UNIVERSITY OF LEEDS

The influence of vegetation on nest site selection and rest in breeding shorebirds. Evidence for management outside of the breeding season?

Joseph Griffin

Biodiversity and Conservation MSc

2023

Abstract

Populations of many shorebird species are declining worldwide, with migratory species most at risk. Reductions in breeding success can be attributed to disturbance, habitat loss and degradation, and increasingly, climate change. Vegetation and dune encroachment could prevent shorebirds from nesting or resting within an area. The management of dune vegetation can be controversial due to its own designations, therefore evidence for the success of management is important. A study of Little Terns (*Sternula albifrons*) and Ringed Plovers (*Charadrius hiaticula*) was conducted within a shorebird colony at Beacon Ponds, a saline lagoon on the Yorkshire coast. The boundary of the dominant vegetation, Marram Grass, and the location of the shorebirds' scrapes were mapped to determine the distance at which birds nest from areas of dense vegetation. Photographs were used to determine the presence of scrapes within Marram Grass and in proximity to microvegetation. The distance and orientation of the shorebirds at rest was observed to determine the influence of vigilance or of other factors (wind direction and thermoregulation). Little Terns preferred nesting and resting with distance between themselves and the Marram Grass. Ringed Plovers showed a preference for nesting within open spaces but no avoidance of Marram Grass when at rest. Wind was the primary influence for their orientation at rest. The removal of encroaching Marram Grass to improve existing breeding sites and create new habitat has the potential to increase breeding success of Little Terns and Ringed Plovers by reducing the risk of predation to eggs and young and allowing shorebirds to nest further from the high tide line, reducing nest loss to high tides, extreme weather, and sea-level rise. Creation of vegetation-free areas will improve roosting habitat for Little Terns, as they can rest further away from vegetation, allowing for faster responses to predators.

Contents Page

Introduction.......... 4

Methods.......... 9

Results.......... 15

Discussion.......... 26

Acknowledgements.......... 31

Bibliography.......... 32

Introduction

Shorebird Background

Globally, the populations of most shorebird species are declining (Koleček *et al*., 2021). Many species' declines are attributed to a range of factors including climate change, disturbance by people, human encroachment into their habitats and over-exploitation (Piersma and Lindström, 2004; Piersma *et al*., 2006; Piersma and Baker, 2000). Migratory shorebird species can be particularly threatened because they are subject to geographically distinct threats and have a greater reliance on suitable habitats at breeding, wintering, and stop-over sites (Cook *et al*., 2021; Koleček *et al*., 2021). The shorebird populations within the UK are no less at risk, with many species of seabirds and coastal waders showing dramatic population declines (JNCC, 2016; Humphreys *et al*., 2020). Two such species of declining shorebird are the Little Tern (*Sternula albifrons*) and Common Ringed Plover (*Charadrius hiaticula*) (hereafter Ringed Plover). In the UK, Little Terns have seen a population decline of 37% since the 1990s (Wilson *et al*., 2020) while Ringed Plovers have seen a 37% decline in the number of breeding pairs between 1984-2007 (Conway *et al*., 2019).

The Little Tern, a member of the Laridae family, is a piscivorous seabird and the smallest of the terns (Green, 2017). They breed across the UK's coasts (Wilson *et al*., 2020), with an estimated 1375 breeding pairs (Eaton *et al*., 2022), before migrating to West Africa for the winter (Cabot and Nisbet, 2013). They are Amber listed under the most recent review of the Birds of Conservation Concern (BoCC5) due to range contraction of over 25% between 1968-71 and 2007-11 and due to breeding localisation (with >50% of the UK population found at ≤ 10 sites during the breeding season) (Stanbury *et al*., 2021). The Little Tern is a Schedule 1 bird under the Wildlife and Countryside Act 1981, meaning it is a criminal offence to intentionally disturb or damage the adults, eggs or young (Tipling, 2011). The Ringed Plover, part of the Charadriidae family, is a small migratory coastal wader (Wiersma *et al*., 2020). The UK has an estimated breeding population of 5450 pairs (Woodward *et al*., 2020) with internationally important numbers during the breeding season (Eaton *et al*., 2009). In the UK the Ringed Plover is Red listed under BoCC5, with a decline of the breeding population of over 25% in the last 25 years (Stanbury *et al*., 2021).

The causes of decline are similar in both species and are centred around reductions in breeding success, of which many factors contribute (Wilson *et al*., 2020; Conway *et al*., 2019). Both species breed in areas of sand and shingle on the coastlines of the UK, with Little Terns in particular nesting very near to the high-tide mark (Tratalos *et al*., 2021; Pickerell, 2004.). The substrate around which they nest acts to camouflage the shorebirds, and as such they select for texture and colour (Fraser *et al*., 2019).

Much of their habitat has been lost because of land use change (Calladine *et al*., 2022), while it is also a popular place for human recreation (Tratalos *et al*., 2021). The shorebirds create scrapes (shallow hollows) in which they lay their eggs (O'Connell *et al*., 2014). The scrapes and the chicks are highly camouflaged and can be easily trampled by humans, while dogs can chase adults and chicks (Tratalos *et al*., 2021). Predation of eggs and young can cause colony failures (Pienkowski, 1984, Avery 1991), which are exacerbated further by human disturbance as chicks become more vulnerable when adults are chased away from them (Wilson *et al*., 2020). Climate change is expected to threaten these species further, as their breeding sites are extremely vulnerable to rises in sea-level and increased occurrence and severity of storms which can wash away a whole colony (Mitchell *et al*., 2020; Power *et al*., 2023).

Nest site selection and vegetation

The choice of where shorebirds nest can impact on their breeding success, even at very small scales. The shorebirds look for a site that promotes the incubation of eggs and brooding of young, reduces the chance of being identified by a predator, yet increases their own predator detection ability (Cunningham *et al*., 2016). The area must also have good foraging opportunities nearby. Ringed Plovers feed on invertebrates in the inter-tidal area with a 'stop-run-peck' method (Pienkowski, 1983). Little Terns are surface feeders of fish at sites close to their colonies with a maximum range of 11km (Power *et al*., 2023; Thaxter *et al*., 2012).

Vegetation can influence nest site selection of both species. Little Terns select colony sites with some sparse vegetation, and too little vegetation cover could result in them avoiding the area (Ratcliffe *et al*., 2008). Conversely, too much vegetation cover at a site can be detrimental to shorebirds. Growth of vegetation has led to the abandonment of some sites by both plovers and terns (Conway *et al*., 2019; Kotliar and Burger, 1984). Little Terns prefer sites with low vegetation cover and shorter plant heights, with an optimum cover of 10% with significant decreases in the number of nests above 42% cover (Jeong *et al*., 2011; Lopes *et al*., 2015). Similarly, Ringed Plovers favour sites with open space and low plant heights, with early succession of microvegetation (Foppen *et al*., 2006). This is likely because of increased chances of nest predation within vegetation, while open space can increase the time and effort spent by predators in detecting them (Medeiros *et al*., 2012; Fraser *et al*., 2019). In addition, some species of plover have been found to be less successful at detecting predators when incubating in a scrape artificially covered with vegetation than when in a scrape in the open (Amat and Masero, 2004). Embryo dune vegetation, such as Marram Grass (*Ammophila arenaria*) and Lyme Grass (*Leymus arenarius*) is known to influence nest site selection (Medeiros *et al*., 2012). Embryo dunes are the primary stage of the development of sand dunes and are formed by the deposition of sand within vegetation (Hesp, 2002).

Shorebirds at Rest

Little Terns and Ringed Plovers are active parents, including through brooding and feeding. Little Terns also mitigate predation risk by dreading (where they flush up into the air en masse and mob any predators present (Erwin, 1989). Ringed Plovers act to protect their young by chasing away anything getting too close to the scrape, or by feigning injury to lure away predators (Gupta *et al*., 2022). Additionally, the birds need energy reserves to migrate following the breeding season. With very high energy demands, Little Terns and Ringed Plovers spend time resting within the colony.

When at rest, individuals are at greater risk of predation as it impacts upon their ability to detect and escape predators. In resting and roosting shorebirds, their head position is primarily stable and the chances of predator detection is diminished compared to when foraging, when the orientation of their head changes frequently (Cantlay *et al*. 2019). Mobile prey are more difficult for predators to catch (Quinn and Cresswell, 2006). During the day, the greatest threat of predation comes from arial predators - birds of prey, e.g., Kestrel (*Falco tinnunculus*) and Sparrowhawk (*Accipiter nisus*). At night the greatest threat comes from nocturnal terrestrial predators, such as Red Fox (*Vulpes vulpes*) and European Badger (*Meles meles*). There is also a risk of predation by smaller predators such as Stoat (*Mustela erminea*) and Grass Snake (*Natrix helvetica*). This means Little Terns and Ringed Plovers must always be vigilant.

Early detection of predators will decrease the risk of adults being predated, while increasing the chances the predators can be deterred before they can take eggs or chicks. The proximity and orientation of the shorebirds to vegetation has the potential to influence predator detection. Shorebirds favour roosting at sites with high visibility for detecting predators and hence prefer open space without tall vegetation (Rogers *et al*., 2006; Zharikov and Milton, 2009). Furthermore, vegetation can inhibit the escape of shorebirds by altering their flight path (Walters, 1990). The visual field of birds is important in the detection of predators. Birds have a narrow binocular field of vision which is made up of the overlap of both eyes, while they also have two monocular fields (making up the cyclopean field) that is the visual field of just one eye (Martin and Piersma, 2009). As visual foragers, the binocular sector in Ringed Plovers and Little Terns is essential for feeding, and as such their bills are positioned in the centre of this field of vision (Martin *et al*., 2007; Martin, 2012). The monocular sectors provide good coverage and provide broad fields of vision; however, this does not cover 360˚, resulting in a 'blind sector' directly behind the head (Timmis *et al*., 2022; Martin and Piersma, 2009). Thus, the orientation of resting shorebirds influences the proportion of their visual field that is facing the vegetation, influencing their ability to detect predators. Ringed Plovers and Little Terns are visual foragers (Pienkowski, 1982; Cunningham *et al.*, 2013). However, differences in how they forage (running, stopping, and pecking and plunge-diving respectively) results in different visual fields, with Little Terns having more forward-facing eyes and hence a larger blind sector (Martin and Piersma, 2009).

Other factors that may influence the vigilance of birds at rest are whether they are resting as part of a group and the frequency of dreading occurrences. Birds within a group have reduced chances of predation and a greater chance of predator detection (Elgar, 1989). When dreading, Little Terns are less at risk of predation due to their unpredictable nature (Meehan and Nisbet, 2002).

Birds may also alter their orientation to correspond with the angle of the sun, to reduce the high energy expenditure that may come with thermoregulation (Cestari and De Melo, 2022; Timmis *et al*., 2022). When ambient temperatures are low, birds may orientate perpendicular to the sun, increasing the surface area exposed (Luskick *et al*., 1978). Alternatively, when ambient temperatures are high, facing the sun can reduce body temperature increases as there is a smaller area of the body (the minor axis) exposed, in addition to the head helping shade some of the body (Fortin *et al*., 2000). Other factors influencing body orientation are wind direction and speed. Resting birds may face the wind to reduce the area exposed to the flow of the air and match with their aerodynamics, reducing air resistance (Cestari and De Melo, 2022; Luskick *et al*., 1978). The orientation of birds may be influenced by interactions between the sun and wind when high wind speeds and low temperatures correlate, in which case more birds orientate perpendicular to the sun (Cestari and De Melo, 2022).

The removal of vegetation

The loss of suitable habitat due to both human and vegetation encroachment has led to calls for more habitat creation or management. The removal of vegetation, including embryo dune vegetation, could allow shorebirds to nest higher up the beach above the zone of flood risk, reducing the risk of losing clutches to the sea during storm surges and higher tides (Moore and Davis, 2004; Charlton, 2003). This could also mitigate the loss of habitat due to sea-level rise (Mitchell *et al*., 2020) and be used in areas where dune encroachment is an issue, such as when shorebirds nest on the side of saline lagoons. Furthermore, the removal of vegetation could allow the growth of early-succession short vegetation (Cooper and Jackson, 2021). This adds another variable to the shorebirds' nest site selection.

Habitat management can, however, experience logistical and financial obstacles (Charlton, 2003). In Britain, the management of sand dunes may be controversial, as they can fall under Annex 1 habitats and therefore have priority conservation status (Rees *et al*., 2019). Another obstacle is the permissions needed to change the landscape, particularly on land set aside for conservation which often have designations for their protection. In the UK ~60% of the breeding population of Little Terns are within Special Protection Areas (SPAs) (Wilson *et al*., 2020) and while this is very important for their protection, it may impede certain management practices.

At certain sites, people may view the removal of vegetation as increasing the flood risk and therefore oppose any management. In areas in which the shorebirds nest on the edge of saline lagoons between embryo dunes and the sea, flooding can be favourable at the right times. In winter, high tides can bring beneficial substrate, creating suitable nesting habitat and replenishing the water-level of the lagoon while diluting the salt concentration, which increases as water evaporates over the summer months. However, flooding during the breeding season can wash away scrapes, in which case the presence of Marram Grass could provide more protection. Therefore, a balance must be struck in any management plan. Despite these logistical and regulatory barriers, due to the potential significant influence of vegetation, its management could be important to the future success of shorebird populations. At present more evidence is needed for this to become standard practice.

Aims and Objectives

Aim: To assess the influence of vegetation on nest site selection and rest behaviours in Little Terns and Ringed Plovers and determine the potential for success of vegetation management outside of the breeding season.

Objective 1: To use measurements, mapping and photographic analysis to assess whether nest site selection of Little Terns and Ringed Plovers is influenced by distance to Marram Grass.

Objective 2: To use behavioural observations to determine whether Little Terns and Ringed Plovers have a preference for resting further away from Marram Grass and whether their orientation at rest is primarily influenced by thermoregulation, wind direction or vigilance (proximity and orientation to Marram Grass).

