

# 1 Regional models of the influence of human disturbance and habitat quality 2 on the distribution of breeding territories of common ringed plover

## 3 *Charadrius hiaticula* and Eurasian oystercatcher *Haematopus ostralegus*

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17  
18 Keywords: wader shorebird nesting coast beach visitor

### 19 20 **Abstract**

21 We estimated the influence of human disturbance and environmental factors on territory  
22 establishment in common ringed plovers *Charadrius hiaticula* and Eurasian oystercatchers  
23 *Haematopus ostralegus*, to inform the conservation of these species. We examined a 212 km stretch  
24 of coastline in the United Kingdom in 2003, mapping all breeding pairs of both study species, as well  
25 as the environmental characteristics of beaches and locations of visitors on the beach, the latter  
26 measured by filming from a light aircraft. Of the 1,003 200m sections of beach surveyed, 183  
27 contained ringed plover territories (267 breeding pairs) and 117 contained oystercatcher territories  
28 (226 breeding pairs). 38,634 human visitors to the beach were mapped from three flights. Population  
29 densities of both ringed plovers and oystercatchers were lower in locations with high visitor numbers,  
30 even when accounting for the influence of the environmental characteristics of the beach. The two  
31 bird species showed similar rates of territory establishment at very low visitor rates, but  
32 oystercatchers showed a stronger negative response when visitor rates reached higher levels. Binary  
33 logistic regression models were used to identify areas where the birds would benefit most from

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reductions in the number of visitors and we illustrate how this information could be used to inform management around sites otherwise favourable for territory establishment.

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## 1. Introduction

Here we study the effect of disturbance on the location of breeding territories in two wading bird species, the common ringed plover, *Charadrius hiaticula* and Eurasian oystercatcher, *Haematopus ostralegus*, which we will generally refer to simply as ‘ringed plover’ and ‘oystercatcher’, respectively. Information on the behaviour and ecology of these species can be found in Thies et al. (2018), Hockey et al. (2020), Wiersma et al. (2020), Allen et al., 2019, Cramp (1983), and Ens and Underhill, 2014).

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Human recreational activities are known to affect nesting birds through egg losses from trampling on nests, abandonment of nests, scattering of chicks, increased predation and energy expenditure (Navedo & Herrera, 2012, Mallord et al. 2007, McGowan & Simons, 2006, Anderson, 1988, Gillet et al., 1975, Safina and Burger, 1983, Carney and Sydeman, 1999, Finney et al., 2004). In addition to these direct effects, population regulation may arise when birds choose to breed in poorer quality but less disturbed sites, or decide not to breed at all, in the face of human disturbance (Liley and Sutherland, 2006). Thomas (2010) found that human disturbance influenced territory choice in American oystercatchers *Haematopus palliatus*.

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In the United Kingdom (UK), ringed plovers are a largely coastal species while a large proportion of the oystercatcher population breed along the coast (Conway et al., 2019, van de Pol et al., 2014). As both species breed on sand and shingle beaches which are also attractive to people, they are exposed to human disturbance, including trampling on nests and pursuit of chicks and adults by dogs. Liley and Sutherland (2006) showed that, over a 9 km stretch of UK coastline, ringed plovers bred less successfully when exposed to disturbance by beach visitors, and population declines in this species have been attributed to human disturbance (Brown and Grice 2005, Pienkowski, 2004). Human

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recreation has also been shown to be associated with reduced breeding success in Eurasian and other oystercatcher species (Tjorve and Tjorve, 2010), and Ens and Underhill (2014) suggest that increased human use of the coastal zone, combined with other possible effects of climate change such as increased risk of nest flooding and loss of wetlands, may threaten the conservation of oystercatcher species. UK breeding populations of ringed plover have declined in recent decades, from a conservative estimate of approximately 8,400 pairs in 1984 to 4,070 in 2007 (Conway et al., 2019) and it has been included in the UK red list as a species of high conservation concern (Eaton et al., 2015). The oystercatcher has undergone considerable Europe-wide decline in recent decades (van de Pol et al., 2014), and has been classified as 'Near Threatened' globally (IUCN, 2020). The UK has also seen a decline in oystercatcher populations since 1997, although locally there have been population increases, especially in inland sites in England (Woodward, 2020).

