Master thesis:

Foraging behaviour of the Eurasian oystercatcher in a challenging breeding site

Isabelle Grieveson

6th September 2018

Supervised by:

Prof. Dr. Stefan Garthe and Dr. Philipp Schwemmer

Declaration of Authorship

I, Isabelle Grieveson, declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

Title of thesis: Foraging behaviour of the Eurasian oystercatcher in a challenging breeding site

I confirm that:

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ABSTRACT

The Eurasian oystercatcher (*Haematopus ostralegus)* population has declined dramatically in the Wadden Sea over the past 20 years. This top predator is an important indicator for the health of the ecosystem as a whole, but the causes behind this dramatic decline are not yet clear. It is thought that low breeding success and food availability may play a role, with the breeding season being a key period where birds must balance their time between foraging trips and defending their breeding territories from rivals or predators. Whilst previous studies have investigated this balance on island-breeding birds, here we aim to discover how this balance is shifted in individuals nesting in a more challenging breeding site. Oystercatchers nesting on the mouth of the river Elbe estuary on the mainland Kaiser-Wilhelm-Koog are subjected to increased levels of predation from nocturnal mammals that are not present on islands, together with an increasing frequency of storm floods that destroy nests. In this study global positioning system (GPS) data loggers were used to investigate oystercatcher foraging behaviour under these conditions, in particular the differences in foraging trip duration and distance during day and night time periods, and during the different tidal stages. Data on the abundance of benthic prey organisms available to the oystercatchers was collected at foraging sites identified using the GPS data, and at random sites on the tidal flats. Visual surveys were carried out in order to determine the hatching success of the oystercatchers in this area. Hatching success was very low, with only 3 chicks observed over the whole area. Although the birds were hypothesized to spend longer periods on the nest at night in order to defend their clutches from nocturnal predation, in fact similar behaviour to individuals breeding on islands was exhibited: foraging trips were of longer duration during the night than during the day. However, in contrast to previous studies on island breeding birds, oystercatchers at Kaiser-Wilhelm-Koog tended to have a relatively high foraging site fidelity and did not travel further when foraging at low tide periods. In addition, unlike several previous studies in different locations, the birds at Kaiser-Wilhelm-Koog did not target areas of high prey density. The most likely reason for this was the uniformly low level of benthic prey abundance across the study site, with an average biomass of only 3.34 gm^{-2} and with several key prey species of the oystercatcher absent entirely. This low-quality breeding site appears to result in significant changes in the foraging behaviour of the Eurasian oystercatcher, however more studies are suggested in order to untangle the multiple factors of low prey availability, high predation and flooding that may be causing these behavioural differences.

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1. Introduction

1.1 Population decline of the Eurasian oystercatcher

The Eurasian oystercatcher (*Haematopus ostralegus)* is a wading bird with a large range across Europe and Asia. The European population is estimated to make up approximately half of the global population, with 568,000-708,000 individuals (Birdlife International 2015; Wetlands International 2012). In turn, the Wadden Sea supports 50% of the East-Atlantic Flyway oystercatcher population(Reineking and Südbeck 2007), and therefore the health of this population is not only of particular conservation concern, but also acts as an important ecological indicator for the quality of the Wadden Sea ecosystem (Reineking and Südbeck 2007).

There has been a declining trend in the population of Oystercatchers in the Wadden Sea since 1997 (CWSS 2010), starting earliest in Schleswig Holstein and the Netherlands. This was thought to have been triggered by a cold winter in 1995/1996, together with shellfish fisheries in the 1990s in the Netherlands (Koffijberg et al. 2015).

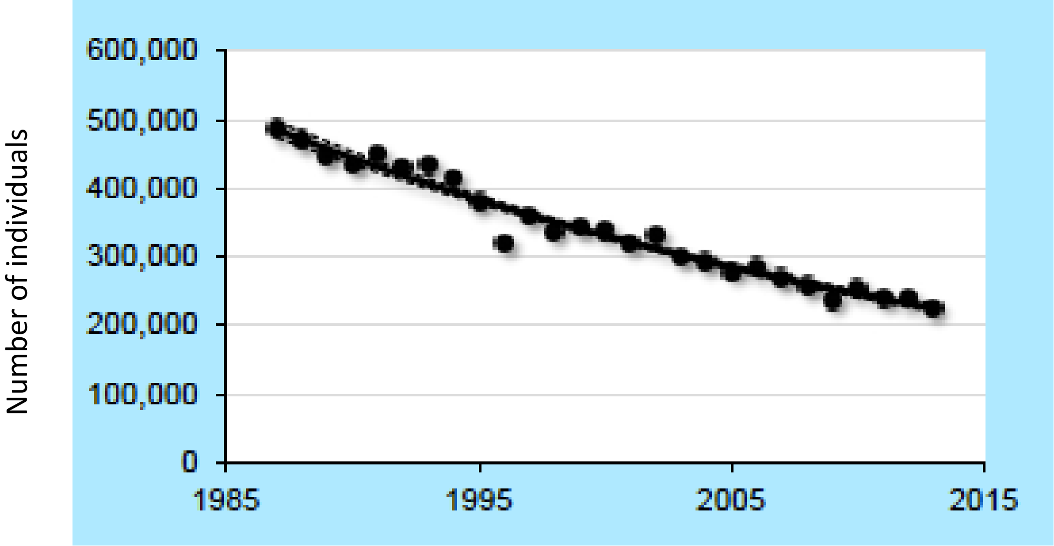

Figure 1. Eurasian oystercatcher abundance in the Wadden Sea (CWSS 2010)

Although this continuing trend can be partially attributed to loss of prey through mussel fisheries in certain locations such as the Netherlands (Piersma et al. 2001; Bruno J. Ens 2006; B. J. Ens, Small, and Vlas 2004), this cannot explain the downward trend in the German Wadden Sea, where these harmful shellfisheries do not exist. It is now thought that low breeding success is a key factor in the declining populations of oystercatcher in the Wadden Sea, however the causes of low breeding success are not entirely clear. Increased predation and flooding are often identified as contributing factors. In fact, oystercatcher breeding success is now so low that it is insufficient to maintain the population at a stable level and, given that oystercatchers are a long-lived species, there is likely to be a delay between the recording of breeding failure and a declining trend appearing in the population (Koffijberg et al. 2016). In particular, hatching success at breeding sites on the mainland coast tends to be very low. In breeding success surveys across the Wadden Sea from 2009-2012 by the Trilateral Monitoring and Assessment Program, the mean hatching success of oystercatchers on the mainland was 5%, with 56% of all cases across sites and years being zero. Hatching success on islands tends to be higher, with a mean of 51%. Where a cause of egg loss was reported, predation was the most common cause at 77%, and the remainder of eggs were lost due to flooding (Thorup and Koffijberg 2016). *Haematopus ostralegus* is under risk of clutch predation by birds such as the Common gull and Herring gull (Verboven, Ens, and Dechesne 2001) throughout its Wadden Sea breeding territories. In addition, those birds that nest on the mainland rather than on islands are also subject to mammalian predation (Langgemach and Bellebaum 2005).

1.2 Balancing clutch defense with successful foraging

Breeding oystercatchers must balance the task of defending their clutch against predation with the need to feed themselves and their chicks. This is additionally complicated by the fact that oystercatchers feed in tidal regions and so foraging is restricted to the times that the tidal flats are exposed. Given the downward trend seen in the oystercatcher breeding success in the Wadden Sea, it is possible that a shift in the levels of predation or efficiency of foraging may have offset this balance and contributed to the declining population. This has been investigated in several previous studies by Philipp Schwemmer et al. focusing on island-breeding oystercatchers, where it was found that these birds use several foraging strategies in order to maximize their breeding success (Schwemmer et al. 2016; Schwemmer and Garthe 2010). Individuals undertook longer foraging trips at night, to sites that were further away from the breeding grounds than those they visited during the day (Schwemmer and Garthe 2010). This is thought to be because the risk of avian predation is reduced at night, giving an opportunity for the birds to leave their nests for longer periods and to prioritise foraging over defense against predators. In addition, it has been shown than oystercatchers are able to identify and specifically target foraging locations with a high prey density (Sutherland 1982; Sutherland and Sutherland 1982; Goss-custard et al. 1991), and during the breeding season they will travel distances over 4km to reach particularly prey dense foraging sites (Schwemmer et al. 2016).

1.3 Kaiser-Wilhelm-Koog as a challenging breeding site

1.3.1 Mammalian predators

The study location chosen is the salt marsh and adjacent mudflats of Kaiser-Wilhelm-Koog, an area bordering the river Elbe estuary in the German Wadden Sea. This is a mainland breeding site of oystercatchers, which has been observed to have a relatively low breeding success (pers. comm. Michael Beverung). Here, one contributor to low breeding success is speculated to be a relatively high level of predation by mammals such as foxes and raccoon dogs. This is a problem that has increased over the last few decades, with predation of oystercatcher nests in western Europe increasing by ~40% from 1980-2006 (Roodbergen, van der Werf, and

Hötker 2012). One possible explanation for this huge increase in nest predation is the dramatic growth of red fox *Vulpes vulpes* and raccoon dog *Nyctereutes procyonoides* populations in Germany following the eradication of rabies in the 1980s-1990s (Bellebaum 2003; Panek and Bresinski 2002). The eradication of rabies reduced the levels of adult mortality in fox and raccoon dog populations, allowing population growth to accelerate and the population to settle at a higher density 6-7 years after the eradication (Langgemach and Bellebaum 2005; Bellebaum 2003). According to a review by MacDonald and Bolton (Macdonald and Bolton 2008), mammalian nocturnal predators currently make up the largest fraction of wader nest predation in Europe. It is currently unknown whether or not oystercatchers breeding in mainland nesting sites such as Kaiser-Wilhelm-Koog have adapted their foraging behaviour in order to combat threats to their clutches from increasing mammalian predation. In order to do so, you would expect the birds to spend as little time as possible away from the nest during the night. However, doing this would also leave their clutch vulnerable to avian predation during the day, and possibly limit their foraging capacity. In taking shorter foraging trips to feeding sites close to their breeding sites, oystercatchers could be passing up the opportunity to forage at sites with a higher prey density.