Methods

Site Description

Beacon Ponds is a saline lagoon located at the northern end of the Spurn peninsula on the Yorkshire Coast. The Beacon Ponds Nature Reserve is majority owned by the South Holderness Countryside Society, with some of the land leased from the Environment Agency. The site is part of the Lagoons Site of Scientific Special Interest (SSSI) and is included in the Humber Estuary SPA and RAMSAR site. A 1970s sea defence wall runs along the western side of the pond, with arable land adjacent to the west and the North Sea to the east. Kilnsea Wetland Nature Reserve is located to the southwest of the pond.

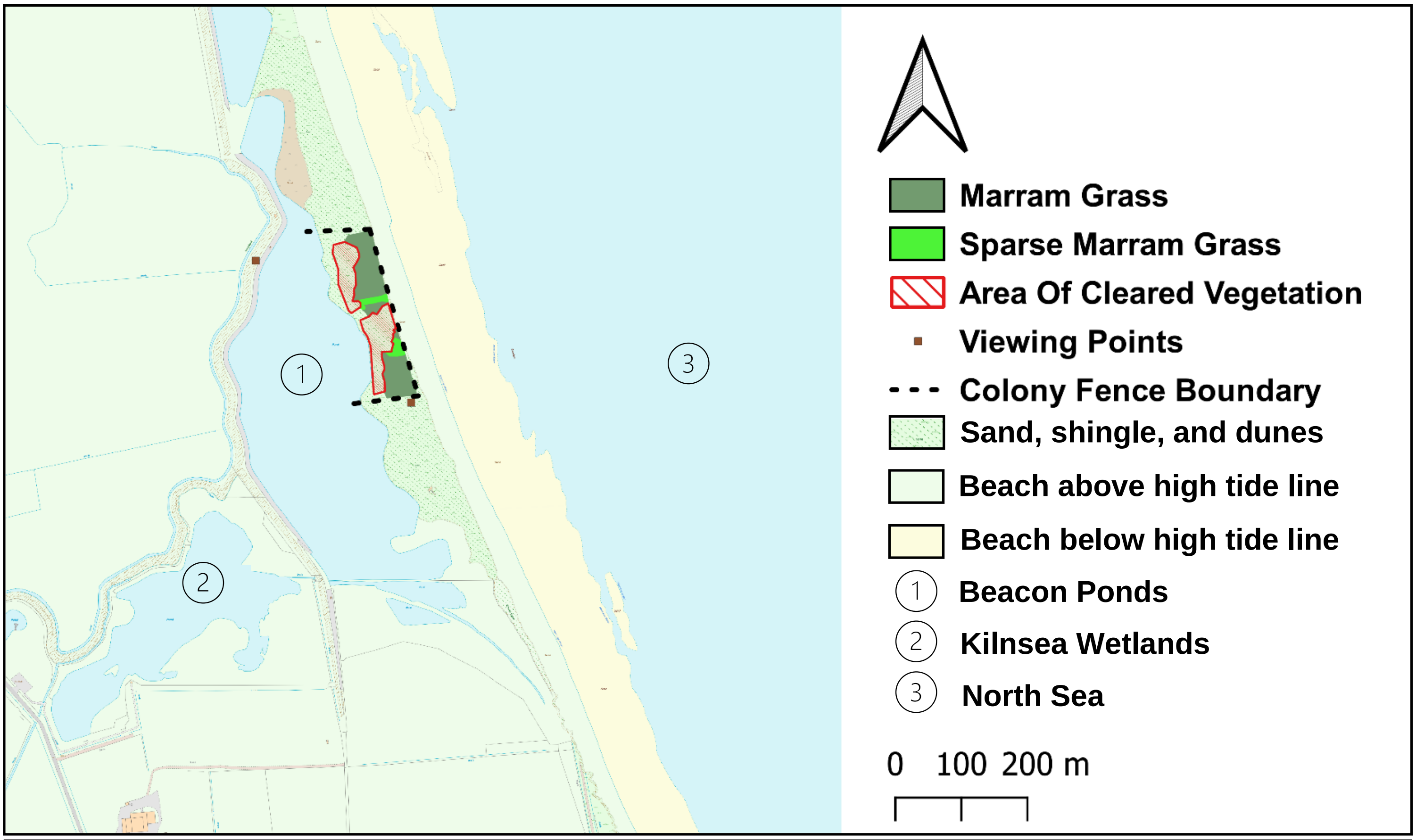

Figure 1: The study site and surrounding area. The fence boundary does not include the electric fence intersecting the colony from north to south or the roped fence to the east. The Marram grass was mapped as part of this study in June 2023 and has only been mapped within the study site, Beacon Ponds.

The study site is an area of sand, shingle, and dunes directly to the east of the pond and is home to the only Little Tern breeding colony in Yorkshire, separated from the beach by sand dunes (fig. 1). Little Terns and Ringed Plovers generally begin to breed here in May, with the last fledglings becoming independent and leaving in August. The colony fence boundary surrounds the shorebird colony and hence forms the boundary of the study area. The colony is managed primarily by the Spurn Bird Observatory Trust, overseen by the Easington Little Terns Protection Scheme. There is a high warden effort at the site, with predators chased away and people prevented from disturbing the shorebirds as far as is practicable. Other species breeding here during the study period were

Black-headed Gull (*Larus ridibundus*), Avocet (*Recurvirostra avosetta*) and Eurasian Oystercatcher (*Haematopus ostralegus*). Each year, winter storms and tide surges act to wash over the dunes, altering the shorebird nesting habitat at the site. The area suitable for nesting can be reduced by dune encroachment here, with dunes historically migrating into open areas. If unmanaged this could lead to reductions in the shorebird breeding numbers and the movement to a new nesting site. Consent was provided by Natural England for the first time to clear an area of embryo dunes in the winter, before the 2023 breeding season (fig. 1).

Nest Site Selection

Geographical Mapping

The scrapes of Ringed Plovers and Little Terns were mapped during two colony walk-throughs on the 15th and 29th June 2023, at which point the number of scrapes would have been at its peak. Participants of the walk-through (wardens and volunteers), walked in a line, evenly spaced, and upon the detection of a scrape, the 'what3words' (What3words, 2023) location was recorded (with an accuracy of 4m). Scrapes were only recorded when eggs were present, to allow for species identification and to avoid the inclusion of unused scrapes in the analysis. Shorebirds frequently create multiple scrapes before deciding on one in which to lay eggs (Hitchcock and Gratto-Trevor, 1997).

During the second colony walk-through, the western edge of the Marram Grass was mapped, with the 'what3words' recorded at various points. The grass was classified into two categories, dense Marram Grass (where the ground coverage was equal or greater than 30% (Blow, 2021)) and sparse Marram Grass (where the ground coverage was less than 30%). The 'what3words' of the distribution of scrapes and the edge of the Marram Grass were then converted into coordinates and uploaded onto QGIS (version 3.28.2) (QGIS Development Team, 2023). Polygons of the Marram Grass were created using the coordinates of the edges as a guide.

The distances (in metres) of all the recorded scrapes to the nearest area of dense Marram Grass and to each other were measured using the measure line tool. The distances of Little Tern scrapes to Marram Grass were also obtained from Blow (2021) to provide a comparison. The colony walk-throughs were conducted under a Schedule 1 licence under the Wildlife and Countryside Act of 1981. Care was taken to prevent the trampling of eggs and chicks and an effort was made to reduce the time spent within the colony to reduce the disturbance. The walk throughs were conducted during periods of warm, still weather to reduce the risk of exposure to unincubated eggs. To prevent the spread of avian flu the shoes of everyone participating were sprayed with disinfectant upon entry and exit of the colony.

To analyse if the observed frequency of nests per metre away from Marram Grass differed from the frequency of nests if the vegetation had no influence and the scrapes were spread evenly across the site, the observed frequencies per metre and expected proportion per metre were compared. To do this, the distance from the Marram Grass to the waterline of the lagoon was measured for every 10m north to south along the colony using GIS and satellite imagery of the lagoon (Google Earth, 2021). The average was calculated, producing an average width of the colony (52m). The expected proportion was taken as the reciprocal of this distance.

Measurements

During the first colony walk-through on the 15th of June 2023, the distance of a small sample of scrapes to vegetation were measured manually to produce an accurate measurement that could then be used to assess the accuracy of using GPS coordinates and GIS to map all the scrapes. A tape measure was held above the scrape and at the edge of denser Marram Grass and the distance recorded. Due to the limited time available, to reduce the time spent disturbing the colony, only a small number of scrapes could be measured. These were selected throughout the whole colony, measuring 30% of the scrapes as identified randomly by the participants of the walk-through.

Photographic analysis

Photographs of Little Tern and Ringed Plover scrapes were taken within the colony at Beacon Ponds when possible and photographs of Ringed Plover scrapes were also obtained from nesting sites at:

- The Breach, another site on the Spurn peninsula at which Ringed Plovers attempt to breed. It is ~3km from the colony at Beacon Ponds and falls within the Humber Estuary SSSI. Success rate is severely hindered here by increased predator presence and human disturbance, with no full-time wardens.
- Gibraltar Point, in Lincolnshire, approximately 60km south from the colony at Spurn. This site has SPA, SSSI and Ramsar status. As at the Breach it also has issues with scrape predation.

These photographs were analysed for the presence of macro or micro vegetation.

Rest – Distance and Orientation

To assess the influence of vegetation on rest behaviour, shorebirds at rest were sampled for a period of 1 hour, 4 times a day (7:30-8:30, 12:30-13:30, 15:00-16:00 and 21:00-22:00), 4 times a week between 13th June to 27th July 2023. The colony was observed from two locations, both of which provided enough distance to prevent disturbance to the colony (fig. 1). The shorebirds were defined as ‘at rest’ when preening, sleeping, or staying still for 60 seconds or longer. This timing was to ensure the birds were not between other activities, for example Ringed Plovers feeding throughout the colony may stand still for short periods of time but continue feeding soon after. Parental duties such as brooding or watching over chicks were not classified as resting, as their distance and orientation may be primarily determined by the chicks rather than external factors. The distance of each resting individual to the nearest area of dense Marram Grass was recorded. This was in a 2m range due to the difficulty of determining the exact distance accurately when viewing from 100m to

280m. Additionally, the body orientation (0-360˚) of each individual to the Marram Grass was recorded at 10˚ intervals, 90˚ being perpendicular to the Marram Grass and 270˚ being face on with the Marram Grass.

From this, the proportion of each bird's visual field on the nearest area of dense grass could be calculated, using the blind sector of each species. This was done by subtracting the degrees of the blind sector that was facing the Marram Grass from the total possible degrees of visual field that could be facing the Marram Grass (180˚). The blind sectors of Little Terns and Ringed Plovers have not been defined, however, but can be estimated. A proxy for the Ringed Plover is the related European Golden Plover, which is another visual feeder and has a blind sector of 20˚ (fig. 2c) (Martin and Piersma, 2009). Due to the similarities in feeding method and skull structure of the two species (fig. 2a and b), the study has also used a 20˚ blind sector for the Ringed Plover.

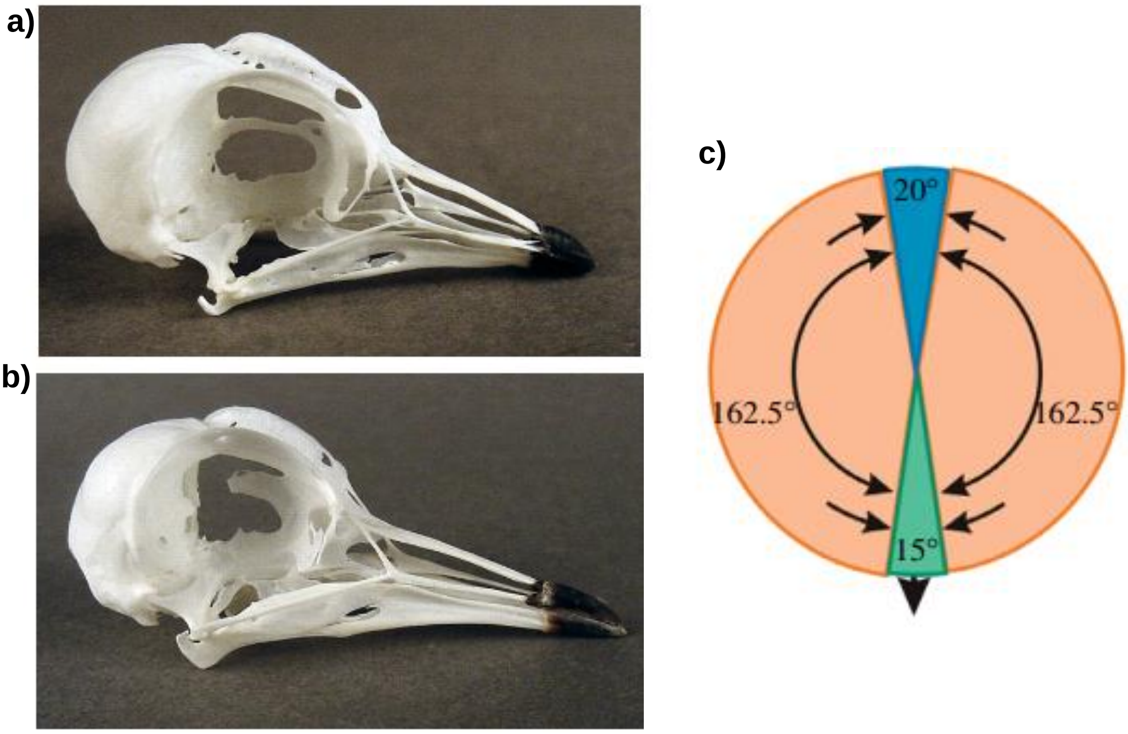

Figure 2: The skulls of a) Ringed Plover and b) European Golden Plover, from the bird skull database 'Skullsite' (2023).

c) The visual field of the European Golden Plover, including the blind sector (blue), binocular sector (green) and monocular sector (pink). The downwards arrow indicates the head orientation. From (Martin and Piersma, 2009).

