of each pit. The average pit sizes per quadrat were used in the statistical analysis.

A sediment core (5 cm deep, 2 cm diameter) was collected per quadrat to estimate soil moisture content. Cores were extracted from undisturbed sediments and then frozen. Sediment moisture content was estimated by weighing individual sediment cores, drying them at 40^{0}C, and re-weighing (to the nearest 0.0001 g). Moisture content was calculated as the moisture mass (difference in mass of wet and dry sediment) divided by the dry mass of the sediment sample.

Sediment profiles were measured at every quadrat. The measuring technique involved attaching a protractor to the base of a transect pole that was held upright, perpendicular to the sediment surface at the high water mark. A string was attached at base of the protractor, and ran to the quadrat, thus allowing the angle of the string from the high water mark to quadrat in question to be read off the protractor.

Statistical analyses

The R statistics program (version 2.15.1, R Core Team 2012) was used to conduct all data analyses. To explore data distributions for pit abundance and pit size, frequency distributions of the sample data were generated. Distributions of both data sets were zero-inflated.

Kruskal-Wallis tests were used to check whether there were significant differences in pit abundance and pit size for site and shore position (with shore position nested within site). To compare the relative effects of soil moisture content and slope on flamingo foraging behaviour, Kruskal-Wallis tests were conducted for site and shore position.

A binomial regression model was generated to examine the probability of feeding in relation to site, shore position, soil moisture content and slope. The validity of the model was examined by running an ANOVA Chi-squared test on the model. The final model was chosen based on the Akaike values.

RESULTS

Foraging pits were present at all four sites sampled at the Heuningnes Estuary (Figure 5.1). Pit abundance and pit size were not significantly different between the sites.

Mean soil moisture content decreased from 29.25% at site A to 28.08% at site D (Figure 5.2). Soil moisture content was significantly different by site (Kruskal-Wallis: $H_{3,48} = 11.34$, $p < 0.05$). Mean slope range between 3.75^0 and 5.42^0, but differences in slope measurements were not significant by site.