1.3.2 Storm floods

An additional challenge that breeding oystercatchers face in this nest site is an increase in storm floods that wash away eggs and young chicks (Van De Pol et al. 2010). Oystercatchers on the mainland may be encouraged to nest closer to the high tide line so their offspring are less vulnerable to mammalian predators (Cervencl et al. 2011), but this leaves the nests exposed to flooding at extreme high tides (Koffijberg et al. 2016). The salt marshes where oystercatchers nest are above the mean high tide levels, however during storms they may be flooded when extreme high tide events occur. Extreme climactic events, such as these storms, have been predicted to continue to increase due to climate change (Easterling et al. 2000; IPCC 2007). Van de Pol *et al.* found in their 2010 study that over the past four decades the maximum high tide has increased twice as fast as the mean high tide, causing more severe and frequent flooding of the salt marsh nest sites during the breeding season. Indeed, they found that in the Cuxhaven area (close to Kaiser-Wilhelm-Koog) the daily probability that the salt marsh will flood has almost doubled in June between the period 1971-1989 and the period 1990-2008 (Figure 2). In addition, the deepening of the shipping channel in the Elbe estuary has allowed the flood tide to move into the river with more energy (Freitag et al. 2007), presumable further increasing the likelihood of flooding of the saltmarsh. Van de Pol *et al.* predict that the risk of flooding of oystercatcher nests will increase in the next decade, even resulting in a level of fledgling success that is too low to sustain a stable population size (Van De Pol et al. 2010). Even if oystercatchers in the Kaiser-Wilhelm-Koog salt marsh are able to adapt to this increase in storm floods by nesting further from the high tide line, other factors, such as proximity to prey, may cause them to continue nesting on sites susceptible to flooding.

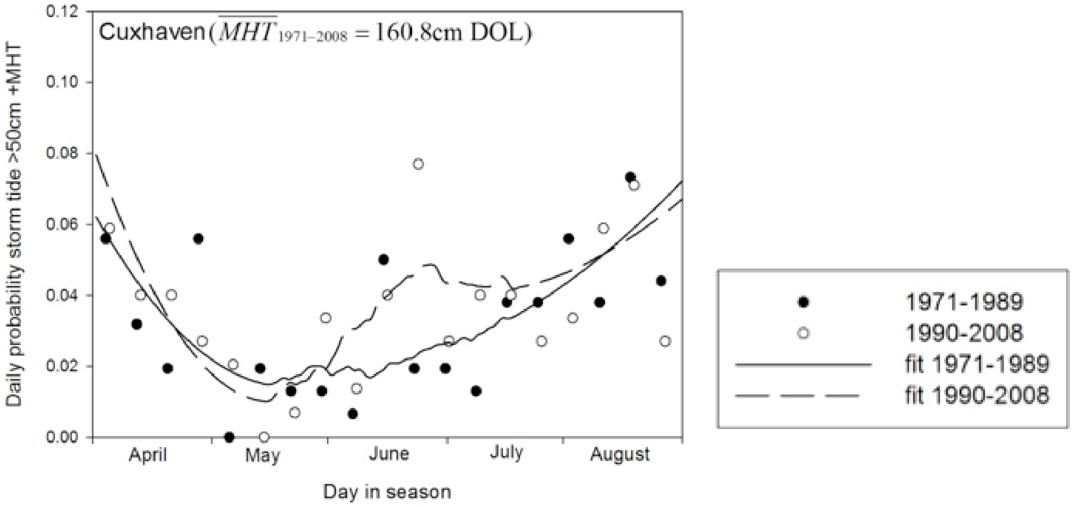

Figure 2. The daily probability that the salt marsh will flood for the periods 1971-1989 and 1990-2008 over the period April-August. Dots represent averages per week. Lines are fitted on raw daily data. All data is for Cuxhaven. Figure adapted from supplementary information of (Van De Pol et al. 2010).

In a fundamental study by Ens et al. in 1992 (Bruno J Ens et al. 1992), the concept of "leapfrog" and "resident" territories in oystercatchers was first conceived. Parent birds that occupy "resident" territories that are adjacent to the mudflats have a reproductive advantage as they must put in less effort to feed their chicks. Parents that occupy "leapfrog" territories are separated from the mudflats by other territories, and so must expend more energy to reach the feeding areas. This concept has also been supported by a more recent study using GPS devices (Schwemmer, Weiel, and Garthe 2017). Significant advantages in terms of breeding success were recorded in "Resident" pairs, but it remains to be seen if these advantages still exist in the wake of rising sea levels and more frequent storm floods of low-lying breeding sites.

1.4. Project Aims

The main goal of this thesis is to better understand the foraging behaviour of the Eurasian oystercatcher *Haematopus ostralegus* during the breeding season. In particular, we aim to shed light on the behaviour of those individuals breeding on a mainland nest site, and thus have the additional pressure of mammalian predators affecting their breeding success. Through the analysis of pre-existing data sets and the collection of new data by fieldwork in the 2017 breeding season, the following questions will be answered:

1. What is the hatching success of oystercatchers breeding in Kaiser-Wilhelm-Koog?
2. Do oystercatchers make foraging trips of longer duration and distance during the day (rather than the night) in order guard against nocturnal mammalian predation?
3. Does tidal stage affect the distance travelled and duration of foraging trips?
4. Do oystercatchers target areas of particularly high prey density when foraging?

2. Materials and Methods

2.1 Study Site

An area of salt marsh in the German Wadden Sea of approximately 4km by 0.4km was chosen as a study site. This is located at Kaiser-Wilhelm Koog, Schleswig Holstein, on the mouth of the River Elbe Estuary (53°55’14N, 8°54’56E) (Figure 3). The foraging behaviour of the oystercatchers was studied on the mudflats adjacent to this salt marsh.

Figure 3. Location of the study site, Kaiser-Wilhelm-Koog on the mouth of the river Elbe. Map created using Google Earth.

2.2 Hatching success

The study site was surveyed for nests using the dike bordering the salt marsh as a viewpoint to help locate incubating birds. All nests within the study site were marked with a bamboo pole and their longitude and latitude recorded with a handheld GPS device. Nests were then visited once weekly throughout the incubation and chick rearing period, and the numbers of eggs or chicks present were noted. If a nest was found empty, the fate of the nest was assessed according to methods proposed by Bregnballe et al. (Bregnballe et al. 2015). If chicks were seen in or near a nest, or there were small egg shell fragments in the nest lining, the nest was classed as hatched. If there are broken eggs inside the nest it would imply the nest was trampled by sheep. If there are signs of recent flooding, the nest was classed as washed away. Finally, if there was an empty nest with no other traces, the nest was identified as predated. Hatching success was then calculated as a percentage of the total number of eggs present.

2.3 Oystercatcher movement data using GPS loggers

In late May and early June 2016, 6 adult Oystercatchers were equipped with GPS data loggers by Philipp Schwemmer and colleagues. The birds were caught whilst incubating, using walk-in traps placed over the nest sites. The loggers used (manufactured by e-obs GmbH) weighed ~10g and were attached to the birds' backs using a harness. All handled birds were also measured, weighed, ringed and then immediately released. Five further birds were also equipped in the same way with GPS loggers at the beginning of June 2017.

The GPS loggers recorded the longitude and latitude of the bird at 10 minute intervals, as well as date, time, heading, speed and temperature. The battery was charged using a small solar panel on the device, therefore during extended periods of low sunshine the logger may have switched to recording data at 20 minute intervals as a result of low battery levels. Data was retrieved from the loggers using an antenna and base station from a distance of up to 4km away (dependent on weather conditions). Therefore, the birds did not need to be recaptured in order to retrieve the data. It is expected that the harness will degrade over a period of time, and the logger will fall off the bird.

The Geographical information system ESRI ArcMap 10.3.1 was used to visualize the spatial patterns of the foraging trips of the birds. A foraging trip was identified by assigning each recording of the GPS logger to one of three categories: "nest", "flying" or "foraging" using the distance travelled from the nest and the speed recorded. A recording of a speed higher than 3.5 m/s was identified as "flying" (Bom 2014; Shamoun-Baranes et al. 2012), a recording closer than 250 meters from the nest was marked as "nest" and recordings at speeds lower than 3.5m/s and further than 250m from the nest were marked as "foraging". Foraging trips were then identified by grouping together consecutive recordings marked as "flying" and "foraging" and confirmed by visualizing the spatial patterns on a map.

Foraging trips were assigned as occurring during the day or night according to civil dawn and dusk times, which were calculated for each day using the maptools R package (Bivand and Lewin-Koh 2017). Foraging trips were also classified according to tidal stage: low tide = 1.5hrs before and after low water, mid tide = between 1.5hrs after low water and 1.5hrs before high water, high tide = 1.5hrs before and after high water. This was calculated using tide tables for the region (Bundesamts für Seeschifffahrt und Hydrographie (BSH) 2016). Differences in trip duration (time spent between leaving and returning to the nest) and trip distance (km) (maximum distance from the nest site reached during the foraging trip) were tested between night and day, as well as between different tidal stages.

Foraging site fidelity of the individuals was estimated by performing kernel density home range analyses using the spatial analyst tools in ArcMap 10.3.1. The total area of foraging habitat in which 25, 50, 75 and 95% of the GPS recordings were located was calculated and plotted as kernels on a map.

2.4 Prey distribution

The distribution of benthic prey in relation to oystercatcher foraging sites was measured. Sites for benthos sampling were chosen from the most important foraging sites indicated by the GPS logger data, selected according to how frequently they were visited by an individual bird, and the time spent at the site. A 15cm deep sediment core was taken, and the sediment was passed through a 1mm sieve. Bivalves were collected in a small plastic bag and then frozen. Polychaetes and small crustaceans were deposited immediately in 70% ethanol. This was also repeated at control sites, three of which were chosen randomly within a 500m radius of each foraging site.