Due to a lack of a suitable proxy for the blind sector of the Little Terns it has been conservatively estimated using skull structure (fig. 3), the positioning of the eye and comparisons with species with known visual fields. As such, a blind sector of 40˚ has been used for Little Terns in this study. Therefore, if a Little Tern was orientated at 10˚ from the Marram Grass, then 30˚ of its blind sector would be facing the Marram Grass and 150˚ of its visual sector would be facing the vegetation.

Figure 3: a) Little Tern skull. From the bird skull database 'Skullsite' (2023). b) Predicted visual field of the Little Tern, blue area indicates the blind spot, downwards arrow indicates the head orientation. The binocular and monocular sectors have not been differentiated.

For each bird sampled it was recorded whether they were in a group (classified as having three or more individuals within 2m). Groups could be conspecific or heterospecific as all species will provide a response to a predator. The number of dreading occurrences of Little Terns within each hour of data collection was recorded, defined as ≥50% of the resting Little Terns flying up (Jørgensen *et al.*, 2007). The number of predators causing these up flights was also recorded. This provides a better understanding of the vigilance of the shorebirds and their predator avoidance behaviours. Ringed Plovers did not participate in these up flights.

To test the influence of thermoregulation on the shorebirds, the temperature was recorded at the start of each sampling session and updated throughout if necessary. Furthermore, the body orientation to the sun (when not obscured by clouds) was recorded. Data collection at 12:30-13:30 acted as a control, as the sun was directly overhead the birds so their orientation would not be influenced by aligning to the sun. For ease of analysis, the body orientation in relation to the Marram Grass and in relation to the sun was condensed so the equivalent orientations were the same, meaning all orientations are within 0-90˚ and 270-350˚ (e.g., 190˚ became 350˚).

To test the influence of wind on the resting orientation of Little Terns and Ringed Plovers, the wind direction was recorded (using the direction of the blades of wind turbines located to the east in the North Sea), and the wind speed obtained from the Met Office (Met Office, 2023). For each resting bird it was recorded whether their body orientation was aligned with the wind direction.

Statistical Analysis

The statistical analysis was conducted using R studio (version 2022.07.02+576) (RStudio Team, 2023). A chi-squared goodness-of-fit test was used to determine if the observed frequencies of Little Tern scrapes at each distance, differed significantly from the expected distribution of scrapes if Marram Grass had no influence (i.e., an even distribution across the area available). The same test was conducted for Ringed Plover scrapes.

A chi-squared goodness-of-fit test was used to determine if the observed frequencies of Little Terns at rest at each distance from the Marram Grass differed significantly with the expected distribution if the terns rested evenly throughout the colony. This was also undertaken for Ringed Plovers at rest. For both species, a general linear mixed model with interaction terms and the sampling session as a random effect was used to analyse the effect of time of day (categorical), the proportion of the birds' visual sector in relation to the nearest area of Marram Grass (categorical) and whether the individuals were within a group (categorical) on the dependent variable, the distance from Marram Grass at which they rested (continuous). The R command 'lmer' was used. Multicollinearity between the predictor variables was tested for by calculating the variance inflation factors of the predictor variables using the R command 'vif()'. For both species, all interaction terms were insignificant and therefore were removed from the model to test the main effects. An ANOVA of the final model and a reduced model for each predictor was used to test for significance.

For both species a generalised linear mixed model with the sampling session as a random effect was used to analyse the effect of the explanatory variables: the proportion of the birds' visual sector on the nearest area of Marram Grass (categorical), their orientation to the sun (categorical) and the wind direction (categorical) on the dependent variable the orientation of the birds to the Marram Grass (categorical). The R command 'glmer' was used, with a Poisson family and log link. Again, multicollinearity between the predictor variables was tested for. Significance was tested by an ANOVA of the model and a reduced model without each predictor variable.

To determine if the proportion of shorebirds resting in alignment with the wind direction correlated with the speed of the wind (as the wind speed was not included in the mixed model), a Spearman rank correlation and a Pearson correlation were used for Little Terns and Ringed Plovers respectively. A Wilcoxon's signed ranks test was used to determine if the orientation of Little Terns in relation to the Marram Grass differed significantly between the times when sun was out of view or directly overhead and the times when they were able to orientate their bodies in relation to the sun.

Results

Nest Site Selection

57 Little Tern scrapes and 11 Ringed Plover scrapes were mapped within the colony (fig. 4). One Little Tern and two Ringed Plover scrapes are shown outside the main colony to the east. These were not included in the analysis as it had not been possible to accurately map the eastern face of the vegetation. All scrapes were located on the sand and shingle, with no birds nesting within the Marram Grass. All 57 Little Tern scrapes within the colony were within a 120m long stretch from north to south and, while the Ringed Plover scrapes were more sparsely distributed, the majority were also within this stretch. 2 Ringed Plover scrapes were, however, located to the south of this main group. 32 Little Tern Scrapes (56% of total) and 6 Ringed Plover Scrapes (54.5% of total) were found within areas that had been cleared of vegetation during winter habitat management. While there were areas to the north, south and east of the cleared areas that had no shorebirds, with the exception of one of the southern Ringed Plover scrapes.

The mean distance of scrapes to the nearest area of dense Marram Grass measured using GIS was 18.49m for Little Terns, with a minimum of 1m and a maximum of 37m (with a standard deviation of 9m) (fig. 5). Only two Little Tern pairs nested within 6m of the Marram Grass. The mean distance to the Marram Grass of scrapes measured with a tape measure was 17.73m, only a 0.76m difference. In 2021, the distance of 26 Little Tern scrapes from the nearest area of Marram Grass were recorded, with a mean distance of 7.04m, a maximum of 26.23m, a minimum of 0.19m and a standard deviation of 5.70m. For Ringed Plover scrapes the mean distance from Marram Grass was 19m, with a minimum distance of 3m and a maximum of 34m (with a standard deviation of 11m) (fig. 2). The mean distance between neighbouring scrapes was 4.60m for Little Terns and 17.03m for Ringed Plovers. The mean distance between Ringed Plover scrapes and their nearest Little Tern neighbour was 17.43m.

Locations of Little Tern (*Sternula albifrons*) and Ringed Plover (*Charadrius hiaticula*) Scrapes within the Beacon Ponds Colony 2023

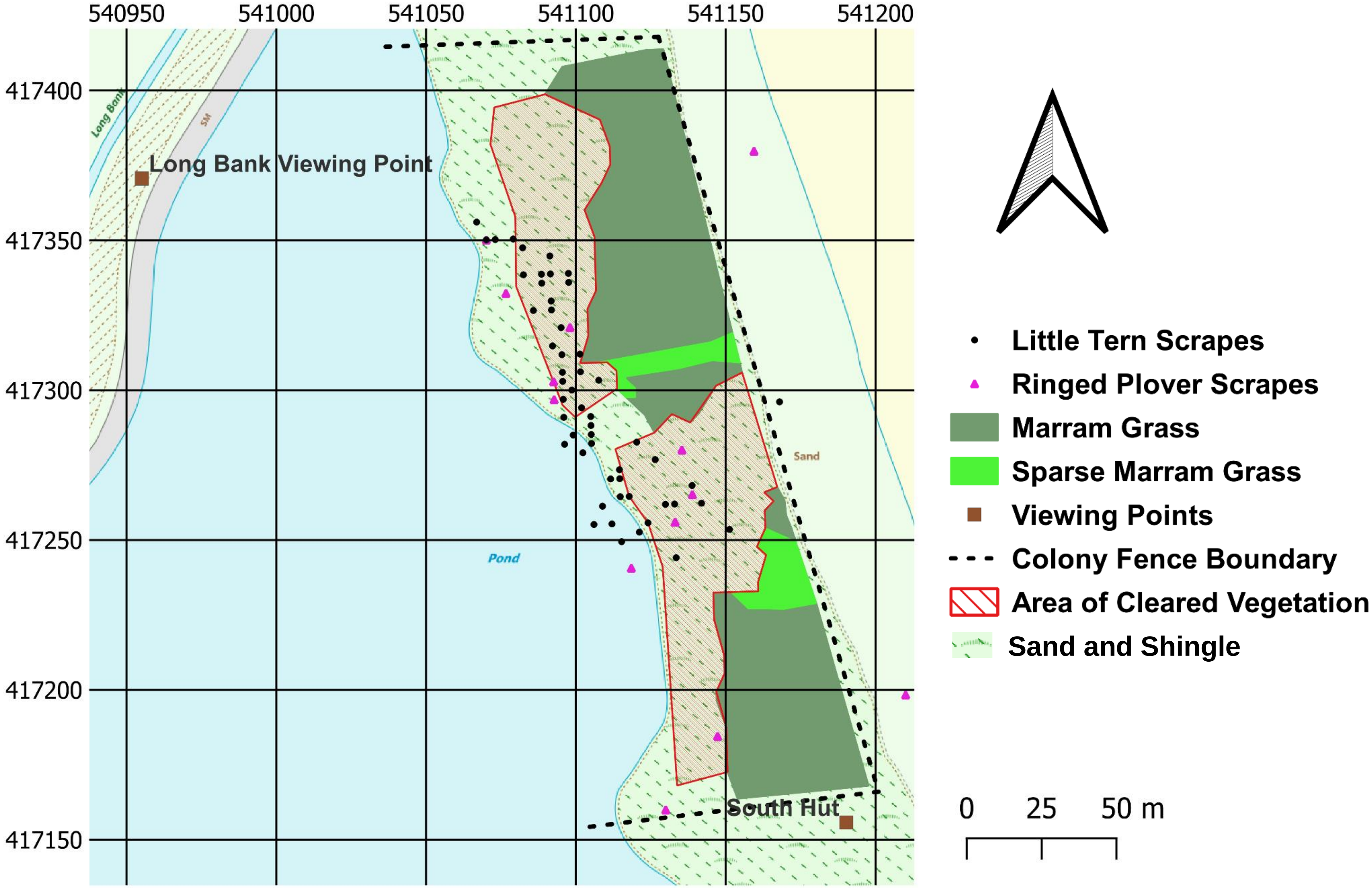

Figure 4: The distribution of Little Tern (*Sternula albifrons*) and Ringed Plover (*Charadrius hiaticula*) Scrapes and the location of dense and sparse areas of Marram Grass (*Ammophila arenaria*) within the shorebird colony at Beacon Ponds in 2023. The fence boundary shown does not include the electric fence intersecting the colony from north to south or the roped fence to the east. The water level in this map is not indicative of that within the study, as it was much lower at this time.

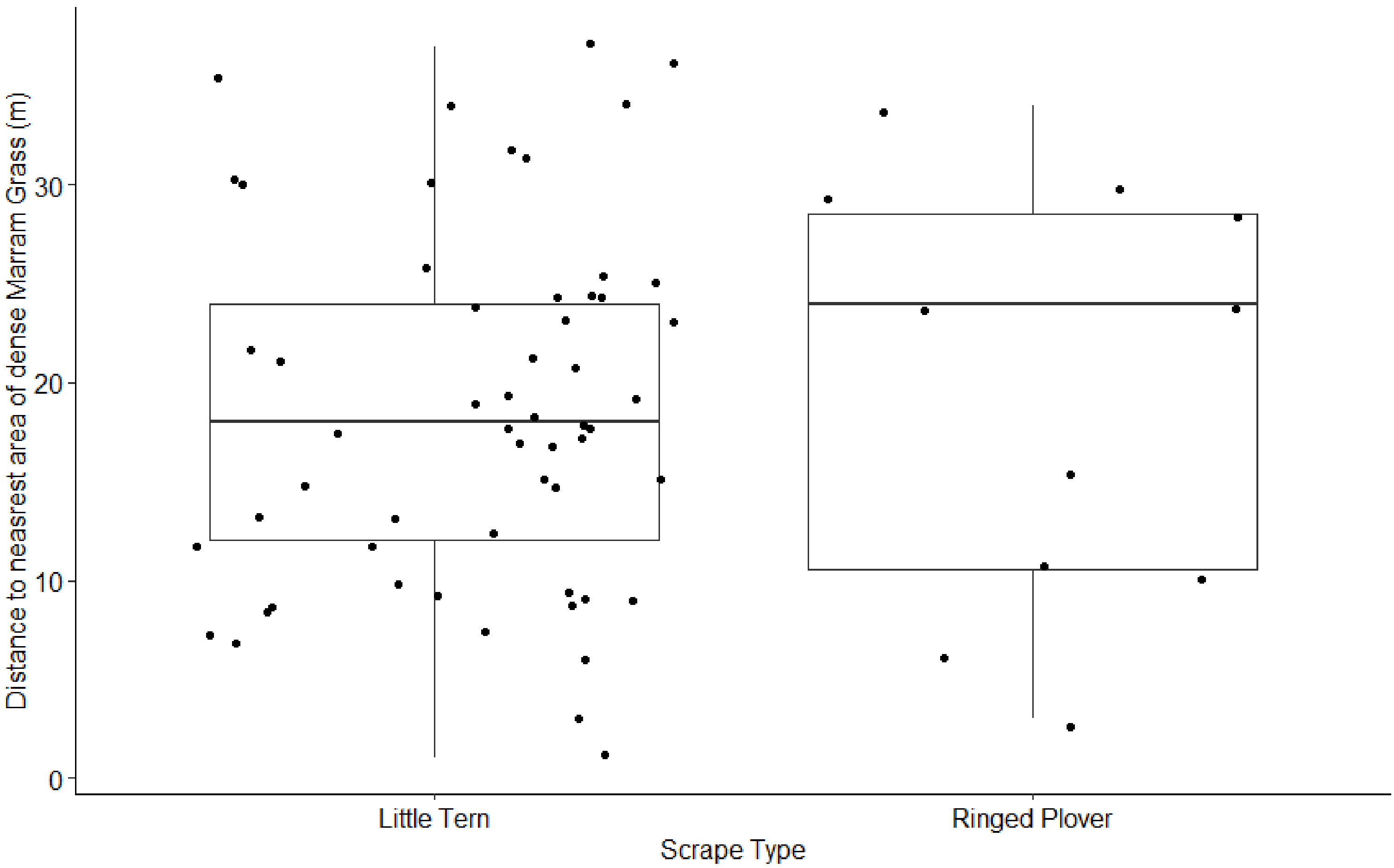

Figure 5: The distance of Little Tern and Ringed Plover scrapes to the nearest areas of dense Marram Grass (*Ammophila arenaria*). Datapoints showing the spread of the data.