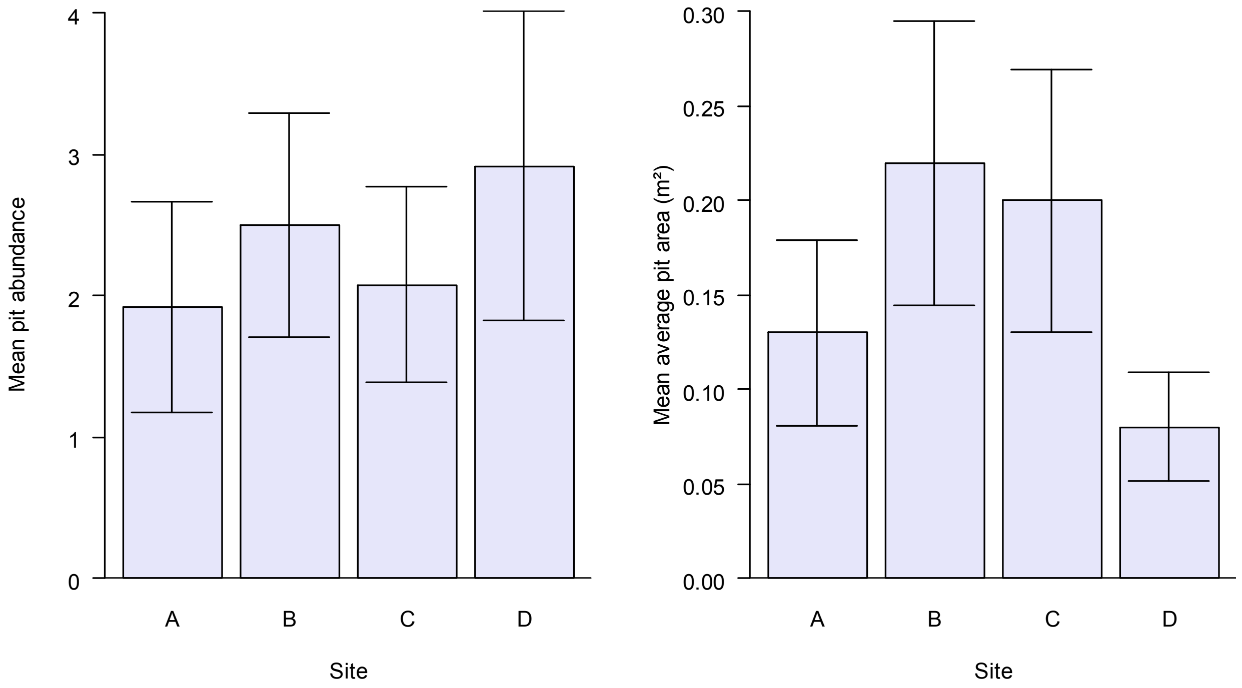

Figure 5.1: Bar plots displaying the means and standard errors of pit abundance and average pit area (m^2) for Greater Flamingo foraging pits as grouped by site (A, B, C and D) along the shoreline of the Heuningnes Estuary.

Figure 5.3 illustrates the absence of foraging pits at the lower mid shore and low shore positions. Pit abundance and pit size were significantly different by shore position (Kruskal-Wallis for pit abundance: $H_{3,48} = 37.87$, $p < 0.001$; Kruskal-Wallis for pit size: $H_{3,48} = 38.71$, $p < 0.001$). However, pit abundance and pit size were not significantly different between the high and upper mid shore positions.

Mean soil moisture content ranged from 28.5% to 29.0%, while mean slope ranged between 4.17^0 and 6.17^0 (Figure 5.4). Soil moisture content was not significantly different between shore positions.

Slope, however, was significantly different between shore positions (Kruskal-Wallis: $H_{3,48} = 10.37$, $p < 0.05$).

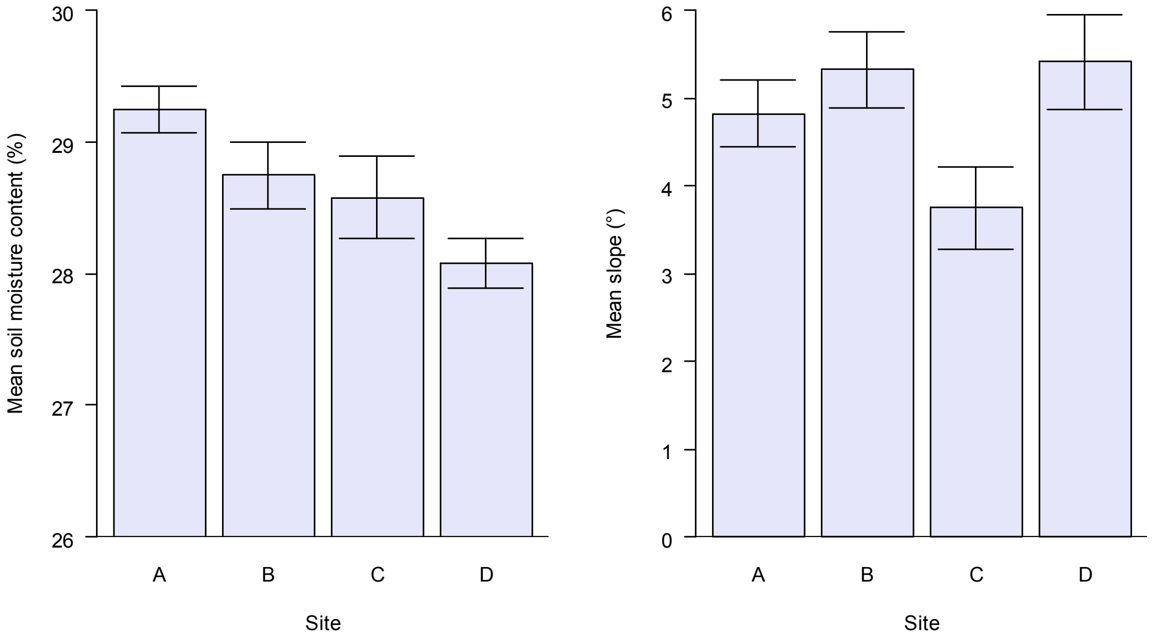

Figure 5.2: Barplots displaying the means and standard errors of soil moisture content (%) and slope (^{o}) for Greater Flamingo foraging pits in the Heuningnes Estuary as grouped by site (A, B, C and D).