Previous studies of the effects of disturbance on the location of breeding territories in birds have usually been based on observations at small study sites but have not considered the phenomenon at a more regional level. One reason for this is the difficulty of obtaining information on human disturbance over large areas. The number of visitors in a given location will vary considerably with temporal factors such as time of day, time of year and day of the week, as well as weather phenomena such as temperature, rainfall and sunshine (Kubo et al., 2020, Tratalos et al., 2013, Coombes and Jones, 2010, Silva, 2008, Dwyer, 1988). For this reason, visitor numbers should ideally be measured across the entire study area simultaneously to obtain an accurate relative measure of disturbance between sites. Another consideration is that environmental factors which influence territory choice might be correlated with human disturbance, as people may find the same places attractive for recreation as birds do for establishing territories, and this is usually not taken into account in disturbance studies.

With these considerations in mind, we acquired information on visitor numbers using aerial videography from a light aircraft, filming the entire coastline of the counties of Norfolk and Suffolk in

1 86 Eastern England in a single flight. This coastline hosts some of the UK's most popular tourist  
2 87 destinations, spans a wide variety of beach types and levels of use by tourists, and is also an important  
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4 88 breeding area for both our study species, which establish breeding territories there during the spring  
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7 89 and summer, when human visitor numbers are also relatively high. It is therefore an ideal study area  
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9 90 to examine the way in which the density of human visitors affects the location of breeding territories.  
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14 92 Further to estimating the effects of habitat and disturbance on the location of ringed plover and  
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16 93 oystercatcher territories, we show how models of these effects can be used in conjunction with site  
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18 94 specific information to distinguish areas where management to reduce visitor numbers would be most  
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21 95 likely to bring about increases in breeding populations of these bird species. Our study is particularly  
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23 96 pertinent in view of proposals to improve visitor access to our study area as sections of the England  
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26 97 Coastal Path, which aims to make the whole coastline of England accessible to walkers. Approximately  
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28 98 half of the study coastline has been included since the fieldwork for this study was conducted, with  
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31 99 the other half currently at the planning stage (Natural England, 2020).  
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## 36 37 38 102 **2. Methods**

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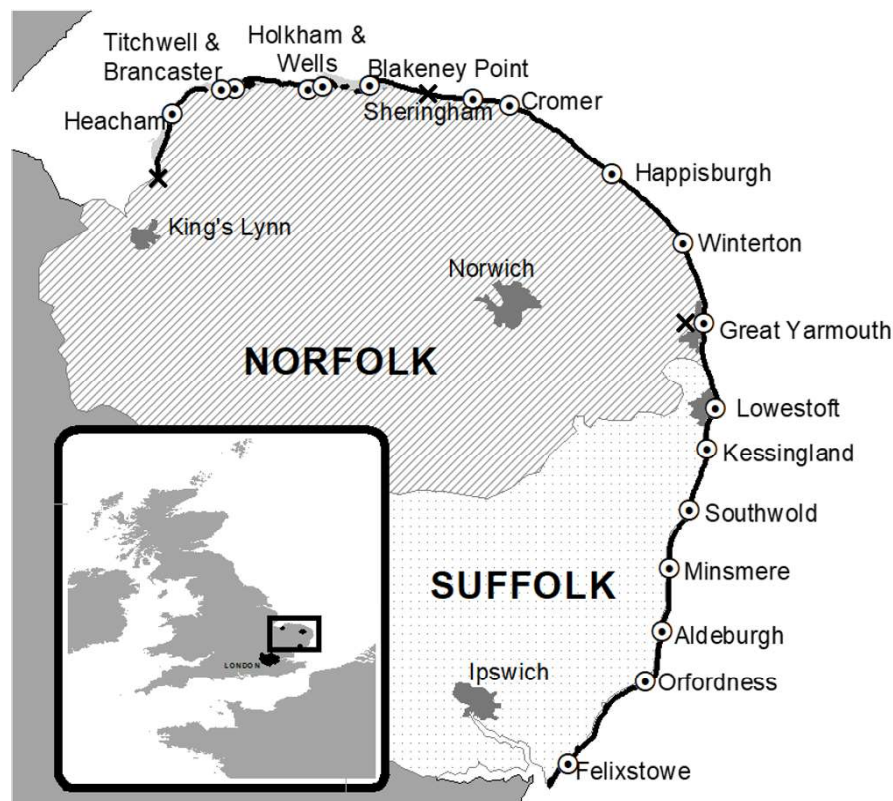
### 41 42 104 *2.1 Beach surveys to obtain breeding bird data*