The ash free dry weight (AFDW) of each benthic species at each sampling site was then calculated. For bivalves, the height, width and length of each individual was measured, the species recorded, and the flesh removed from the shell. For polychaetes and crustaceans, each individual was identified to the species level and the length was measured. Any fragments of the same species in one sample were counted and then grouped together for further analysis. The organisms were then dried for 12hrs at 55°C and weighed to determine the dry weight. This dried benthos was then burned in a Muffel furnace for 12hrs at 450°C and weighed to give the mass of inorganic matter. In order to obtain the biomass in the form of AFDW, the weight of inorganic matter was taken away from the dry weight. The biomass (g/m^2) and count of prey (individuals/m^2) found at foraging sites was then compared to the biomass and count at control sites. This analysis was carried out for total prey biomass and count, polychaete biomass and count, and bivalve biomass and count.

2.5 Statistical analyses

Generalised linear mixed effect models (GLMMs) were used to analyse both the GPS foraging trip data and the links between prey density and oystercatcher foraging locations. This method not only allows for non-normally distributed data, but also for individual variation, as it allows individuals to be included in models as random effects (Bolker et al. 2009). GLMM models were carried out using the lme4 package in R (Bates et al. 2015). Due to a high proportion of zero values when comparing bivalve biomass density between foraging and control sites, a hurdle model was used in combination with a GLMM. This combines two models, one that estimates the occurrence probability, and another that estimates the number of individuals given that the species is present (Oppel et al. 2012). All statistical analyses were carried out in the program R (version 3.3.3), and the models used are provided in the appendix.

3. Results

3.1 Foraging Behaviour

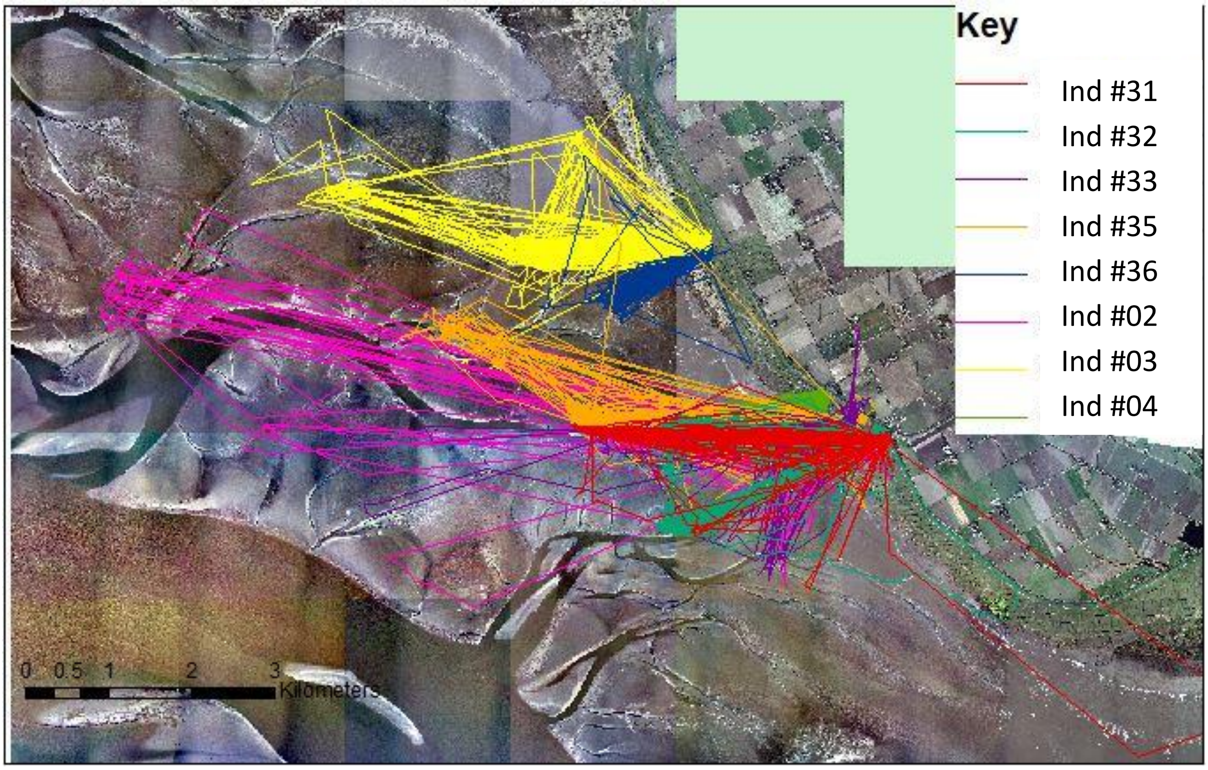

Figure 4. Foraging trips of 8 oystercatchers during the spring/summer incubation period. Individuals 31-36 were tracked in 2016 and individuals 02-04 were tracked in 2017.

A total of 691 foraging trips were recorded from 8 birds during the spring/ summer incubation periods of 2016 and 2017. All birds were caught whilst incubating eggs on the saltmarshes of Kaiser-Wilhelm-Koog, with two individuals (#03 & #36) caught ~2km further to the north. All individuals visited the adjacent mudflats during the study period, with some degree of overlap between the areas visited by the individual birds (Figure 4). A large variation was recorded in both trip distance from the nest, and the duration of each trip. The longest trip distance from the nest was 9.14km, the shortest 0.07km. The mean overall trip distance was 2.17km (SD ± 1.57km). The longest trip duration was 1180 minutes, the shortest <10 minutes. Since the logging interval of the GPS devices was 10 minutes, foraging trips of a shorter length may not have been detected. The mean overall trip duration was 137.18 minutes (SD ± 141.83 mins) (Table *1*).

Table 1.

The number of foraging trips logged for each individual oystercatcher.

		Distance			Duration		
Ind. #	***n* trips**	**Mean**	**Min**	**Max**	**Mean**	**Min**	**Max**
02	111	2.81 (SD ± 2.73)	0.07	9.14	108.73 (SD ± 98.82)	10	470
03	147	2.10 (SD ± 1.01)	0.31	5.53	144.15 (SD ± 161.23)	10	590
04	54	1.66 (SD ± 0.44)	0.57	2.15	117.59 (SD ± 91.4)	10	440
31	46	3.20 (SD ± 0.90)	0.69	5.49	238.26 (SD ± 136.5)	10	580
32	71	2.39 (SD ± 0.67)	0.41	2.91	214.65 (SD ± 187.26)	20	1180
33	135	1.12 (SD ± 0.79)	0.08	5.95	63.04 (SD ± 78.07)	10	470
35	69	3.60 (SD ± 1.22)	0.33	5.66	219.12 (SD ± 135.98)	10	680
36	58	1.21 (SD ± 0.25)	0.29	2.11	92.24 (SD ± 123.13)	10	640

There was also a high level of variation between individual birds in the patterns of foraging behaviour they exhibited. For example, individual #02 repeatedly visited a foraging site that was 8.8km from the nest, as well as occasionally foraging closer to the nest. In contrast, individual #32 foraged at sites within only 3km of the nest throughout the entire incubating period. Seven out of eight individuals showed a preference for foraging in the day rather than at night, with the vast majority of foraging trips carried out during daylight hours in all individuals except individual #31 (Table 2).
Despite this higher frequency of daytime foraging trips, trip duration was significantly longer during the night, with a mean trip duration of 273.88 minutes (SD ± 128.07 mins), as opposed to 89.4 minutes (SD ± 112.24 mins), during the day. There was no significant difference in maximum distance travelled away from the nest between day and night periods (Figure 5).

As expected, very few foraging trips were carried out during high tide periods. The majority (65%) of trips were carried out during the mid-tide period, followed by 28.94% of foraging trips at low tide and only 2.75% of trips during high tide. The tidal stage did not have a significant effect on the maximum distance from the nest travelled during the trip, however tidal stage does explain the differences in trip duration (Figure 6). Trip duration is significantly longer in low and mid-tide than during the high tide. The mean duration for trips during high tide was 47.40 minutes (SD ± 65.31 mins), contrasted with 82.35 minutes (SD ± 76.63 mins) during low tide and an even greater mean of 156.58 minutes (SD ± 145.83 mins) during mid tide periods.

Table 2.

The distance travelled from the nest and duration (minutes) of foraging trips for each individual oystercatcher

Ind. #	**Total minutes logged**	**Number of foraging trips**					
		Day	**Night**	**High tide**	**Low tide**	**Mid tide**	**Total**
02	12069	98	13	2	34	73	111
03	21190	113	34	4	42	91	147
04	6350	46	8	0	25	28	54
31	10960	22	24	2	7	35	46
32	15240	38	33	2	17	48	71
33	8510	104	30	7	41	86	135
35	15119	42	27	1	9	58	69
36	5350	48	9	1	25	32	58
		511	**178**	**19**	**200**	**451**	**691**

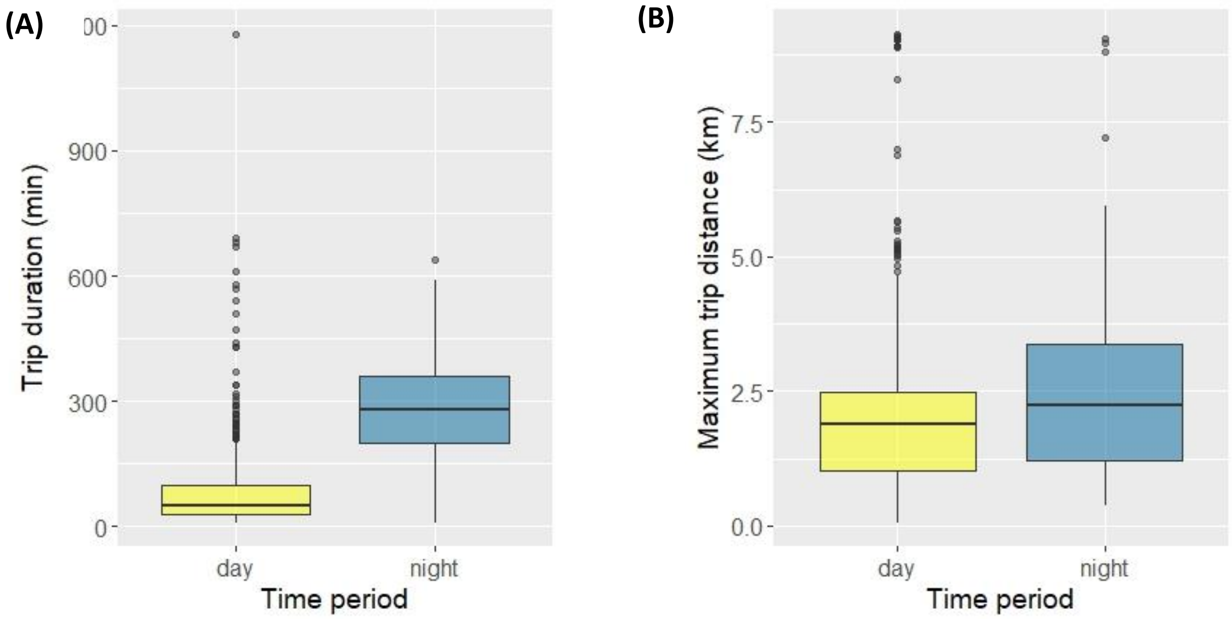

Figure 5. (A) Trip duration over day/night periods. GLMM significantly improved by adding time class (ANOVA: $\chi2$ =284.6, P<0.001). (B) Time class of trip had no significant effect on the maximum distance of the trip.