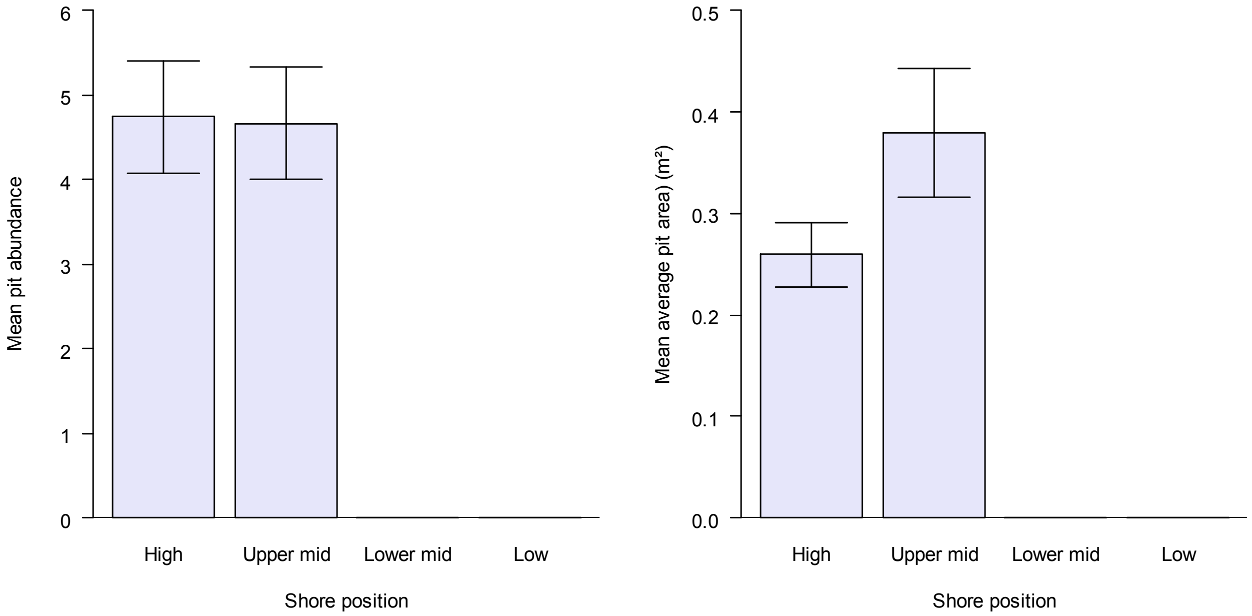

Figure 5.3: Bar plots displaying the means and standard errors of Greater Flamingo foraging pit abundance and average pit area (m^2) as grouped by shore position (High, Upper mid, Lower mid and Low) along the Heuninges Estuary.