There is a significant difference between the distances of Little Tern scrapes from the nearest area of Marram Grass and the expected distribution of scrapes if vegetation had no effect (X^2= 100.82, df = 51, p < 0.001).

There is no significant difference between the distances of Ringed Plover scrapes from the nearest patch of Marram Grass and the expected distribution of scrapes if vegetation had no effect (X^2 = 50.454, df = 51, p = 0.4952).

Photographic Analysis

As previously stated, no scrapes were found within the Marram Grass at Beacon Ponds. However, on the Breach on the Spurn Peninsula, Ringed Plover eggs were found within the grass (fig. 6a and b), in addition to at Gibraltar Point (fig. 6c). The presence of four eggs within two of the three scrapes (figs 3a and 3c) indicates that it was the pair's first attempt at breeding this year, as a female is unable to lay four eggs after the energy exertion of a first brood.

a) b) c)

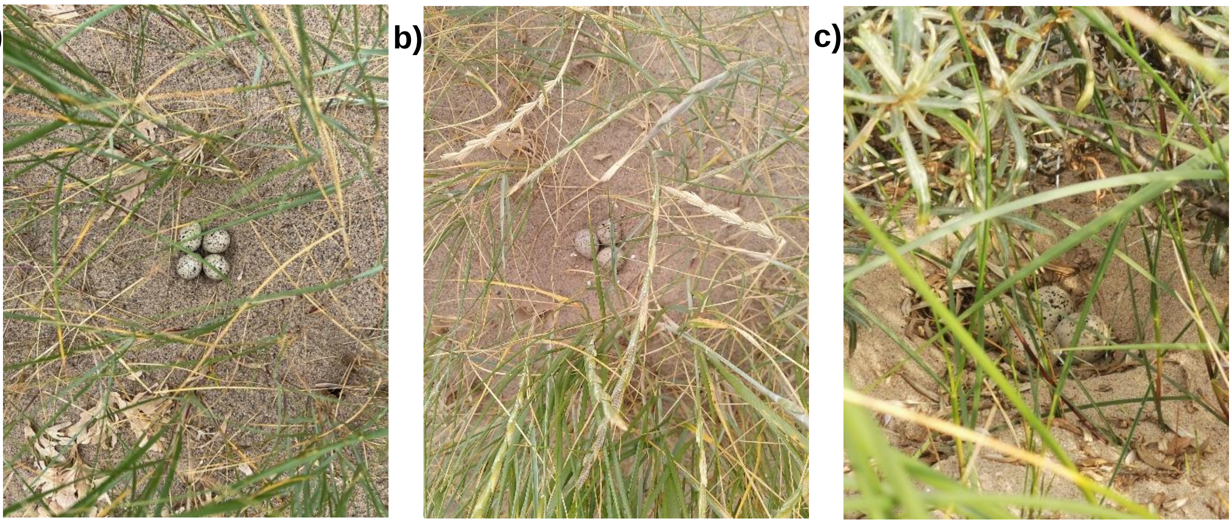

Figure 6: Ringed Plover Scrapes within Marram Grass. a) Four eggs on the Breach on the Spurn Peninsula, b) Three eggs on the Breach on the Spurn Peninsula, c) Four eggs at Gibraltar Point, Lincolnshire.

a) b) c) d)

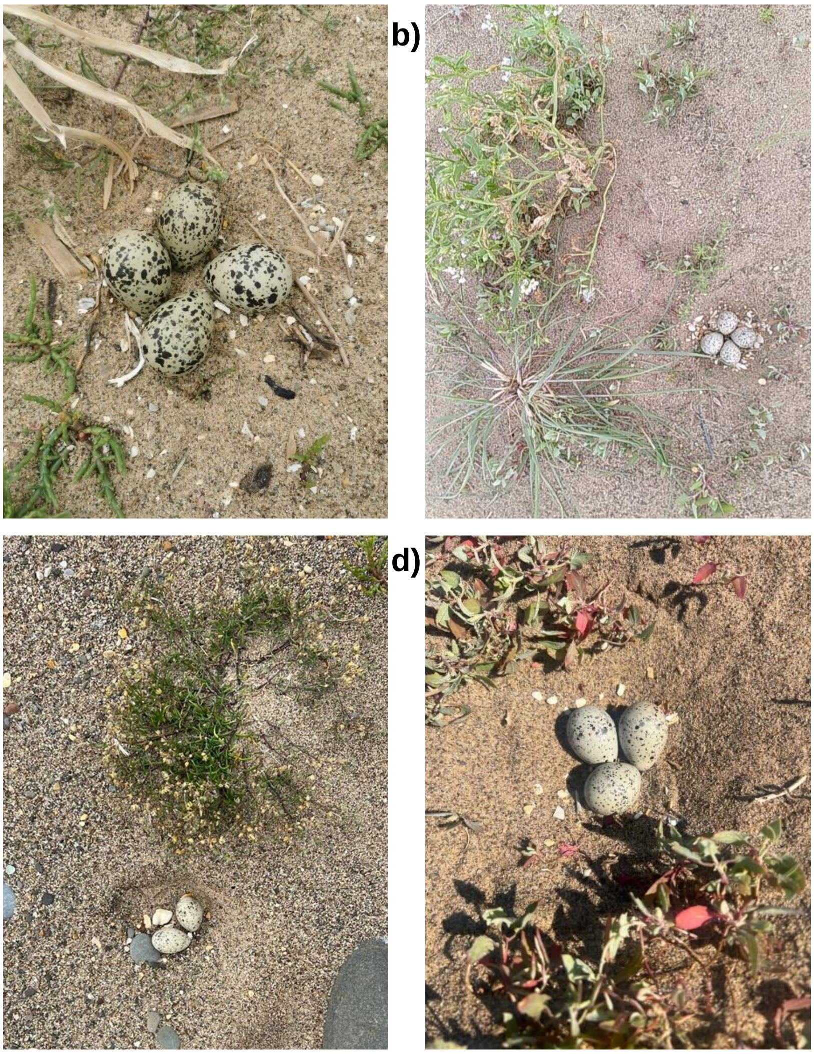

Figure 7: Scrapes within proximity to microvegetation within the colony at Beacon Ponds. Ringed Plover scrapes (a and b) and Little Tern scrapes (c and d).

Although no Little Tern scrapes were found within the macro vegetation, the photographic evidence suggests that the presence of microvegetation does not stop Little Terns or Ringed Plovers from nesting (fig. 7). The true relationship of Little Tern nest site selection and microvegetation cannot, however, be concluded from this alone.

Rest – Distance and Orientation

Little Terns

6309 instances of rest were recorded for Little Terns, with an average of 30.26 resting at a time, reaching a maximum of 119 individuals. Dreading was recorded on average 5.01 times per hour, with predators being the cause of these fly ups on average only 0.256 times per hour.

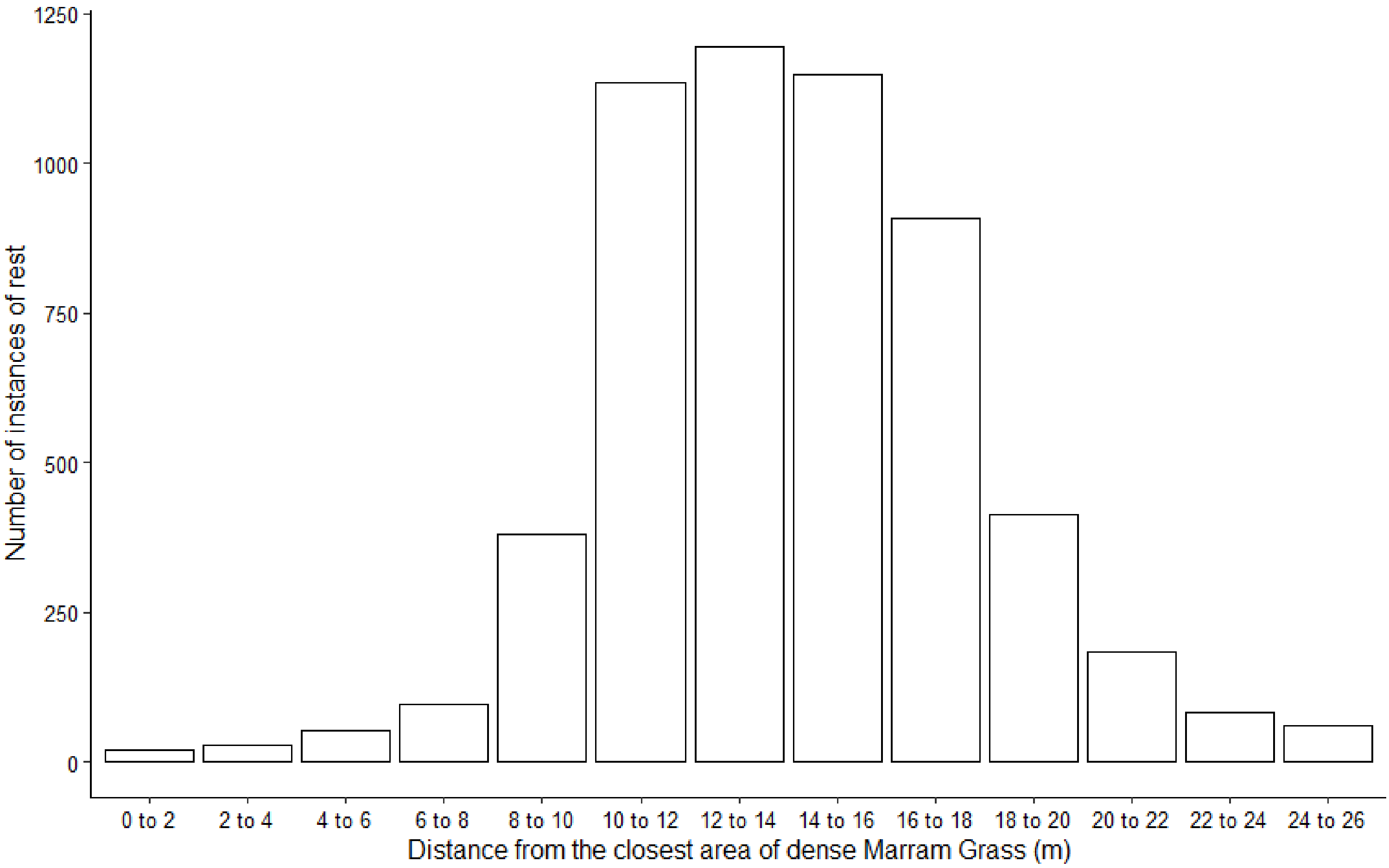

Figure 8: The distance at which Little Terns rest from the nearest area of dense Marram grass within the colony at Beacon Ponds.

Little Tern Distance of Rest

There is a significant difference between the frequency of the distances from vegetation of Little Terns at rest and the expected frequency if there was an even spread across the colony, depending on the available area between the Marram Grass and the lagoon (X^2= 23386, df = 26, $p < 0.001$).

The distance at which the Little Terns rest is greatest at the middle distances from the nearest vegetation, the most frequent distance being 12-14m, with few terns choosing to rest closer to the Marram Grass than 8m (fig. 8). However, despite there being space to rest at greater distances from the vegetation, the terns rarely chose to.

Table 1: The results of two mixed models on the rest behaviour of Little Terns and their equivalent reduced models.

Response variable	Predictor variables	ANOVA	F	DF
Distance from Marram Grass	Part of a group or not	p < 0.001***	25.012	3
	Time of Day	p < 0.001***	25.01206	3
	Proportion of visual sector on nearest Marram Grass	p= 0.1485	2.0875	1
Orientation to Marram Grass	Wind Direction	p < 0.001***	25697	14
	Orientation to the sun	p < 0.001***	5233	19
	Proportion of visual sector on nearest Marram Grass	p < 0.001***	45158	1

There was no significant interaction between the predictor variables (part of a group, time of day and proportion of visual sector on nearest Marram Grass) so the interaction terms were removed from the first model. The time of day has been shown to affect the distance at which the Little Terns rest (Table 1), with the terns resting at greater distances from the Marram Grass at 21:00-22:00 in comparison with the other sampling times (fig. 9).