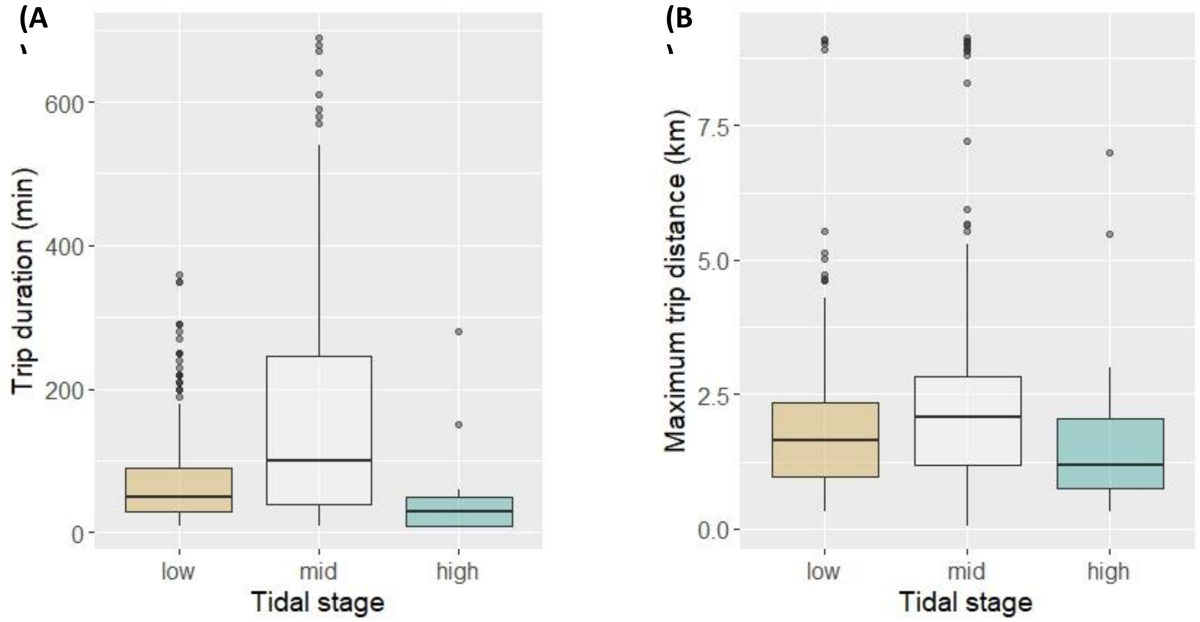

Figure 6. (A) Variation in trip duration over tidal stages. GLMM significantly improved by adding tidal stage as an explanatory variable (ANOVA: χ2 = 41.949, P<0.001). (B) The effect of tidal stage on maximum trip distance. Tidal stage had no significant effect on trip distance.

Foraging site fidelity varied between individuals, however all individuals seemed to have a high return rate to specific foraging sites, with all birds having a less than 0.05 km^2 area of foraging habitat at the 95% encounter probability (Table 3, Figure 10). Some, such as individual #04, had a small overall range (at 25% encounter probability) as well has a high rate of return to foraging sites. However, at the other end of the spectrum, individual #02 had a large 25% range of 45.6 km^2, whilst retaining a relatively small area of foraging habitat at the 95% encounter probability.

Table 3.
The area of habitat used while foraging, expressed in probabilities calculated by kernel density home range analysis. Smaller values suggest a higher foraging site fidelity.

		Area of foraging habitat at given encounter probabilities (km^2)			
Ind. #	**no. of trips**	**25%**	**50%**	**75%**	**95%**
02	111	45.644	0.101	0.054	0.041
03	147	18.567	0.234	0.077	0.026
04	54	1.834	0.058	0.027	0.011
31	46	36.640	0.051	0.023	0.014
32	71	11.956	0.163	0.066	0.028
33	135	18.739	0.087	0.014	0.010
35	69	27.310	0.249	0.094	0.043
36	58	6.378	0.032	0.013	0.003

3.2 Benthic prey

The main prey species sampled at all sites were the polychaetes *Hediste diversicolor* and *Marenzelleria viridis*, as well as the bivalve *Limecola balthica* (Table 4). Other prey species were found in very small densities. In most sampling sites, *L. balthica* was the only species of bivalve found. The bivalves found tended to be on the small side, with 67.7% of *L. balthica* being smaller than 10mm (*L. balthica* grows up to 25mm (Budd and Rayment 2001)). The shrimp *Crangon crangon* was also found in many sites sampled, however this is not a typical prey species of the oystercatcher.

Table 4.

The count and AFDW (g) of benthos prey species found in foraging and control sites.

	Mean count per m²		**Mean AFDW per m²**	
	c	**f**	**c**	**f**
All	710.2 (SD ± 630.89)	736.78 (SD ± 454.32)	2.95 (SD ± 2.46)	3.74 (SD ± 1.81)
Bivalves	39.87 (SD ± 50.13)	54.63 (SD ± 47.94)	0.97 (SD ± 1.07)	1.31 (SD ± 1.13)
Limecola balthica	39.87 (SD ± 50.13)	53.15 (SD ± 49.17)	0.97 (SD ± 1.07)	1.3 (SD ± 1.14)
Mya arenaria	0 (SD ± 0)	1.48 (SD ± 6.77)	0 (SD ± 0)	0.01 (SD ± 0.05)
Polychaetes	670.33 (SD ± 625.96)	682.15 (SD ± 458.23)	1.98 (SD ± 2.15)	2.43 (SD ± 1.30)
Hediste diversicolor	448.86 (SD ± 403.64)	437.05 (SD ± 326.66)	1.46 (SD ± 1.28)	2.01 (SD ± 1.44)
Marenzelleria viridis	197.85 (SD ± 509.25)	228.86 (SD ± 375.48)	0.48 (SD ± 1.46)	0.4 (SD ± 0.58)
Nereis sp.	5.91 (SD ± 12.48)	1.48 (SD ± 6.77)	0.01 (SD ± 0.01)	0 (SD ± 0.01)
Phyllodoce mucosa	1.48 (SD ± 6.77)	2.95 (SD ± 13.53)	0 (SD ± 0)	0 (SD ± 0.01)
Nereis virens	2.95 (SD ± 9.33)	0 (SD ± 0)	0.01 (SD ± 0.04)	0 (SD ± 0)
Arenicola marina	0 (SD ± 0)	2.95 (SD ± 9.33)	0 (SD ± 0)	0.01 (SD ± 0.02)
Nephtys hombergii	1.48 (SD ± 6.77)	0 (SD ± 0)	0.01 (SD ± 0.04)	0 (SD ± 0)
Crangon crangon	11.81 (SD ± 20.74)	8.86 (SD ± 17.38)	0.01 (SD ± 0.03)	0 (SD ± 0.01)

In the case of all benthos species present, there was no significant difference in prey count or AFDW between foraging and control sites sampled (Figure 4). There was also no significant difference found between foraging and control sites sampled when only bivalves (Figure 8) or only polychaetes (Figure 9) were considered. Notably, there is very little spread of biomass found between sites, with AFDW varying by a standard deviation of only 2.17g/m^2. Overall, the prey density sampled at both control and foraging sites was strikingly low, with an average biomass of only 3.34g/m^2.

The species composition of benthic organisms was fairly similar across the study site (Figure 11). In almost all sites, the most common species found was *Hediste diversicolor*, followed by *Limecola balthica*. In some areas the invasive polychaete *Marenzelleria viridis* was also a dominant species, however it appeared to be more localised than either *H. diversicolor* or *L. balthica*. Together with *Crangon crangon*, these three most commonly found species were the only species with a higher abundance than three individuals across the whole study site.

Figure 10 shows the foraging home ranges of the oystercatchers during the incubating period of 2016, together with the quantity of benthic prey organisms found across the study site. When combined with the count of prey individuals, there is little correlation between high prey densities and sites frequently visited by the birds. In the case of one individual (#32), its home range corresponded to areas of high prey density. However, the remaining birds showed no correlation with the foraging sites visited most and higher densities of benthic prey (either count of individuals or biomass). The area of mudflat closest to the nest sites of the birds (the southeast of the study site) had low prey densities, compared to areas sampled further away from the nest sites. Areas bordering tidal creeks appear to be visited most frequently by the foraging oystercatchers.