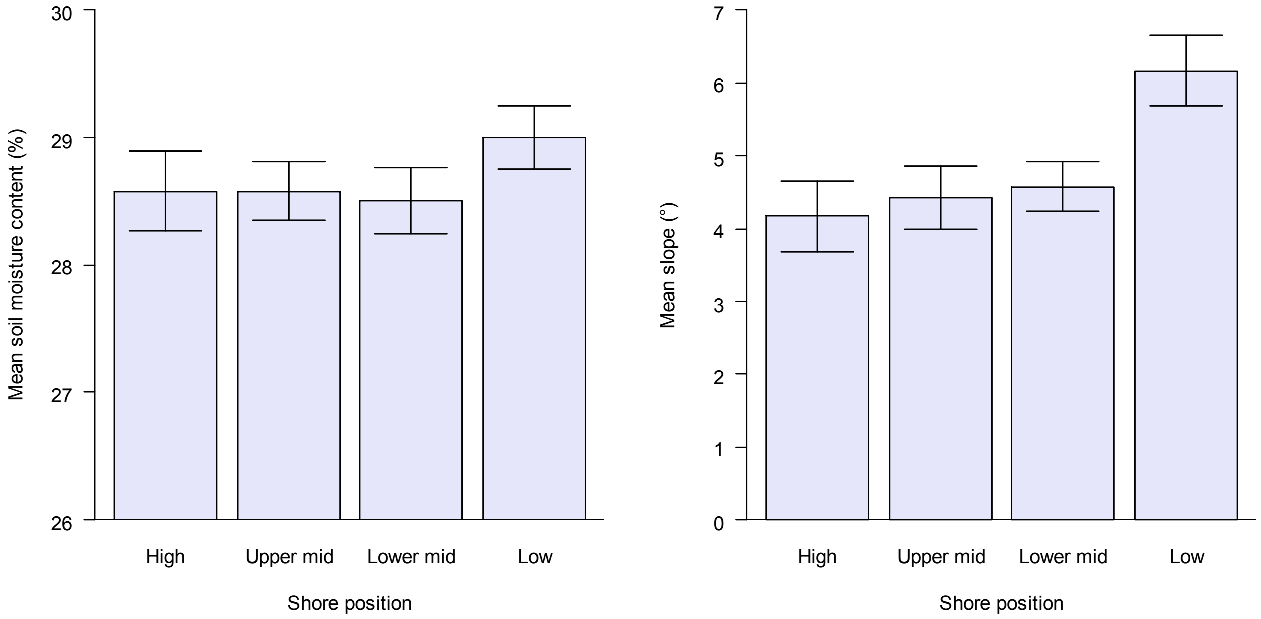

Figure 5.4: Bar plots displaying the means and standard errors of soil moisture content (%) and slope (^{o}) of Greater Flamingo foraging pits as grouped by shore position (High, Upper mid, Lower mid and Low) along the shoreline of the Heuningnes Estuary.

Table 1: A summary of the Chi-squared ANOVA test of the binomial model. The probability of feeding was the response variable, while soil moisture content, site, slope and quadrat were the model parameters.

Parameter	Degrees of freedom	Residual degrees of freedom	Akaike value	Deviance	Residual deviance	Variation explained	Pr(>Chi)
NULL		47	68.46	66.459			
Soil moisture content	1	46	70.27	0.185	66.274	34%	0.667
Site	3	43	76.13	0.141	66.133	34%	0.986
Slope	1	42	73.52	4.617	61.515	32%	0.032
Quadrat	3	39	18.00	61.515	0.000	0%	<0.001

Quadrat and slope were the only parameters that were significant in determining the probability of feeding by Greater Flamingos in the Heuningnes Estuary ($p < 0.05$ and $p < 0.001$ respectively). Soil moisture content and site were responsible for 34% of the variation explained by the model, while slope was responsible for 32% of the variation explained by the model.

DISCUSSION

The abundance and size of Greater Flamingo foraging pits were not significantly different between the four sampled sites, despite the significant differences in soil moisture content by site. This result may suggest that every site was equally utilised as flamingo foraging grounds. The intertidal widths and sediment profiles were similar for all sites. The difference in soil moisture content could probably be attributed to the weather conditions over the sampling period because rainy and overcast weather was experienced on the first two sampling days (site A and B), while the third and fourth days were dry (site C and site D).