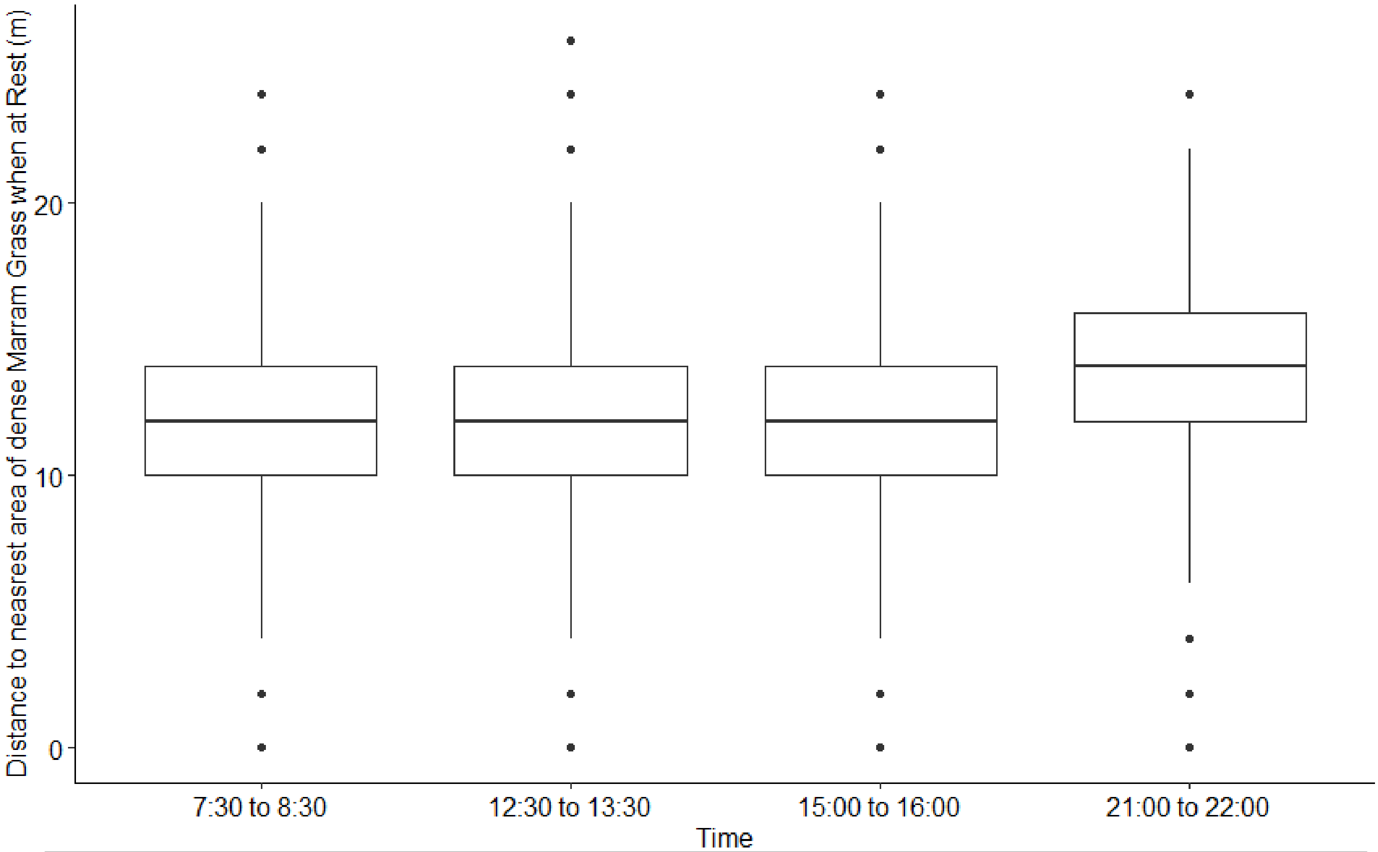

Figure 9: The distance at which Little Terns rest from the nearest area of dense Marram Grass at the four sampling times throughout the day.

77.4% of Little Terns rested in a group of three or more individuals. Whether Little Terns rest in groups, does show an effect on the distance of Little Terns at rest (Table 1), with a general trend of greater proportions of terns resting in groups at greater distances from vegetation up to 12-14m before declining again (with the exception of 24-26m) (fig. 10).

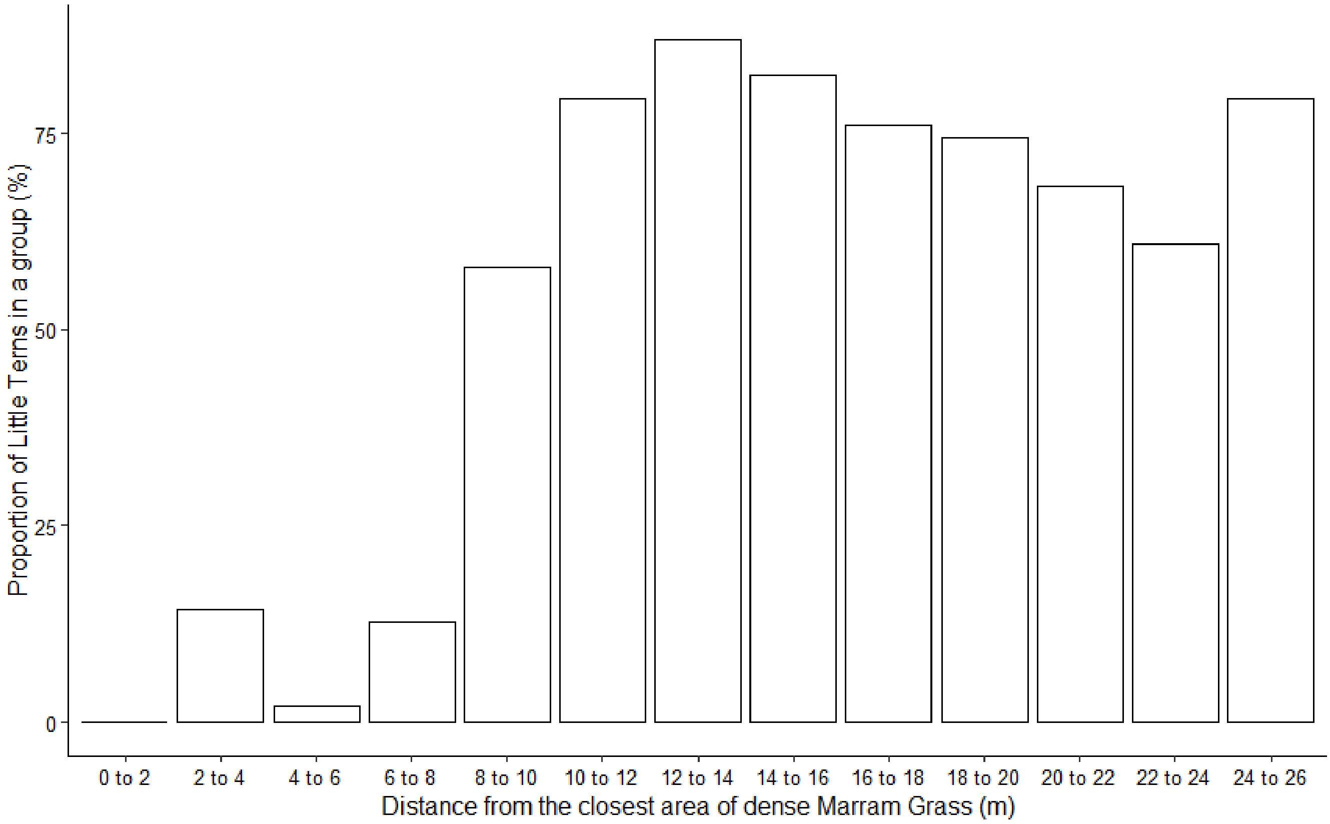

Figure 10: The proportion of Little Terns resting in a group at each distance from the nearest area of dense Marram Grass.

The distance at which the Little Terns rest has not been found to interact with their orientation to the Marram Grass, with the proportion of their visual field on the nearest area of Marram Grass having no significant effect on the distance (Table 1).

Little Tern Orientation when at rest

The proportion of the Little Tern's visual field on the nearest area of Marram Grass does, significantly interact with the orientation of the Little Terns (Table 1). The orientation of the terns was more frequently aligned with the nearest Marram Grass in such a way that the proportion of their visual field facing the Marram Grass was the lowest possible, with 65% of the terns orientated with just 140° of their visual sector on the nearest Marram Grass.

The orientation of Little Terns when resting was significantly affected by the wind direction (Table 1), with 84.7% of Little Terns orientated facing into the wind. The proportion of Little Terns that were aligned to the direction of the wind was found to strongly correlate with the speed of the wind ($r(16) = 0.78$, $p < 0.001$) (fig. 11).

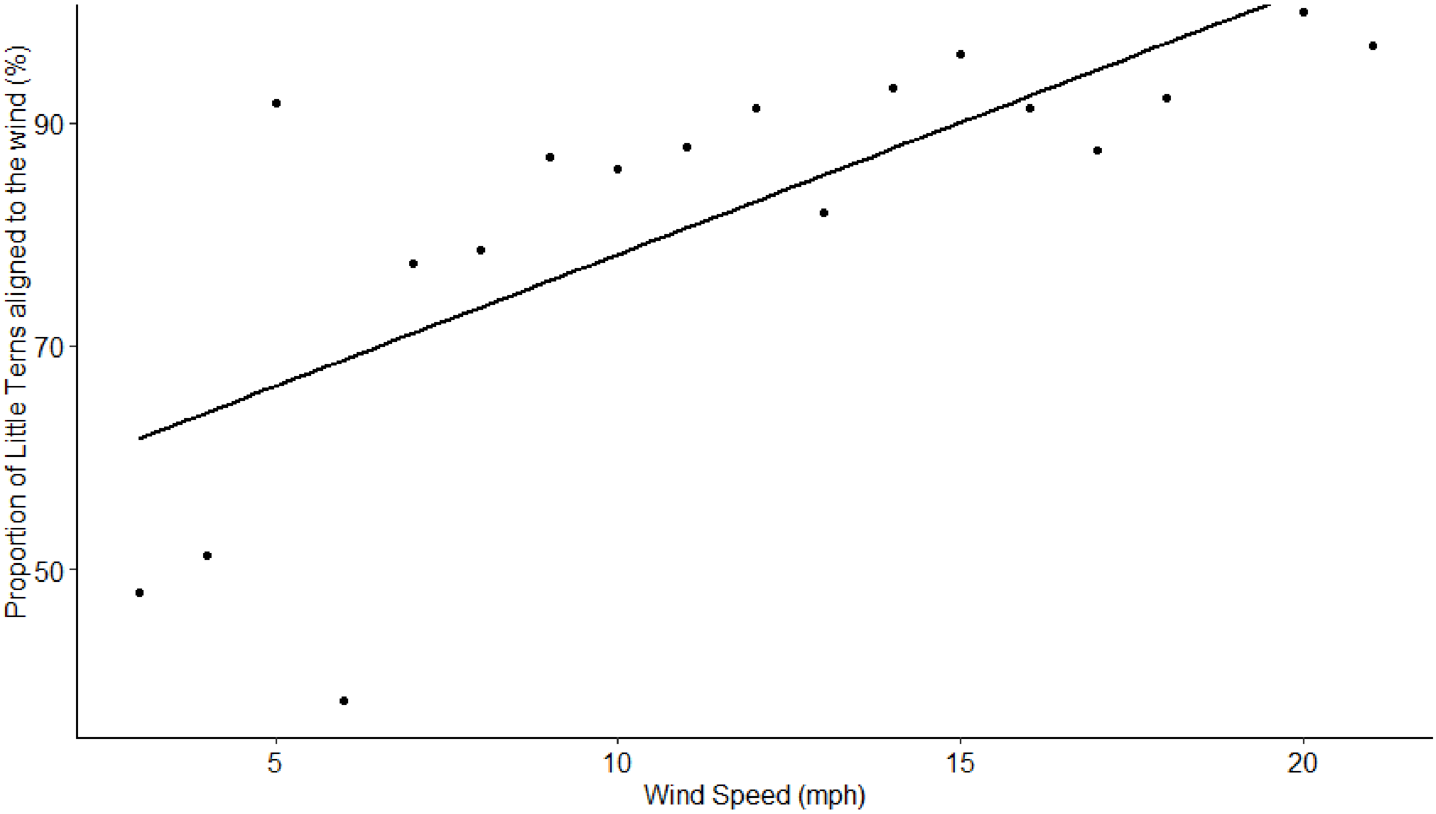

Figure 11: The relationship between wind speed and the proportion of Little Terns resting in alignment to the wind direction. The line of best fit was produced by a linear model.

3012 Little Terns were recorded at rest when it was possible for them to align themselves to the angle of the sun, while 3387 Little Terns were recorded at rest when the sun was directly overhead or cloud cover prevented the sun from showing. The orientation of Little Terns to the sun has been found to significantly interact with the Little Terns orientation in relation to the Marram Grass (Table 1), and there is a significant difference between the orientation of Little Terns when the sun is showing and when it is overhead or obscured (V = 1445690, p < 0.001).

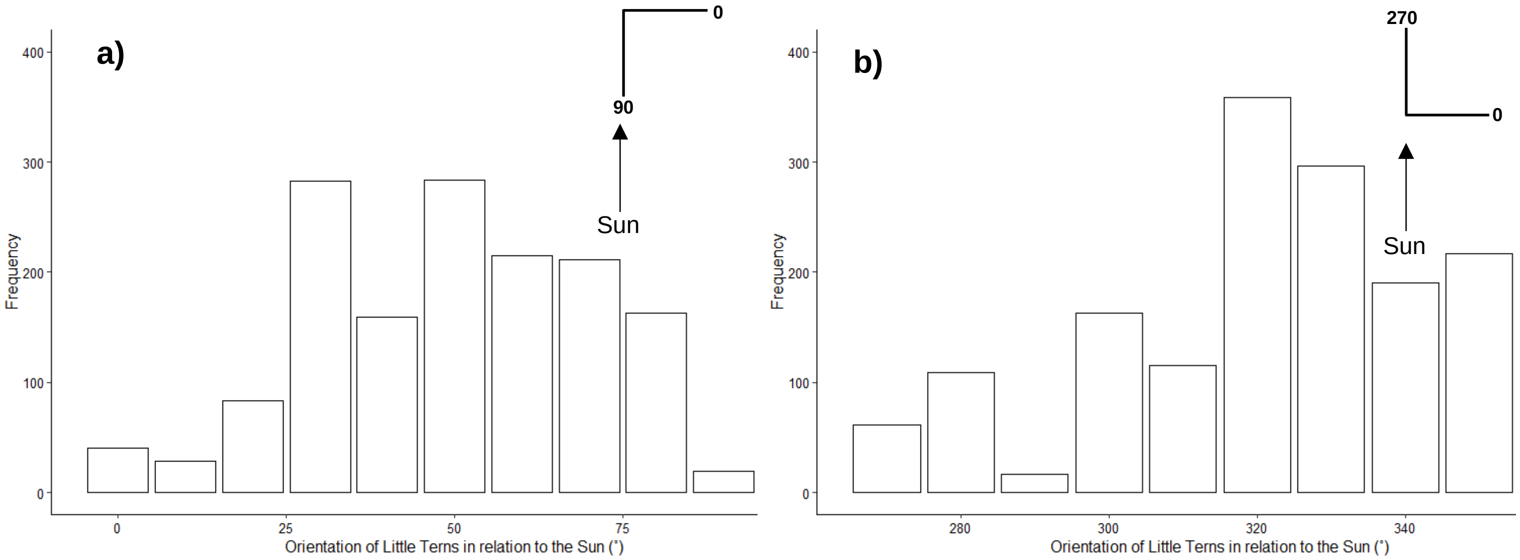

Figure 12: The frequency of Little Terns resting at different alignments to the sun. a) Orientation to the sun at 0 to 90˚. b) Orientation to the sun at 270 to 350˚.