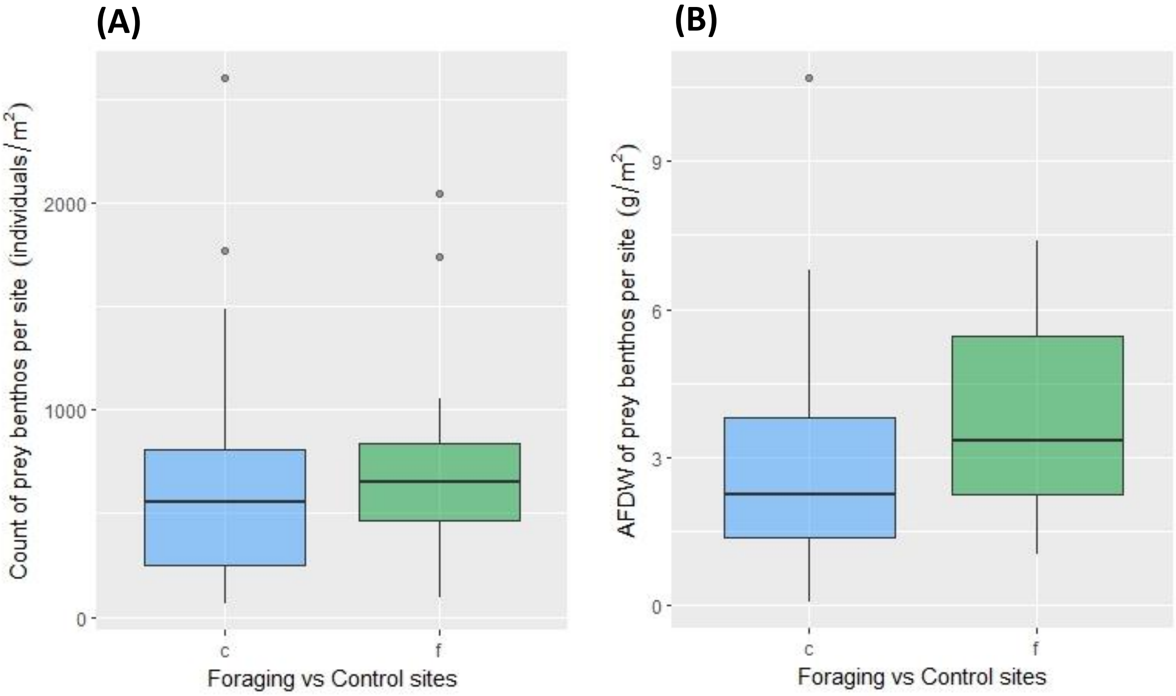

Figure 7. The abundance of all benthic prey organisms found at foraging and control sites. Abundance was measured in (A) count, and (B) biomass (AFDW g/m2).

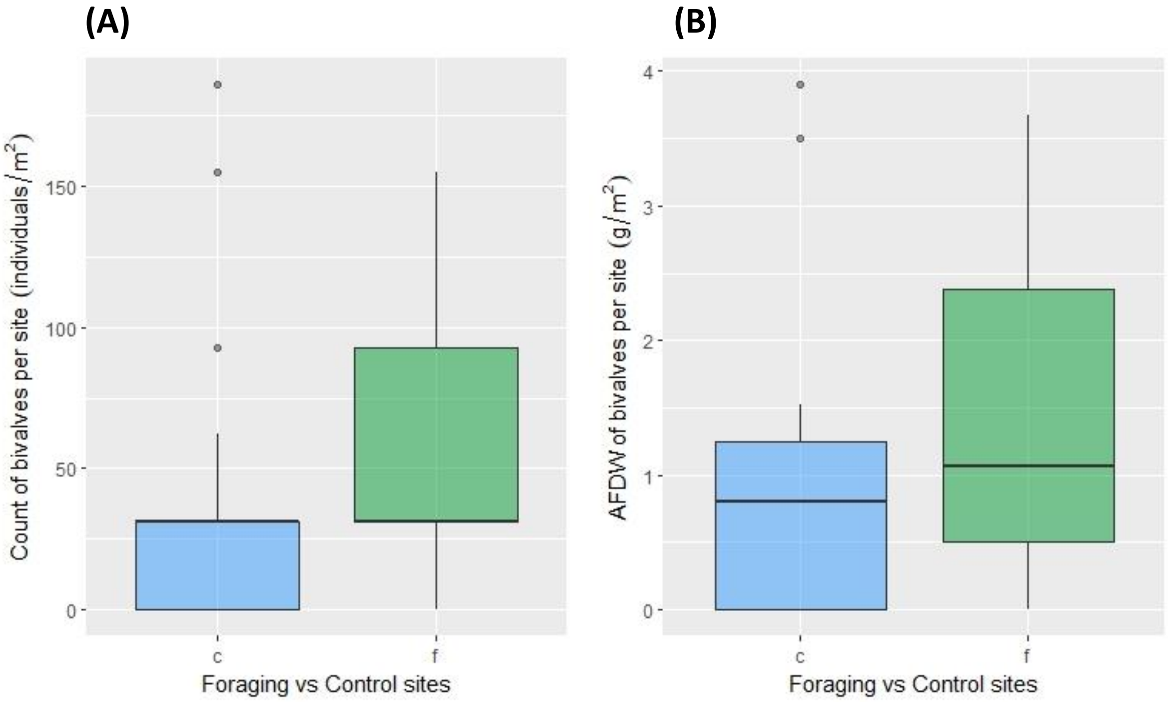

Figure 8. The abundance of all bivalve prey organisms found at foraging and control sites. Abundance was measured in (A) count, and (B) biomass (AFDW g/m^2).

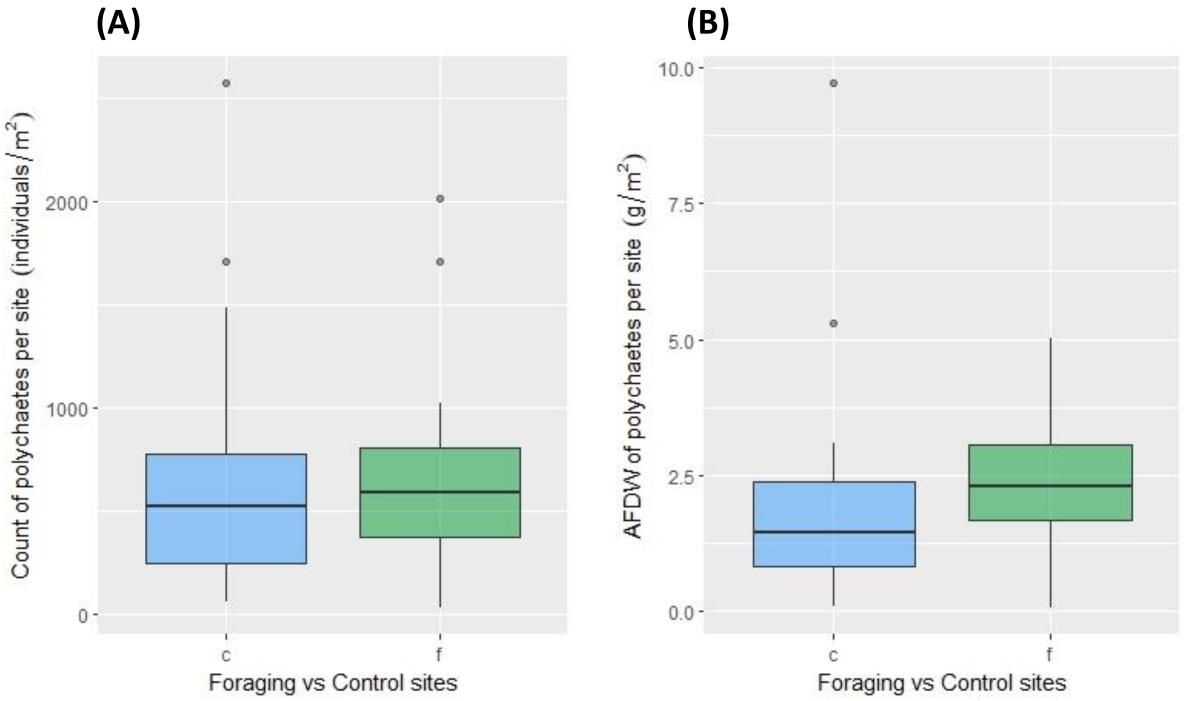

Figure 9. The abundance of all polychaete prey organisms found at foraging and control sites. Abundance was measured in (A) count, and (B) biomass (AFDW g/m2).

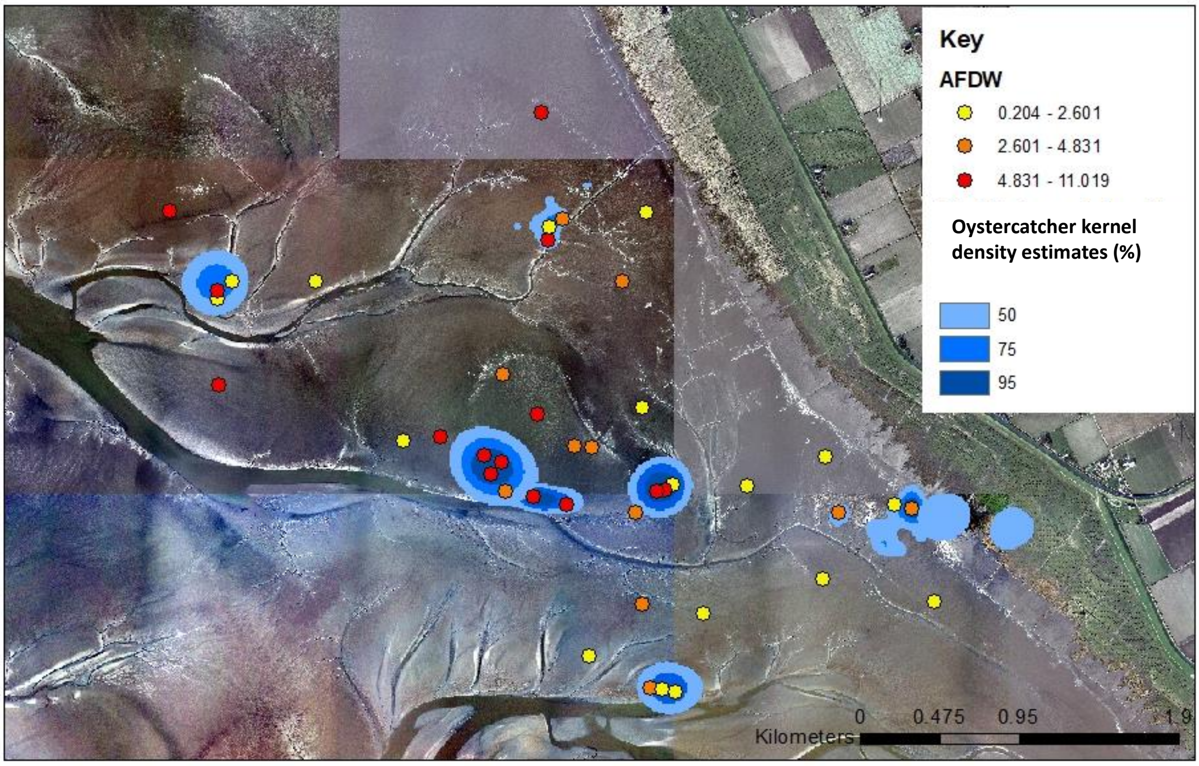

Figure 10. The Kernel density estimates of oystercatchers overlayed with the abundance of benthic prey sampled. Prey abundance is measured in Ash free dry weight (AFDW) per square meter.