Flamingos choose their foraging grounds according to habitat conditions and prey availability (Hutto 1985; Greene & Stamps 2001; Jones 2001; Clark & Mangel 1984). Soil moisture content is regulated by tidal fluctuations, which influences the availability of prey (Ribeiro et al. 2004; Summers & Kalejta-Summers 1996; Velasquez & Hockey 1992). Soil moisture content relates to sediment compaction and sediment resistance. Sediment that is less compact increases the living space of infauna (Finn et al. 2008). As a result, sediment moisture tends to be a good indicator of prey density (Yates et al. 1993). Sediment that is less resistant is more easily penetrated by probing shorebirds, thereby reducing the prey searching time required (Myers et al. 1980, Gerritsen & van Heezik 1985, Finn et al. 2008). The same conditions should also be upheld for flamingos making use of stamp-feeding behaviour. Therefore, foraging efficiency should be increased in sediments with greater soil moisture content. However, the homogenous flamingo feeding pattern observed between the four sites may be indicating that soil moisture content was unlikely to be a major driver of flamingo foraging choice. This result was supported as soil moisture content was not significant in the binomial regression model.

The abundance and size of Greater Flamingo foraging pits were significantly different between shore positions. Interestingly, flamingo foraging pits were only evident at the high shore and upper mid shore positions of the intertidal for all four sites. However, pit abundance and size was not significantly different between the high shore and upper mid shore positions, suggesting that these two regions were utilised equally. Differences in flamingo foraging patterns along the intertidal were predicted because of the intertidal zonation of the benthic community, which is influenced by physical and biological factors (Peterson 1991). Preference for the high shore and upper mid shore positions could possibly be attributed to the sediment profile conditions or the prey assemblages that were favoured.

Sediment profile was significantly different between shore positions, and is likely to be influencing flamingo foraging behaviour as it was also significant in the binomial model. The intertidal elevation was very flat for all sites, ranging between 1^{o} and 8^{o}. The higher elevations of the lower mid shore and low shore positions could be indicative of a dissipative and accreting shoreline, in which the rates of sediment deposition are greater compared to erosion (Menn 2002). It was predicted that the Greater Flamingos would prefer foraging in flatter regions of the intertidal because of the expected accumulation of organic matter, which should support more macrofauna (Menn 2002). Intertidal macrofaunal abundance data obtained during the same sampling period by Gihwala (2014) showed that certain taxa were greater in the high shore zones compared to the low shore zones. Polychaete worms were the most abundant taxon for all sites and shore positions, but were on average 3.6 times greater in abundance for the high shore and upper mid shore positions compared to the lower mid shore and low shore positions. In addition, isopods were on average 2.5 times more abundant in the high shore and upper mid shore positions. The flamingos may have chosen to limit their feeding to the high shore and upper mid shore because the shallower slope was an environmental indicator of higher prey density.

Alternatively, the flamingos could have chosen their foraging patches based on shore position alone. Flamingos possess sensitive tactile organs within their bills, and make use of taste and sight when searching for prey (Johnson & Cézilly 2007; Jenkin 1957; Zweers et al. 1995; Martin 2011). In order to know whether a foraging ground is suitable, predators are required to sample the foraging ground (Clark & Mangel 1984). Interestingly though, there was no evidence of foraging structures in the lower mid shore or low shore positions for the duration of the study, suggesting that the flamingos would have chosen to avoid these areas based on prior knowledge. Clark & Mangel (1984) suggest that vertebrate predators have the ability to compare the length of time spent searching for prey in a particular patch relative to previous patches that they have searched in, and can choose to abandon a current feeding patch if the search for prey is exceeding that of a previous patch. Therefore, over time, predators should learn which patches are more profitable. Perhaps the Greater Flamingos did not need to sample the lower shore regions of the intertidal, because they had learnt from experience that prey in the upper shore were more plentiful.

It has been suggested that flamingos distribute themselves across a foraging ground according to the ideal free distribution model (Johnson & Cézilly 2007; Arengo & Baldassarre 2002). Flamingo spatial distribution is therefore dictated by prey distribution and the degree of interference of conspecifics (Folmer et al. 2010; Sutherland 1983; Ribeiro et al. 2004). Interference is a function of the distance between individuals (Folmer et al. 2010). Despite increased levels of interference and the depreciation of patch quality, flocking improves predator detection, and can be an indicator of favourable foraging patches for conspecifics (Arengo & Baldassarre 2002; Folmer et al. 2010).