Furthermore, the mean temperatures for each orientation have a range of only 3.8˚C, despite the temperature range during the study being 10˚C. This suggests that temperature does not have a large influence on the orientation of terns towards the sun.

Ringed Plovers

216 instances of rest were recorded of Ringed Plovers.

Ringed Plover Distance of Rest

The observed distance at which Ringed Plovers rest from Marram Grass is significantly different to if they rested evenly throughout the colony ($X^2 = 378.75$, df = 26, $p < 0.001$).

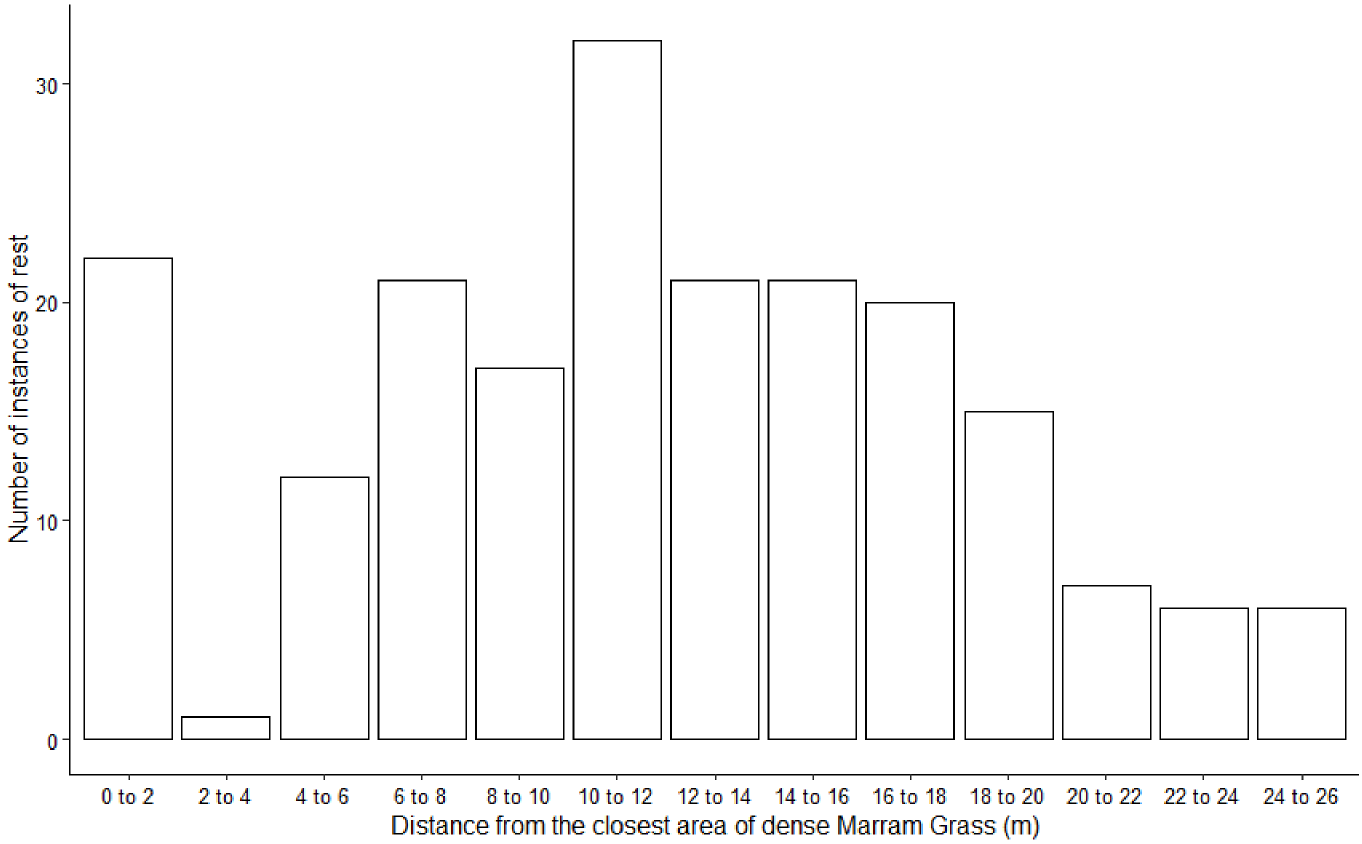

Figure 13: The distance at which Ringed Plovers rest from the nearest area of dense Marram grass within the colony at Beacon Ponds.

The most common distances from vegetation at which Ringed Plovers rest are, in the middle distances, much like in Little Terns, with 10-12m being the most frequent distance, with the frequency declining as distance increases from here (fig. 13). However, there is also a considerable number that rested between 0-2m from the Marram Grass.

Table 2: The results of two mixed models on the rest behaviour of Ringed Plovers and their equivalent reduced models.

Response variable	Predictor variables	ANOVA	F	DF
Distance from Marram Grass	Part of a group or not	p= 0.1468	3.8369	2
	Time of Day	p= 0.0138*	10.646	3
	Proportion of visual sector on nearest Marram Grass	p= 0.0603	45158	1
Orientation to Marram Grass	Wind Direction	p < 0.001***	37.141	14
	Orientation to the sun	p= 0.1648	485.84	19
	Proportion of visual sector on nearest Marram Grass	p < 0.001***	2043.7	1

There was no significant interaction between the predictor variables (part of a group, time of day and proportion of visual sector on nearest Marram Grass) so the interaction terms were removed from the first model.

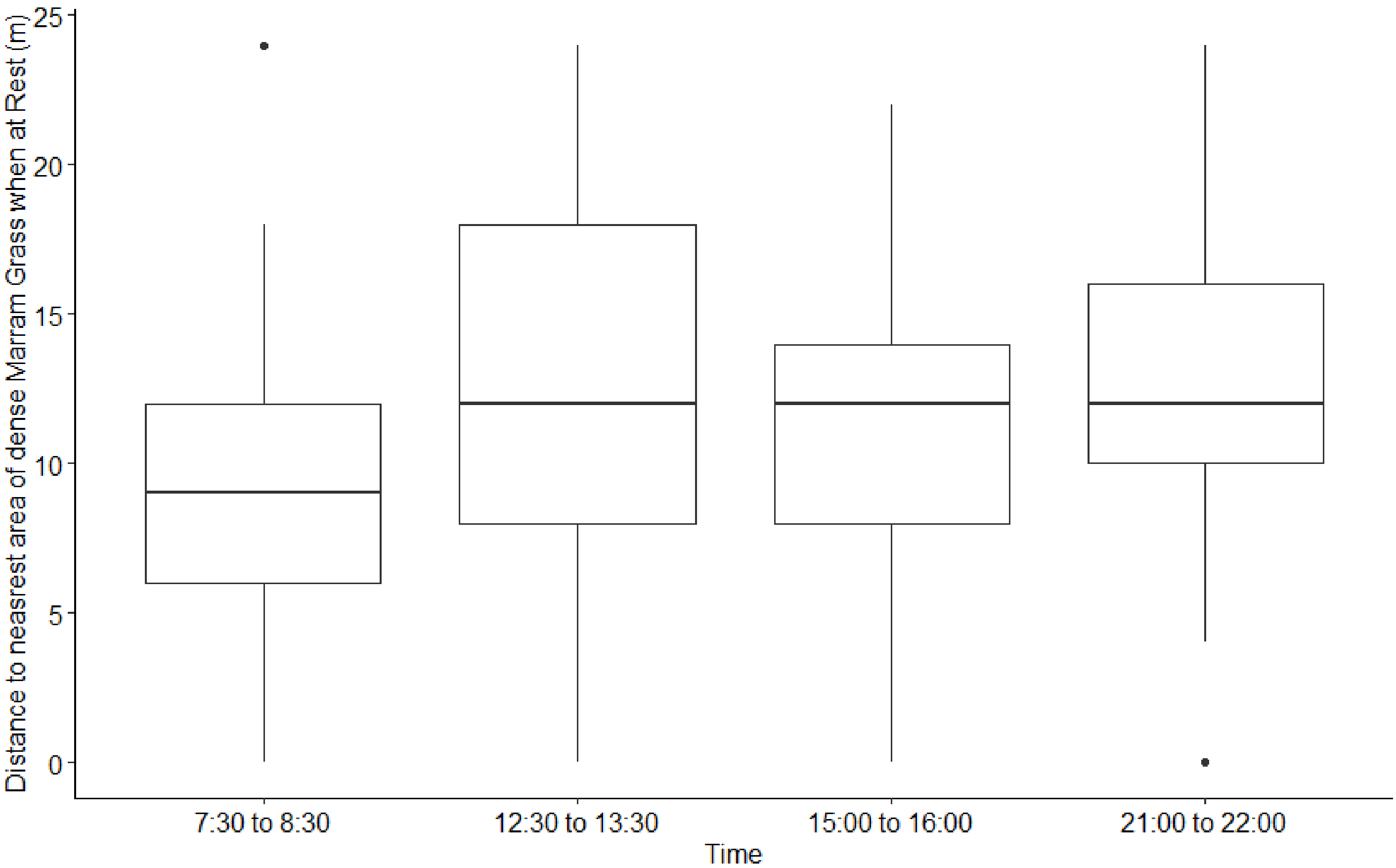

Figure 14: The distance at which Ringed Plovers rest from the nearest area of dense Marram Grass at the four sampling times throughout the day.

Although the time of day has a slightly significant effect on the distance at which Ringed Plovers rest with a significant p value (Table 2), the AIC values of the model with and without the time of day, are within two values, suggesting the time of day has limited influence. There are no strong trends throughout the day in which Ringed Plovers changed their resting distance, but they did rest slightly closer to the Marram Grass at 7:30 to 8:30 when compared to the other sampling times (fig. 14).

Only 15.7% of Ringed Plovers rested in groups of three or more. There is no significant effect of whether Ringed Plovers rested in groups on the resting distance of the Ringed Plovers (Table 2). The orientation of Ringed Plovers, and therefore the proportion of their visual field on the nearest area of Marram Grass has no significant influence on the distance at which the Ringed Plovers rest (Table 2).

Ringed Plover Orientation when at Rest

The angle at which Ringed Plovers faced the sun had no significant association with their orientation, with the reduced model without the orientation to the sun fitting the data better (Table 2). There was a significant effect of wind direction on the orientation of Ringed Plovers (Table 2) and there is a significant positive correlation between wind speed and the proportion of Ringed Plovers that are facing the wind ($t = 2.4959$, $df = 15$, $p = 0.0247$) (fig. 15).

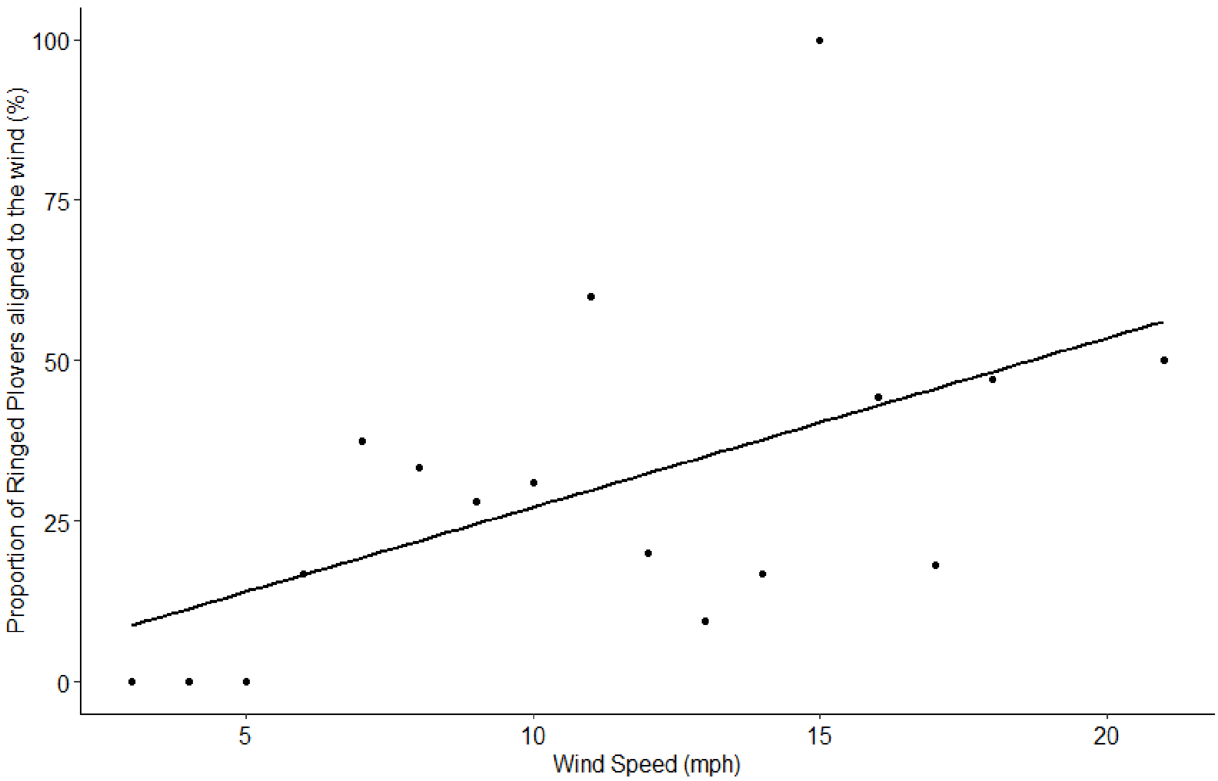

Figure 15: The relationship between wind speed and the proportion of Ringed Plovers resting in alignment to the wind direction. The line of best fit was produced by a linear model.