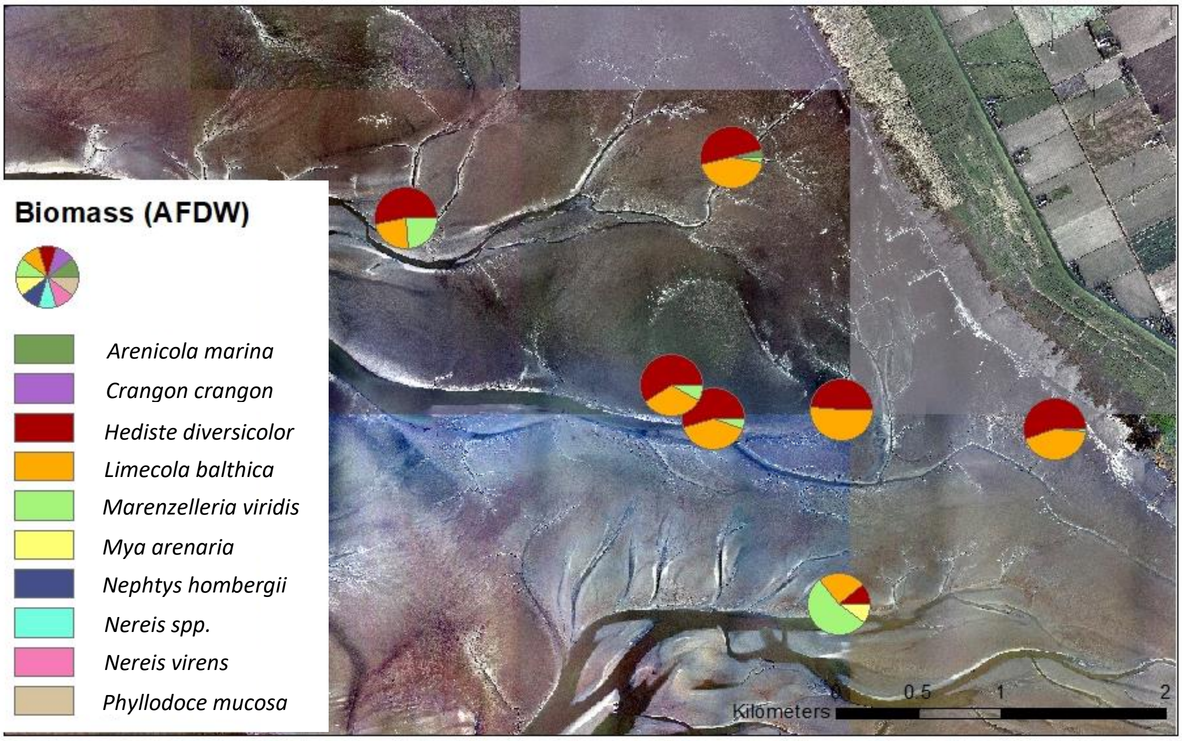

Figure 11. Species composition of benthic prey organisms sampled. The map shows species composition measured by biomass, suing Ash free dry weight (AFDW) per m^2. Each pie chart represents the mean prey biomass per species found at a particular foraging site and its corresponding control sites.

3.2 Hatching success

The area of salt marsh bordering the mudflats at Kaiser-Wilhelm-Koog were surveyed for oystercatcher nests from mid-May till the end of July 2017. The first eggs were discovered later than expected, on 6th June. Overall only 13 nests with eggs were found (Figure 12), with between 1 and 3 eggs in each nest. This came to a total of 31 eggs. Clutch loss was high, caused by flooding of the saltmarsh and by predation. In most cases it was not possible to tell the cause of egg loss, however predators such as crows (*Corvus corone*), the common gull (*Larus canus*) and the red fox (*Vulpes vulpes*) were observed in the area. Given that the breeding area was only visited once a week and the rate of egg loss was high, it was often not possible to tell if the eggs seen were the first brood, or subsequent breeding attempts after egg loss. Therefore, the number of clutches counted is likely to be an underestimate, and this is also a possible cause of the late laying date observed. Only 3 chicks were observed, belonging to two different families. It was not possible to identify which nests the chicks were from as by this time they had already left the nest. It is not known if any of these chicks survived to adulthood, however at least one reached four weeks old. This gives a hatching success of 9.7% of all eggs observed, but the true hatching success of all clutches in the area must be presumed to be significantly lower than this, since the frequency of clutch loss was higher than the frequency of surveys taken.

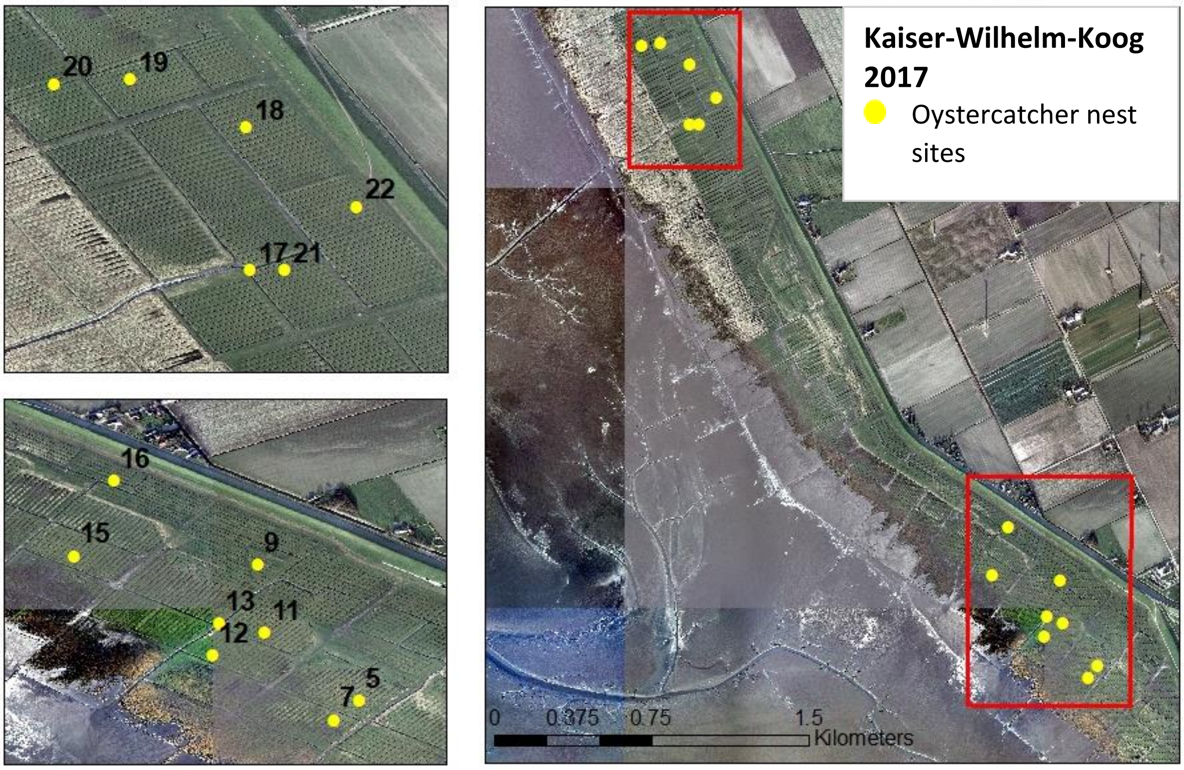

Figure 12. Locations of oystercatcher nest sites in the study area of Kaiser-Wilhelm-Koog.

4. Discussion

4.1 Foraging behaviour

In this study it was found that oystercatcher foraging behaviour is influenced by both tidal and day-night cycles.

4.1.1 Tidal

As expected, foraging trips were of longer duration during mid and low tide periods, when the mudflats are exposed, and thus benthic prey organisms are most accessible. This confirms the results of previous studies (Schwemmer and Garthe 2010; Zwarts, Ens, et al. 1996). There was, however, no difference found in the distance travelled by oystercatchers to foraging sites during different tidal stages. This is in direct contrast with the findings of Philipp Schwemmer *et al*. in a previous study carried out on oystercatchers breeding on the island of Oland (further north in the Wadden Sea), where the birds foraged at sites further away from their nests during low tide than in mid tide periods (Schwemmer and Garthe 2010). This may be explained by the fact that intertidal flats bordering Kaiser-Wilhelm-Koog are fairly high compared to those surrounding Oland, therefore the mudflats at Kaiser—Wilhelm-Koog remain uncovered by the tides for a longer period than those at Oland ("Navionics Chart Viewer" 2018). This may allow oystercatchers at Kaiser-Wilhelm-Koog to use the same areas of mudflat to forage on for the majority of the tidal cycle.

4.1.2 Site fidelity

This difference foraging trip distance seems to be linked to contrasting site fidelity between the two breeding areas. All birds breeding in Kaiser-Wilhelm-Koog showed a moderate to high foraging site fidelity, with each bird returning to specific foraging sites, and thus supporting the idea that oystercatchers have foraging territories during the breeding season (Bruno J Ens et al. 1992). In contrast, birds breeding in Oland showed lower site fidelity despite the fact that data was collected over a shorter period of time. Despite these differences, birds in both this study and earlier studies (Goss-custard et al. 1991; Schwemmer and Garthe 2010) showed a marked preference for foraging on the borders of tidal creeks.