Greater Flamingo densities at the Heuningnes Estuary were low, with less than 20 individuals observed per sampling day. Provided that the ideal free distribution model was upheld by this population, the flamingos should have only utilised the best foraging sites. Therefore, in conjunction with the prey data obtained by Gihwala (2014), it is likely that the high shore and upper mid shore regions were the most profitable sites for flamingo foraging.

Differences in flamingo feeding relative to the four shore positions measured could coincide with the foraging depth required for stamp-feeding behaviour. Stamp-feeding requires a water depth of up to 50cm (as estimated from the study by Mascitti & Castañera 2006), and can occur in the intertidal and subtidal (Johnson & Cézilly 2007). The intertidal sandflat was completely exposed at low tide, so the Greater Flamingos would not be able to forage at any of the shore positions during this time. Foraging at the lower mid shore and low shore positions would have had to occur within the period between high and low tide. However, foraging at the upper mid shore and high shore positions would have probably occurred during high tide, in order for this region of the tidal flat to be covered with enough water to allow for stamp-feeding. In their study, Glassom & Branch (1997a) found that Greater Flamingo foraging in the intertidal only occurred at high tide. Alternatively, Khaleghizadeh (2011) found that Greater Flamingo foraging occurred at low tide in the early morning and evening, and at high tide at midday.

High tide foraging could be linked to the time of day at which flamingo foraging was optimal. Greater Flamingos were observed to be resting in the subtidal during low tide (between 09:00 and 15:00) on the sampling days. It was therefore suspected that the Greater Flamingos at the Heuningnes Estuary were foraging mainly at dawn (approximately 06:00) and dusk (approximately 18:00) within the intertidal, following the high tide. Flamingo feeding usually occurs day and night and varies according to the season and the location of the foraging ground (Johnson & Cézilly 2007). Britton et al. (1986) found that the daily feeding cycle of Greater Flamingos in the Camargue (France) tracked the circadian rhythms of their main prey item in this region, the brine shrimp (*Artemia* sp). In Britton et al.'s study (1986), Greater Flamingos fed almost exclusively at night because the brine shrimps would migrate to the surface waters and therefore be more attainable by skim-feeding. Night foraging is said to sometimes be preferred for improved thermoregulation or predator and human disturbance avoidance (Yosef 2000; Brown et al. 2005). As temperatures during the day did not exceed 23^{o}C, human disturbance was low, and flamingo predators were absent from the Heuningnes Estuary, the Greater Flamingos would not need to forage at night. Therefore, it is more likely that flamingo foraging patterns were linked to the high tide in relation to the greater prey density located in the upper mid shore and high shore regions of the intertidal.

Conclusion

Greater Flamingos overwintering at Heuningnes Estuary foraged uniformly between the four study sites, but restricted their foraging to the high shore and upper mid shore regions of the intertidal. The high shore and upper mid shore regions were utilised equally as foraging grounds as flamingo foraging frequency (pit abundance) and effort (pit size) were similar between them. Soil moisture content was not a significant driver of flamingo foraging behaviour, but sediment profile was significant. It was proposed that flamingo foraging preference for the high shore and upper mid shore regions was because: (1) the sediment profiles were flatter, (2) the macrofaunal prey densities were greater and (3) these shore positions coincided with the required depth for stamp-feeding, which was linked to the high tide and the time of day at which foraging occurred. This study has provided novel information regarding the environmental drivers of Greater Flamingo foraging behaviour and the spatial use of the intertidal sandflats of the Heuningnes Estuary. This knowledge could be useful for the management of flamingo foraging grounds within the De Mont Nature Reserve. It also adds to the limited knowledge of Greater Flamingo foraging behaviour for South Africa. To build on this research, I would recommend the addition of sediment grain size and anoxia measurements so that further connections to the prey community could be made.

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