The proportion of the Ringed Plovers visual field on the nearest area of Marram Grass does significantly interact with the orientation of the Little Terns (Table 2). The Ringed Plovers were orientated with the smallest proportion of their visual field on the nearest vegetation in most cases, with 60.6% of the plovers orientated in such a way that only 160˚ of their visual field was facing the nearest vegetation.

Discussion

Summary

Maco vegetation in the form of Marram Grass has shown a clear influence on nest site selection, with Little Terns displaying a preference for nest sites further away and Ringed Plovers also preferring to nest in open areas (although the influence of distance from vegetation is less important). In general, Little Terns rest away from vegetation to reduce predation risk while Ringed Plovers do not show a clear avoidance when at rest. No pattern of alignment for vigilance from the nearest area of Marram Grass was found in either species. Wind direction was the primary driver of orientation. Vegetation clearance for the purpose of creating more suitable habitat for nest site selection could provide benefits to the breeding success of both species and improve the habitat for resting and roosting Little Terns and potentially other shorebird species.

Nest Site Selection

The accuracy of the GIS can be considered sufficient when comparing the means of the GIS and tape measure measurements of scrapes to the nearest area of Marram Grass with the difference being less than 1m. The distances at which the Little Terns and Ringed Plovers select their nest sites from the nearest area of Marram Grass varied between the species (fig. 5). In general, Little Terns showed a preference for nest sites at distances away from the Marram Grass with a mean of 18.49m. With only two pairs out of 57 nesting within 6m of the Marram Grass, there is a clear pattern of avoidance, in line with the current understanding (Jeong *et al*., 2011; Lopes *et al*., 2015; Medeiros *et al*., 2012). However, not all Little Terns nested away from the vegetation (fig. 5), with one pair nesting as close as 1m from the vegetation. This indicates that, although the majority of Little Tern pairs selected sites further away, the presence of vegetation is not intolerable to all, and a small number of pairs have been found to endure high vegetation cover (Lopes *et al*., 2015). Data from Beacon Ponds in 2021 showed Little Terns selected nest sites considerably closer to vegetation than during this study, with the mean distance of scrapes to the nearest Marram Grass being 2.6 times smaller. This could have been because there may have been less available vegetation-free land in 2021, with no vegetation clearance the prior winter, and therefore the shorebirds had less choice of where to select their nests.

Ringed Plovers appeared to have an even spread of distances from the Marram Grass throughout the available area of shingle and, as with Little Terns, there were cases of Ringed Plovers nesting close to the vegetation with a minimum distance of 3m (fig. 5). This does not necessarily mean they show no relationship with the vegetation, as being in an open area may be acceptable to Ringed Plovers regardless of their distance to vegetation. Unexposed nest sites can allow the detection of predators by plovers, even when distance to vegetation is not considered (Amat and Masero, 2004).

The high number of scrapes found within areas that had been cleared of vegetation in this study is a strong indication of the success of this management practice. The avoidance of vegetation found here suggests that had the management not been undertaken, the shorebirds may have been forced to select poorer quality nest sites or may have selected sites outside of the colony. However, the full extent of the area cleared of vegetation was not utilised by the shorebirds. One possible explanation for this could be a lack of suitable substrate within the shingle; shorebirds can be very specific when choosing nest sites (Fraser *et al*., 2019). While there was shingle within this area, it may take more high winter tides to bring additional substate to create preferable habitat. Thus, the continuation of this study over another season may provide more answers as to the success of vegetation clearance. Another reason for the shorebirds to not nest further within the cleared area may be because of the improved predator detection that can be associated with nesting closer together (Evans *et al.*, 2016). This could also explain why most shorebirds nested within a 120m stretch and not further to the north or south where there was still some appropriate habitat. Additionally, increased exposure to the prevailing winds coming off the sea could have dissuaded the shorebirds from nesting within the eastern extent of the cleared area where there were no dunes in between the colony and the sea.

Photographic analysis was not extensive and cannot alone provide a comprehensive picture of nest site selection. However, it can highlight objective truths such as the presence of scrapes within Marram Grass. Photographs at Gibraltar Point and the Breach on the Spurn Peninsula show Ringed Plovers do nest directly within Marram Grass (fig. 6), with the presence of first broods indicating that these sites were their first choice. It is not evident why these were chosen as nesting locations as there was sand and shingle in the vicinity, but they could have been selected to increase the distance from human visitors to the site (Tratalos *et al*., 2021; Coombes *et al*., 2008). With no scrapes found within the Marram Grass at Beacon Ponds where there was a large area of sufficient habitat clear of grass and limited human disturbance, it would suggest that although Ringed Plovers show a preference for vegetation free nesting sites, where necessary they can nest in Marram Grass. This contradicts Conway *et al*. (2019) as excessive vegetation has not led to these Ringed Plover abandoning the site, although there may be a time lag in the abandonment of sites. If these nests were unsuccessful this year due to increased predation within vegetation (Amat and Masero, 2004; Medeiros *et al*., 2012), they may choose an alternative the following year.

Although not explicitly tested within this study, the influence of microvegetation could be important to nest site selection, with instances of both Little Terns and Ringed Plovers nesting within 5cm of small plants (fig. 7). Foppen *et al*. (2006) indicates some shorebird species are dependent on early succession vegetation. Further research on the preference, indifference or avoidance of small vegetation may be necessary, particularly given the likelihood of vegetation succession following Marram Grass clearance (Cooper and Jackson, 2021). However, this is a positive indication that early vegetation succession will not prevent the shorebirds from nesting.

Distance and Orientation from Vegetation when at Rest

Little Terns infrequently rested within 8m of Marram Grass, opting to rest further away, likely because this gives them more opportunity to detect any predators and more time to evade a predator or chase it away from any eggs or young (Rogers *et al*., 2006; Zharikov and Milton, 2009). However, Little Terns did not frequently rest at the furthest possible distances from the Marram Grass (fig. 8), possibly as the threshold of perceived predation risk was exceeded past this point as they already had a clear view of their surroundings.

Ringed Plovers were observed to rest less frequently, possibly because of their lower energy demands in comparison with Little Terns. Despite 10-12m being the most frequent distance at which Ringed Plovers rest there is no obvious relationship with distance from vegetation, until above 17-20m at which the frequency of instances deceases (fig. 13). Furthermore, they did frequently rest within 2m of the Marram Grass; instances of rest between 0-2m being the second most frequent distance. This is possibly because they were often observed foraging at the boundary between the shingle and the Marram Grass and may not move to a different area to rest. This suggests Ringed Plovers do not show a preference for resting further away from vegetation indicating their perceived predation risk is lower, potentially stemming from their larger visual field.

Little Terns showed an increased likelihood to rest in groups at distances above 8m from the Marram Grass (fig. 10). This cannot solely be explained by increased numbers of Little Terns at increased distances (and therefore resting groups by chance) as the relationship with instances of rest does not match at distances above 18m (fig. 8 and 10). Yet it is not clear why this pattern has been found as the need for increased aggregation is lower further away from the vegetation where predation risk is lower and increased vigilance is less important (Rogers *et al*., 2006; Elgar, 1989). Ringed Plovers infrequently rested in groups (whether conspecific or heterospecific), and whether they were in a group or alone had no influence on the distance at which they rested. One explanation is their low population density and low instances of rest, meaning few were resting at the same time and therefore less likely to be resting in proximity to each other.

Throughout the daylight hours studied (7:30 to 16:00), the distance at which the Little Terns rest did not change (fig. 9). However, at dusk when the light levels were decreasing, the Little Terns tended to rest at distances further away from the Marram Grass. This could be as a response to the increased threat of nocturnal terrestrial predators such as the Red Fox, which is increasingly likely to be active as the sun sets (Díaz-Ruiz *et al*., 2016). This adds further weight to the argument that the Little Terns use increased distance from the Marram Grass as a predator avoidance behaviour. Further study into the site selection of roosts and body orientation overnight could support this argument. For Ringed Plovers, the time of day has a limited influence on the distance at which they rest, resting at slightly shorter distances from the Marram Grass from 7:30 to 8:30 (fig. 14), although it is unclear why this is the case.

Both species showed a significant effect of the proportion of their visual sectors on the nearest area of vegetation, being orientated facing away most frequently. This shows a lack of vigilance to threats that could come from the vegetation or that the shorebirds may instead decrease their predation risk in other ways, for example resting away from the Marram Grass. The shorebird species did not change their orientation to cover more of the Marram Grass when at close distances. Increased wariness, leading to higher instances of dreading, will decrease their chances of being predated (Meehan and Nisbet, 2002), which is worth the risk of increased energy expenditure from false alarms. This could negate the need for vigilance of the vegetation when at rest. The time spent at rest at each distance could provide some further insight into the perceived predation risk of the shorebirds and may benefit from further study. The shorebirds may spend less time resting in areas with increased risk of predation as they are less at risk when mobile (Quinn and Cresswell, 2006). Perhaps in more enclosed vegetation vigilance would increase (Metcalfe, 1984).

The mixed model suggests significant effects of orientation to the sun for Little Terns, with no association for Ringed Plovers (table 2). However, the direction of this effect is not clear, as there is no obvious preference of alignment when at rest, with cases of both similar frequencies of terns orientating at very different angles to the sun and large differences in frequency even when the orientation only changes by 10˚ (fig. 12). The small range in the mean temperature for each orientation would suggest thermoregulation is not an important factor, in addition to the temperatures experienced in this study being relatively benign to the adults (13 to 23˚C). Additionally, in July the sun is higher in the sky, therefore reducing the impact changing orientation will have on the thermoregulation of shorebirds (Luskick *et al*., 1978). In more extreme temperatures, the orientation of shorebirds to the sun may become more pronounced as there is greater need for thermoregulation (Ryeland *et al*., 2021). Instead, the primary reason for the orientation of both shorebirds was the wind. The majority of shorebirds rested facing into the wind, with the frequency of both species aligning with the wind increasing with wind speed (fig. 11 and 15). This allowed the shorebirds to sit comfortably, not getting buffeted, as they are orientated in alignment with their aerodynamics (Cestari and De Melo, 2022; Luskick *et al*., 1978). This relationship was stronger in Little Terns.

Management implications

This study provides evidence that, although vegetation does not influence the orientation of terns, the creation of clear areas may allow them to nest and rest at greater distances from the vegetation, potentially improving adult survival rates and improving their breeding success, thereby assisting the prevention of population declines (Wilson *et al*., 2020; Conway *et al*., 2019). This management practice also has the potential to aid other shorebird species.

Despite the potential benefits for shorebird species, the protection of rare and threatened habitat types such as embryo dunes must also be considered in any management plan. At sites exclusively inhabited by Ringed Plovers, management can be less extensive, with less vegetation removal as the distance from vegetation is less important. For Little Terns vegetation clearance in patches will likely be less effective than fewer larger areas of clearance as this allows greater distances from vegetation and enables the terns to nest in closer proximity to their neighbours. Vegetation should never be cleared completely, as sites with no vegetation are avoided (Ratcliffe *et al*., 2008). Furthermore, vegetation could be built up in places to provide greater shelter to scrapes from the prevailing winds from the sea.

Limitations

As Little Terns are a Schedule 1 species, restraint was necessary when photographing their scrapes (despite acting under a licence), reducing the extent of photographic analysis. Due to the time pressures during the colony walk-throughs, it was not possible to measure all the scrapes within the colony. Mapping of the most important aspects of the site prior to the breeding season would have increased accuracy from GIS and established the water-level of the lagoon (although this did drop throughout the study). Furthermore, early measurement of different features would have increased the accuracy of the measurements by eye from across the lagoon during the study. Without this, there may be some inaccuracy in the distances at which the shorebirds rested from the vegetation. Additionally, association with the water level of the lagoon was not tested for within this study, but in some cases can influence nest site selection (Blow, 2021).

Acknowledgements

I would like to give thanks to my supervisor Dr Rupert Quinnell for his invaluable support and advice throughout this study. I would also like to thank the wardens, volunteers, the Easington Little Tern committee, and everyone associated with the protection of the shorebirds at Beacon Ponds for their advice, support and because without their efforts, there would be no colony to study. Special mention goes to Liam Andrews, Richard Boon, Josh Brown, Harry Coghill, Paul Collins, Eva Finney, Erin Gold, Rob Hunton, Matt Livsey, Jacob Spinks and Tom Wright. Thank you to Oliver Blow for providing the data on the Beacon Ponds colony from 2021. Thanks to Josh Brown and Tom Wright for providing the photographs on the title page.

Bibliography

Amat, J.A. and Masero, J.A. 2004. Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. *Animal Behaviour*. **67**(2), pp.293–300.

Avery, M 1991. Little Tern. In C. Loyd, M. L. Tasker, and K. Partridge (Eds.). *The Status of seabirds in Britain and Ireland*, pp. 234-242. A&C Black.

Blow, O. 2021. Factors Effecting Nest Site Selection and Predator Visitation of Little Terns (*Sternula albifrons*) at Beacon Ponds Reserve. MSc Dissertation, Leeds University.

Cabot, D. and Nisbet, I. 2013. Terns. Collins New Naturalist Library, Book 123. London, UK: Harper Collins.

Calladine, J., Border, J., O'Connell, P. and Wilson, M. 2022. Modelling important areas for breeding waders as a tool to target conservation and minimise conflicts with land use change. *Journal for Nature Conservation*. **70**, p.126267.

Cantlay, J.C., Portugal, S.J. and Martin, G.R. 2019. Visual fields and foraging ecology of Blacksmith Lapwings *Vanellus armatus*. *Ibis*. **161**(4), pp.895–900.