4.1.3 Day-night

More surprisingly, foraging trips were of longer duration at night than during the day, despite the fact that there was no difference in distance of the foraging sites from the nests. Therefore, the hypothesis that oystercatchers would respond to high levels of predation by nocturnal mammals by maximising their time near the nest at night must be rejected. It has been found in previous studies that night feeding plays an important role in fulfilling the energy needs of oystercatchers (Sitters 2000), as it is not possible for oystercatchers to gain enough energy during a single low tide period (Zwarts, Ens, et al. 1996). In addition, according to Sitters 2000, tactile feeding is less time efficient than foraging by sight, and so more time may need to be invested to reap the same rewards as during the day. Sitters also observed that oystercatchers foraged on the same mussel beds during the day as at night. Indeed, when birds were found to have a lower site fidelity (Schwemmer and Garthe 2010), not only were trips of longer duration during the night, but oystercatchers visited sites that were further away from their nests at night. This was hypothesised to be a behavioural adaptation to high levels of clutch predation during the day by avian predators such as gulls.

In this, and previous studies (Schwemmer and Garthe 2010), there were a higher number of foraging trips during the day. This may also be caused by a higher efficiency of foraging during the day, leading to more frequent, shorter foraging trips than at night.

4.2 Benthos

4.2.1 Prey density targeting

Contrary to the findings of several previous studies (Schwemmer 2015, Goss-custard 1991, Goss-custard 1977, Hulscher 1976), in this study oystercatchers did not appear to target areas of high prey density when foraging. This may be because no areas of particularly high prey density were found, with the maximum biomass being 9.72gm^{-2}. Previous studies were carried out in regions with a higher overall prey density, and oystercatchers where only found to target areas with a prey density higher that 80 gm^{-2} (Schwemmer 2011). Therefore, perhaps in Kaiser-Wilhelm-Koog the variation in prey density was not large enough that any areas were worth targeting. This low prey density does not appear to affect the fitness of the oystercatchers breeding in Kaiser-Wilhelm-Koog, as all oystercatchers caught to attach GPS loggers were weighed and found to be within a normal weight range (Hockey, Kirwan, and Boesman 2018). However, many birds face problems of low food availability during the chick rearing period and not during the incubation period (Koffijberg et al. 2016) and as we caught birds during the incubation period we do not know their body condition during chick rearing.

4.2.2 Low prey density

In this study a low prey density of benthic prey organisms was found in the tidal mud flats of Kaiser-Wilhelm-Koog, both in terms of biomass and count of individuals. Compared to other regions of the Wadden sea, the difference in density of benthic biomass is dramatic: the average biomass of macrozoobenthos across the Wadden sea has varied from 40 to 60 gm^{-2} since 1989 (Drent et al. 2017), compared to the average biomass of 3.34 gm^{-2} found in Kaiser-Wilhelm-Koog. There was also a notable absence of certain species, particularly commonly occurring bivalves such as *Cerastoderma edule* and *Mya arenaria*, both of which are prey species of the Eurasian oystercatcher (Zwarts and Wanink 1984). Although there have been a few previous studies sampling in nearby areas that have found similar results (Leyrer 2011; Wetzel et al. 2012), there have been few attempts to discuss or discover possible reasons for this low diversity, low density community. The most apparent contributing factor to this difference in density compared to other areas of the Wadden Sea is the fact that Kaiser-Wilhelm-Koog is situated on the mouth of the river Elbe estuary. This results in changes to a variety of physical conditions such as salinity and pollution levels.

Salinity. Salinity at sites close to the mouth of the Elbe estuary (including Kaiser-Wilhelm-Koog) can fluctuate dramatically from 1.2-22PSU, depending on the time of year, tidal stage and river run-off (Carstens et al. 2004). This creates a challenging environment for biota, and few benthic species can cope with fluctuations through such a wide range of salinities. A previous study on a different Wadden Sea estuary (the river Ems) found that a lower salinity correlates to a decrease in growth rates of the bivalves *Cerastoderma edule* and *Mytilus edulis*, whereas the species *Limecola balthica* was much less affected (Essink and Bos 1985). Indeed, it has been discovered that *L. balthica* has an exceptional ability to tolerate low salinities, with its growth rate remaining unaffected when transplanted to salinities as low as 3 PSU (Jansena et al. 2009). This may explain the low diversity of bivalves present, however it does not fully explain the low density of *L. balthica* found. It has been shown in estuarine environments that there is a decrease in species richness, diversity and total benthic biomass as salinity decreases (Ysebaert et al. 1993; Ysebaert and Herman 2002; Ysebaert et al. 1998), and this may be one contributing factor to the low benthic biomass found at Kaiser-Wilhelm-Koog. However, this does not explain the absence of certain species such as *C. edule* which are found in similar sites on other European estuaries such as the Ems and Schelde Estuary (Ysebaert et al. 1993; Ysebaert and Herman 2002). In addition, Kaiser-Wilhelm-Koog is situated relatively near to the mouth of the Elbe estuary, and similar sites on other estuaries usually show much higher levels of benthic biomass.

***Pollution*.** Wetzel *et al*. (2013) reveal that benthic organisms in the Elbe estuary are much more affected by pollution than previously thought. Furthermore, benthic biomass has been found to correlate with water quality in similar estuaries (Ysebaert et al. 1993). Although sites further upstream are impacted the most, chronic effects are expected for benthic communities throughout the whole estuary, caused by sediment pollution. Sediment-bound pollutants are often persistent and so can accumulate in sediments and organisms over a time-frame of years. In fact, a previous study on the presence of contaminants in oystercatcher tissues in the Wadden Sea found that although overall levels of contaminants have declined in recent years, they still remain at significant levels in oystercatcher tissues (Schwemmer et al. 2014). In addition, higher levels were found in birds resident at Kaiser-Wilhelm-Koog, compared to birds resident on Hallig Oland, an area 90km away from the Elbe Estuary. This supports the idea that benthic prey organisms are also subjected to pollutants. In a recent study of pesticides and biocides the sediments of major European river mouths, the highest number of pollutants were detected at Cuxhaven, opposite to Kaiser-Wilhelm-Koog on the Elbe estuary (Massei et al. 2018). Concentrations of pollutants were measured using Toxic Units (TU), with TUs higher than 0.001 associated with a decline of the invertebrate community structure, and Tus higher than 0.1 thought to pose acute risks to invertebrates. At Cuxhaven the photosynthesis inhibitor Acetochlor was found to be a major pollutant, with a TU of 3.3. Significant levels of fungicides (TU=0.3) were also found accumulated in the sediments at Cuxhaven. These are known to be highly toxic to zooplankton, inhibiting processes such as protein synthesis, endocrine signalling and disturbing development and growth. Thus, negative impacts to phytoplankton at the bottom of the food chain are likely to influence to growth and community structures to the whole benthic community.

4.2.3 Prey composition

Given that the majority of prey species available were polychaetes and the biomass of bivalves was so low, it is likely that all birds were worm specialists. In addition, the majority of bivalves present (almost all *Limecola balthica*) were smaller than 10mm, whereas oystercatchers are known to feed only on individuals with a length greater than 10mm ((Hulscher 1981; Zwarts, Cayford, et al. 1996). However this lack of bivalves may not be a problem, given that it has been discovered that oystercatchers in some areas of the Wadden Sea tend to switch from feeding on *L. balthica* during May, to feeding mainly on polychaetes such as Hediste *diversicolor* during the incubation and chick rearing periods of June-July (Wanink and Zwarts 1993). This is thought to be due to the combined effects of *L. balthica* burying deeper during the summer, and Hediste feeding closer to the surface.

***Marenzelleria*.** In addition to *Nereis*, another common species of polychaete present was *Marenzelleria viridis. Marenzelleria* in a non-native species that originates from the Atlantic coast of North America, and was first observed on the European North Sea coastline in the early 1970s (Elliott and Kingston 1987; Blank et al. 2004). *Marenzelleria* was the third most common species found in Kaiser-Wilhelm-Koog, although it is less common in other parts of the Wadden Sea (Leyrer 2011). This may be linked to the observations of Wimm Wolf, that invasive species tend to be more common in brackish waters (Wolff 1998). He proposes three likely hypotheses to support these findings: firstly, that ports are often situated in brackish waters (i.e. estuaries), and therefore brackish-water species are more likely to be picked up or released in ballast water. Secondly, brackish-water species have a better chance of surviving transport in ballast water tank conditions. Thirdly, brackish waters tend to have fewer species present and so this may leave more openings for an invasive species to establish itself. Given that such a low abundance of benthic organisms was found at Kaiser-Wilhelm-Koog, it is likely that the third hypothesis is particularly relevant in this case. The *Marenzelleria* individuals found during this study were of similar length and biomass to *Hediste diversicolor* individuals found, which is a common prey species of *H. ostralegus* (Goss-custard 1996). This indicates that the oystercatchers at Kaiser-Wilhelm-Koog may also take advantage of *Marenzelleria* as a prey item.

4.3 Hatching success

In the breeding season of 2017 a very low hatching success was observed, with only two breeding pairs successfully hatching chicks in Kaiser-Wilhelm-Koog. This was compounded by the fact that there were very few nests observed in the area, compared to other mainland breeding sites of a similar size (Hofeditz and Hoppe 2016). In Kaiser-Wilhelm-Koog (a study site of 1.6 km^2) only 31 nests were observed in the course of the breeding season, compared to 60 nests in Hedwigenkoog, (a site of 1.92 km^2) approximately 40km northwards. This, together with the late laying date that was also apparent throughout the breeding site is likely to be an indicator of high predation pressure on oystercatcher eggs. In the majority of cases, failed nests were found empty, with no fragments of eggshell. This points towards predation being the cause of egg loss (Bregnballe et al. 2015). In addition to high levels of predation, several flooding events were observed during extreme high tides. These destroyed multiple nests and the eggs were washed away. These storm floods have been speculated to form an "evolutionary trap". In the "leapfrog – resident" concept developed by Ens *et al*. (Bruno J Ens et al. 1992) and later corroborated by Schwemmer *et al.* (Schwemmer, Weiel, and Garthe 2017), birds nesting on territories bordering the mudflats ("residents") have an advantage over those nesting further away ("leapfrogs"). However, an increase in storm floods over recent years may mean that birds nesting in resident territories that were historically most desirable may now be at a disadvantage due clutch loss from flooding (Van De Pol et al. 2010). Given that the Eurasian Oystercatcher is a long-lived bird that can reach 40 years old or more, such a low breeding success can have a delayed impact on the population levels and so the true impact may not be apparent until the consequences are too severe to reverse by conservation efforts. Flooding may have a higher impact on breeding success on mainland sites in comparison to island breeding territories in the German Wadden Sea, as islands such as Oland tend to be protected from flooding by breakwaters or even small dikes ("Sommerdeiche").