Cestari, C. and De Melo, C. 2022. Shorebirds adjust resting orientation in response to solar radiation and wind speed. *Austral Ecology*. **47**(4), pp.765–769.

Charlton, P. 2003. Habitat creation for little terns. In R. I. Allcorn (Ed.). *Proceedings of a symposium on Little Terns Sterna albifrons* (pp. 34-41). RSPB Research Report 8.

Conway, G.J., Austin, G.E., Handschuh, M., Drewitt, A.L. and Burton, N.H. 2019. Breeding populations of Little Ringed Plover *Charadrius dubius* and Ringed Plover *Charadrius hiaticula* in the United Kingdom in 2007. *Bird Study*. **66**(1), pp.22–31.

Cook, A.S., Burton, N.H., Dodd, S.G., Foster, S., Pell, R.J., Ward, R.M., Wright, L.J. and Robinson, R.A. 2021. Temperature and density influence survival in a rapidly declining migratory shorebird. *Biological Conservation*. **260**, p.109198.

Coombes, E.G., Jones, A.P. and Sutherland, W.J. 2008. The biodiversity implications of changes in coastal tourism due to climate change. *Environmental Conservation*. **35**(4), pp.319–330.

Cunningham, S.J., Corfield, J.R., Iwaniuk, A.N., Castro, I., Alley, M.R., Birkhead, T.R. and Parsons, S. 2013. The anatomy of the bill tip of kiwi and associated somatosensory regions of the brain: comparisons with shorebirds. *PLoS one*. **8**(11), p.e80036.

Cunningham, J.A., Kesler, D.C. and Lanctot, R.B. 2016. Habitat and social factors influence nest-site selection in Arctic-breeding shorebirds. *The Auk: Ornithological Advances*. **133**(3), pp.364–377.

Díaz-Ruiz, F., Caro, J., Delibes-Mateos, M., Arroyo, B. and Ferreras, P. 2016. Drivers of red fox (*Vulpes vulpes*) daily activity: prey availability, human disturbance or habitat structure? *Journal of Zoology*. **298**(2), pp.128–138.

Eaton, M.A., Brown, A.F., Noble, D.G., Musgrove, A.J., Hearn, R.D., Aebischer, N.J., Gibbons, D.W., Evans, A. and Gregory, R.D. 2009. Birds of conservation concern 3. *British Birds*. **102**(45), pp.296–341.

Eaton, M.A. 2022. Rare breeding birds in the UK in 2020. *British Birds*. **115**, pp.623–686.

Elgar, M.A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews*. **64**(1), pp.13–33.

Erwin, R.M. 1989. Responses to human intruders by birds nesting in colonies: experimental results and management guidelines. *Colonial Waterbirds*., pp.104–108.

Evans, J.C., Votier, S.C. and Dall, S.R. 2016. Information use in colonial living. *Biological reviews*. **91**(3), pp.658–672.

Foppen, R.P., Majoor, F.A., Willems, F.J., Meininger, P.L., Van Houwelingen, G.C. and Wolf, P.A. 2006. Survival and emigration rates in Kentish *Charadrius alexandrinus* and Ringed Plovers *Ch. hiaticula* in the Delta area, SW-Netherlands. *ARDEA-WAGENINGEN-*. **94**(2), p.159.

Fortin, D., Larochelle, J. and Gauthier, G. 2000. The effect of wind, radiation and body orientation on the thermal environment of greater snow goose goslings. *Journal of Thermal Biology*. **25**(3), pp.227–238.

Fraser, J.D., Catlin, D.H., Colwell, M.A. and Haig, S.M. 2019. Habitat ecology and conservation of Charadrius plovers. *The population ecology and conservation of Charadrius plovers*. (52), pp.217–243.

Google Earth Version 9.194.0.0 (2021) *Beacon Ponds, Kilnsea, 53.632604, 0.1340056*. [online]. Available from: https://earth.google.com/web [Accessed 3rd September 2023].

Gupta, S., Agrawal, A. and Saxena, K. 2022. Defense Strategies in Birds of Charadriidae Family *In*: *Proceedings of the Zoological Society*. Springer, pp.1–18.

Hesp, P. 2002. Foredunes and blowouts: initiation, geomorphology and dynamics. *Geomorphology*. **48**(1–3), pp.245–268.

Hitchcock, C.L. and Gratto-Trevor, C. 1997. Diagnosing a shorebird local population decline with a stage-structured population model. *Ecology*. **78**(2), pp.522–534.

Humphreys, E.M., Austin, G.E., Frost, T.M., Mellan, H.J., Boersch-Supan, P., Burton, N.H.K. and Balmer, D.E. 2020. Wader populations on the United Kingdom's open coast: results of the 2015/16 Non-Estuarine Waterbird Survey (NEWS-III) and a review of population trends. *Bird Study*. **67**(3), pp.371–384.

Jeong, K.-S., Jang, J.-D., Kim, D.-K. and Joo, G.-J. 2011. Waterfowls habitat modeling: Simulation of nest site selection for the migratory Little Tern (*Sterna albifrons*) in the Nakdong estuary. *Ecological modelling*. **222**(17), pp.3149–3156.

JNCC. 2016.Seabird Population Trends and Causes of Change: 1986-2015. Report, Joint Nature Conservation Committee.

Jørgensen, P.S., Kristensen, M.W. and Egevang, C. 2007. Red Phalarope *Phalaropus fulicarius* and Red-necked Phalarope *Phalaropus lobatus* behavioural response to Arctic Tern *Sterna paradisaea* colonial alarms. *Dansk Oritologisk Forenings Tidsskrift*. **101**, pp.73–78.

Koleček, Jaroslav, et al. 2021. "Global Population Trends in Shorebirds: Migratory Behaviour Makes Species at Risk." The Science of Nature. **108**(2), 2021, p. 9.

Kotliar, N.B. and Burger, J. 1984. The use of decoys to attract Least Terns (*Sterna antillarum*) to abandoned colony sites in New Jersey. *Colonial Waterbirds*., pp.134–138.

Lopes, C.S., Ramos, J.A. and Paiva, V.H. 2015. Changes in vegetation cover explain shifts of colony sites by little terns (*Sternula albifrons*) in Coastal Portugal. *Waterbirds*. **38**(3), pp.260–268.

Luskick, S., Battersby, B. and Kelty, M. 1978. Behavioral thermoregulation: orientation toward the sun in herring gulls. *Science*. **200**(4337), pp.81–83.

Martin, G.R. 2012. Through birds' eyes: insights into avian sensory ecology. *Journal of Ornithology*. **153**(1), pp.23–48.

Martin, G.R., Jarrett, N. and Williams, M. 2007. Visual fields in Blue Ducks *Hymenolaimus malacorhynchos* and Pink-eared Ducks *Malacorhynchus membranaceus*: visual and tactile foraging. *Ibis*. **149**(1), pp.112–120.

Martin, G.R. and Piersma, T. 2009. Vision and touch in relation to foraging and predator detection: insightful contrasts between a plover and a sandpiper. *Proceedings of the Royal Society B: Biological Sciences*. **276**(1656), pp.437–445.

Mitchell, I., Daunt, F., Frederiksen, M. and Wade, K. 2020. Impacts of climate change on seabirds, relevant to the coastal and marine environment around the UK.

Medeiros, R., Ramos, J.A., Pedro, P. and Thomas, R.J. 2012. Reproductive consequences of nest site selection by Little Terns breeding on sandy beaches. *Waterbirds*. **35**(4), pp.512–524.

Meehan, T.D. and Nisbet, I.C. 2002. Nest attentiveness in common terns threatened by a model predator. *Waterbirds*. **25**(3), pp.278–284.

Metcalfe, N.B. 1984. The effects of habitat on the vigilance of shorebirds: is visibility important? *Animal Behaviour*. **32**(4), pp.981–985.

Met Office. 2023. *Met Office Weather Forecast* (version 2.31.0) [Mobile app]. [Accessed 13th June 2023].

Moore, P. and Davis, A. 2004. Marram grass *Ammophila arenaria* removal and dune restoration to enhance nesting habitat of Chatham Island oystercatcher *Haematopus chathamensis*, Chatham Islands, New Zealand. *Conservation evidence*. **1**, pp.8–9.

O'Connell, D.P., Power, A., Doyle, S. and Newton, S.F. 2014. Nest movement by Little Terns *Sternula albifrons* and Ringed Plovers *Charadrius hiaticula* in response to inundation by high tides. *Irish Birds*. **10**(1), pp.19–22.

Pickerell, G., 2004. Little tern *Sterna albifrons*. *Seabird Populations of Britain and Ireland, Poyer, London*, pp.339-449.

Pienkowski, M.W. 1984. Breeding biology and population dynamics of Ringed plovers Charadrius hiaticula in Britain and Greenland: nest-predation as a possible factor limiting distribution and timing of breeding. *Journal of Zoology*. **202**(1), pp.83–114.

Pienkowski, M.W. 1983. Changes in the foraging pattern of plovers in relation to environmental factors. *Animal behaviour*. **31**(1), pp.244–264.

Pienkowski, M.W. 1982. Diet and energy intake of Grey and Ringed plovers, *Pluvialis squatarola* and *Charadrius hiaticula*, in the non-breeding season. *Journal of Zoology*. **197**(4), pp.511–549.

Piersma, T., Boere, G.C., Galbraith, C.A. and Stroud, D.A. 2006. Migration in the balance: tight ecological margins and the changing fortunes of shorebird populations. *Waterbirds around the world*., pp.74–80.

Piersma, T. and Baker, A.J. 2000. Life history characteristics and the conservation of migratory shorebirds *In*: *Behaviour and conservation*. Cambridge University Press, pp.105–124.

Piersma, T. and Lindström, Å. 2004. Migrating shorebirds as integrative sentinels of global environmental change. *Ibis*. **146**, pp.61–69.

Power, A., Newton, S., Burke, B., Tierney, D. and O'Connor, I. 2023. *Seabirds*. Marine Institute.

QGIS Development Team. 2023. QGIS Geographic Information System (version 3.28.2) QGIS Association. http://qgis.org

Quinn, J.L. and Cresswell, W. 2006. Testing domains of danger in the selfish herd: sparrowhawks target widely spaced redshanks in flocks. *Proceedings of the Royal Society B: Biological Sciences*. **273**(1600), pp.2521–2526.

Ratcliffe, N., Schmitt, S., Mayo, A., Tratalos, J. and Drewitt, A. 2008. Colony habitat selection by Little Terns *Sternula albifrons* in East Anglia: implications for coastal management. *Seabird*. **21**, pp.55–63.

Rees, S., Angus, S., Creer, J., Lewis, H., Mills, R., 2019. Guidelines for the selection of biological SSSIs. Part 2 Detailed guidelines for Habitats and Species. Chapter 1a Coastlands (coastal saltmarsh, sand dune, machair, shingle, and maritime cliff and slopes, habitats).

Rogers, D.I., Piersma, T. and Hassell, C.J. 2006. Roost availability may constrain shorebird distribution: exploring the energetic costs of roosting and disturbance around a tropical bay. *Biological Conservation*. **133**(2), pp.225–235.

RStudio Team (2023). RStudio (version 2022.07.02+576). Integrated Development for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/.

Ryeland, J., Weston, M.A. and Symonds, M.R. 2021. The importance of wetland margin microhabitat mosaics; the case of shorebirds and thermoregulation. *Journal of Applied Ecology*. **58**(2), pp.382–391.

Skullsite. 2017. *Bird Skull Collection*. [Online] [Accessed 1st August 2023] Available from: https://skullsite.com/.

Stanbury, A., Eaton, M., Aebischer, N., Balmer, D., Brown, A., Douse, A., Lindley, P., McCulloch, N., Noble, D. and Win, I. 2021. The status of our bird. *British Birds*. **114**, pp.723–747.

Thaxter, C.B., Lascelles, B., Sugar, K., Cook, A.S., Roos, S., Bolton, M., Langston, R.H. and Burton, N.H. 2012. Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. *Biological Conservation*. **156**, pp.53–61.

Timmis, A.D., Symonds, M.R. and Weston, M.A. 2022. The influence of resting posture and orientation on alertness and escape in shorebirds. *Journal of Ornithology*. **163**(2), pp.509–521.

Tipling, D. 2011. Bird photography—A new code of practice. *British Birds*. **104**(4), p.223.

Tratalos, J.A., Jones, A.P., Showler, D.A., Gill, J.A., Bateman, I.J., Sugden, R., Watkinson, A.R. and Sutherland, W.J. 2021. Regional models of the influence of human disturbance and habitat quality on the distribution of breeding territories of common ringed plover *Charadrius hiaticula* and Eurasian oystercatcher *Haematopus ostralegus*. *Global Ecology and Conservation*. **28**, p.e01640.

Walters, J.R. 1990. Anti-predatory behavior of lapwings: field evidence of discriminative abilities. *The Wilson Bulletin*., pp.49–70.

What3Words. 2023. *What3words: Navigation & Maps* (version 4.28) [Mobile app]. [Accessed 29th June 2023].

Wiersma, P., Kirwan, G.M., Boesman, P. 2020. Common Ringed Plover (*Charadrius hiaticula*). In Handbook of the Birds of the World Alive. ed. J. del Hoyo, Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. Lynx Edicions, Barcelona.

Wilson, L.J., Rendell-Read, S., Lock, L., Drewitt, A.L. and Bolton, M. 2020. Effectiveness of a five-year project of intensive, regional-scale, coordinated management for Little Terns *Sternula albifrons* across the major UK colonies. *Journal for Nature Conservation*. **53**, p.125779.

Woodward, I., Aebischer, N., Burnell, D., Eaton, M., Frost, T., Hall, C., Stroud, D.A. and Noble, D. 2020. Population estimates of birds in Great Britain and the United Kingdom. *Br. Birds*. **113**, pp.69–104.

Zharikov, Y. and Milton, D.A. 2009. Valuing coastal habitats: predicting high-tide roosts of non-breeding migratory shorebirds from landscape composition. *Emu-Austral Ornithology*. **109**(2), pp.107–120.