In this study, all birds that were tracked with GPS loggers lost their clutch during the incubation period. Although this is to be expected in an area with such a high rate of breeding failure, it must also be considered that birds who have lost their eggs and are therefore no longer incubating may show a different pattern of foraging behaviour to those that are still incubating eggs. In contrast to previous studies of the foraging patterns of incubating oystercatchers, for example on the island of Oland (Schwemmer and Garthe 2010), the individuals studied at Kaiser-Wilhelm-Koog no longer needed to invest time into defending a clutch or breeding territory. Therefore, this is likely to contribute to the differences in foraging behaviour observed between the two studies.

4.4 Study limitations and future studies

Given the confounding factors of low prey availability, nest sites vulnerable to increasingly frequent storm-floods and high levels of predation, it is difficult to pin any causation on the foraging behaviours found in this study. Therefore, for any conclusions to be drawn on the influence of increased nocturnal nest predation on the foraging behaviours of the Eurasian oystercatcher, it would be necessary to carry out a similar study in an area where prey is more abundant and nest sites are less prone to destruction by flooding. This would enable the impact of nocturnal predation by mammals to be seen more clearly.

In this study it was only possible to visit the breeding site once a week due to logistical reasons. To gain a true understanding of the causes of breeding failure, future studies should be set up so that daily visits are possible, and ideally cameras should be used to record any predation events. This is especially important in order to observe any nocturnal predation of eggs, as although in this study I aimed to examine nest remains, there was insufficient evidence to identify the cause of egg loss, let alone the type of predator.

It would also be advantageous in future studies to collect benthos data in the same year as the GPS foraging data is collected, as there is some evidence that although species composition remains the same, there is variation of prey density from year to year (Leyrer 2011). This is particularly dependent on the harshness of the previous winter and the level of larval recruitment that year (Strasser, Reinwald, and Reise 2001). Therefore, in order to get a better understanding of oystercatcher foraging behaviour in response to particular prey densities it would be advantageous to collect benthos prey samples in the same season and year as the foraging data of interest. Interannual variability in benthic prey density as discussed above may also go a small part of the way to explaining the low prey abundance found in this study, given that the prey base was only sampled once.

5. Conclusion

In conclusion, the oystercatchers in this study were found to be breeding in an extremely challenging environment which led to some unexpected differences in oystercatcher foraging behaviour from birds previously studied in different locations. Not only was the density of prey organisms low, but there was also a high rate of clutch loss due to flooding of the salt marshes and predation by both mammalian and avian predators. Surprisingly, the oystercatchers studied did not target areas of high prey density when foraging, as previously thought to be the rule. This may be explained by the uniformly low density of prey available, caused by conditions found on the Elbe estuary. Despite this, all individuals showed a moderate to high site fidelity when foraging, and foraging trip distance did not vary between the tidal periods or from day to night periods. This contradicts the findings of studies on island breeding birds. Predictably, foraging trips were of longer duration during the low and mid-tide periods compared to high tide periods. However, contrary to the hypothesis that oystercatchers may spend more time on their nests at night when their clutches are threatened by nocturnal predators, it was found that the duration of foraging trips was longer at night than during the day. In comparison to previously studied breeding sites located on islands, this mainland breeding site is of particularly low quality, leading to notable differences in the foraging behaviour of the Eurasian oystercatcher.

6. Acknowledgements

First of all, I would like to thank Prof. Dr. Stefan Garthe for giving me the opportunity to do my master’s thesis in his group and for being a committed and helpful supervisor. I would also like to thank Dr Philipp Schwemmer for helping me with every stage of this project, from planning the project, to carrying out fieldwork, to the final stages of writing up. Thank you for your support, advice and patience. Next, I would like to thank Leonie Enners for her help with my benthos sampling, and always being happy to answer my questions. For their invaluable help with my fieldwork I would like to thank Daniela Koch, Leonie Enners, Tabea, Kai Borkenhagen, Stefan Weiel and Philipp Schwemmer. Many thanks to Dr. Ulrike Schückel for her guidance in polychaete identification. Lastly, I would like to thank everyone at the FTZ for their friendly support and advice.

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8. Appendix

Statistical models used:

Foraging

1. Trip duration and day/night

```
Models:
fit2.lmr: sqrt(Trip_length) ~ 1 + (1 | Individual)
fit1.lmr: sqrt(Trip_length) ~ Time_class + (1 | Individual)
         Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
fit2.lmr  3 4194.8 4208.4 -2094.4   4188.8
fit1.lmr  4 3912.2 3930.4 -1952.1   3904.2 284.57      1  < 2.2e-16 ***
```

2. Maximum trip distance & day/night

```
Models:
fit2.lmr: log(Trip_dist) ~ 1 + (1 | Individual)
fit1.lmr: log(Trip_dist) ~ Time_class + (1 | Individual)
         Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
fit2.lmr  3 1240.8 1254.4 -617.39   1234.8
fit1.lmr  4 1242.7 1260.9 -617.36   1234.7 0.0578      1     0.8101
```

3. Trip duration & tidal stage

```
Models:
fit2.lmr: sqrt(Trip_length) ~ 1 + (1 | Individual)
fit1.lmr: sqrt(Trip_length) ~ Tide_class + (1 | Individual)
         Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
fit2.lmr  3 4035.8 4049.3 -2014.9   4029.8
fit1.lmr  5 3997.9 4020.4 -1993.9   3987.9 41.949      2  7.777e-10 ***
```

4. Maximum trip distance & tidal stage

```
fit2.lmr: log(Trip_dist) ~ 1 + (1 | Individual)
fit1.lmr: log(Trip_dist) ~ Tide_class + (1 | Individual)
         Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
fit2.lmr  3 1209.3 1222.8 -601.65   1203.3
fit1.lmr  5 1211.2 1233.7 -600.59   1201.2 2.1218      2     0.3462
```

Benthos

1. All benthos foraging (f) and control (c) AFDW. Slightly right skewed, so square root transformed.

```
Models:
fit2.benthos_sqrt: sqrt(AFDW) ~ 1 + (1 | bird_ID)
fit1.benthos_sqrt: sqrt(AFDW) ~ f_c + (1 | bird_ID)
                  Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Ch
isq)
fit2.benthos_sqrt  3 80.961 86.174 -37.480   74.961
fit1.benthos_sqrt  4 80.114 87.065 -36.057   72.114 2.8467    1  0.09156
```

2. All benthos foraging (f) and control (c) count. Right skewed so log transformed.

```
Models:
fit2.benthos_log: log(count) ~ 1 + (1 | bird_ID)
fit1.benthos_log: log(count) ~ f_c + (1 | bird_ID)
                 Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chis
q)
fit2.benthos_log  3 108.04 113.26 -51.022   102.04
```

```
fit1.benthos_log  4 108.96 115.91 -50.481   100.96 1.0816      1     0.29
83
```

3. Polychaetes foraging (f) and control (c) AFDW. Right skewed so square root transformed

```
Models:
fit2.polychaetes_sqrt: sqrt(AFDW) ~ 1 + (1 | bird_ID)
fit1.polychaetes_sqrt: sqrt(AFDW) ~ f_c + (1 | bird_ID)
                      Df    AIC    BIC logLik deviance  Chisq Chi Df Pr(>
Chisq)
fit2.polychaetes_sqrt  3 76.381 81.594 -35.19   70.381
fit1.polychaetes_sqrt  4 76.521 83.472 -34.26   68.521 1.8598      1
0.1726
```

4. Polychaetes foraging (f) and control (c) count. A little right skewed so square root transformed

```
Models:
fit2.polychaetes_sqrt: sqrt(count + 1) ~ 1 + (1 | bird_ID)
fit1.polychaetes_sqrt: sqrt(count + 1) ~ f_c + (1 | bird_ID)
                      Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(
>Chisq)
fit2.polychaetes_sqrt  3 315.27 320.49 -154.64   309.27
fit1.polychaetes_sqrt  4 317.08 324.03 -154.54   309.08 0.1928      1
0.6606
```

5. Bivalves foraging (f) and control (c) AFDW: Large number of zero values therefore used a hurdle model.
    i. Binomial presence/absence data

```
Models:
b2: binom ~ 1 + (1 | bird_ID)
b1: binom ~ f_c + (1 | bird_ID)
   Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
b2  2 49.986 53.462 -22.993   45.986
b1  3 50.614 55.827 -22.307   44.614 1.3723      1     0.2414
```

   ii. All data >0. Right skewed, used gamma distribution

```
Models:
m2: AFDW ~ 1 + (1 | bird_ID)
m1: AFDW ~ f_c + (1 | bird_ID)
   Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
m2  3 83.967 88.269 -38.984   77.967
m1  4 85.733 91.469 -38.866   77.733 0.2345      1     0.6282
```

6. Bivalves foraging (f) and control (c) count. Data right skewed so used square root transformation.

```
Models:
fit2.bivalves_sqrt: sqrt(count) ~ 1 + (1 | bird_ID)
fit1.bivalves_sqrt: sqrt(count) ~ f_c + (1 | bird_ID)
                   Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Ch
isq)
fit2.bivalves_sqrt  3 240.42 245.63 -117.21   234.42
fit1.bivalves_sqrt  4 240.69 247.65 -116.35   232.69 1.7227      1  0.1893
```