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47 106 Our study area was composed of all habitats suitable for territory establishment by our study species  
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49 107 along the coastline of Norfolk and Suffolk, UK. It was therefore restricted to sand and shingle beaches,  
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52 108 amounting to 83 % of the total coastline of these counties. This coast contains a number of protected  
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54 109 sites of significant conservation value and is a nationally important breeding area for both species.  
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111 To obtain data on the location of bird territories, these habitats were walked between early April and  
 112 mid-June, 2003; this time period was chosen on the basis of published information on the breeding  
 113 behaviour of these species in the study area and elsewhere (Cramp & Simmons, 1983, Liley, 1999,  
 114 Prater, 1974, 1976, Rooney & Eve, 1993). By this time individuals, even if not yet commencing nesting,  
 115 would still exhibit behaviour indicative of territoriality; however, to minimise temporal bias, three  
 116 starting points at approximately equal intervals along the coast were selected. Sections were then  
 117 walked alternately from these points. Fig. 1 shows the coastline surveyed.



131 **Figure 1. Map of the study area, showing the coastline surveyed (black line), key locations,**  
 132 **the start point of walked sections (black crosses) and (inset) the location of the study area**  
 133 **within the UK.**

137 Each day, a different section of beach several kilometres in length was surveyed. The locations of all  
 138 breeding pairs of ringed plovers and oystercatchers were recorded using a GPS (Global Positioning  
 139 System), both on the outward and the return journey, to minimise the probability of pairs being

140 missed. Breeding was determined on the basis of indications of the presence of a nest (a scrape with  
141 eggs, an incubating adult, an adult distraction display or the presence of young) or on territorial  
142 behaviour, which included slow wing beat butterfly flights in either species, as well as, in  
143 oystercatchers, piping displays in ground confrontations with neighbouring and intruding birds of the  
144 same species, alarm calling and mobbing and, in ringed plovers, agitated behaviour (e.g. head-  
145 bobbing), sometimes with breast 'puffing' and tail fanning (see Cramp et al., 1983) . Single birds were  
146 included if they behaved in a manner indicative of territoriality, as one adult of a pair might be absent  
147 if feeding elsewhere in cases where the feeding territory was not within the nesting territory, but  
148 flocks were not.

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150 At beaches where large expanses of mud or sand are exposed at low tide, birds may move some  
151 distance from the territory to feed. Localities with a very wide intertidal zone were therefore surveyed  
152 at least once during high tide or on a rising tide approaching high tide. No surveys were undertaken in  
153 winds exceeding a moderate breeze (Beaufort Scale 4) or during periods of prolonged rain, due to  
154 poor visibility and to the reduce the risk of chilling of eggs or young if incubating or brooding adults  
155 were disturbed. Access was not permitted during the breeding season to three localities: the tern  
156 colonies located at the western tips of i) Scolt Head Island and ii) Blakeney Point, covering stretches  
157 of beach c. 500 m and 1 km in length respectively, and iii) Orford Ness Nature Reserve - a 16 km shingle  
158 spit. At these localities, bird data were provided by Natural England, the National Trust and the  
159 Landguard Bird Observatory. At other localities at which sections of beach had been roped to reduce  
160 disturbance to breeding terns and waders, suitable vantage points around their periphery allowed  
161 adequate coverage to survey for ringed plovers and oystercatchers. At a few sites, where bird breeding  
162 densities were high, a second visit was made within three days of the first, and a repeat bird survey  
163 was undertaken. In mapping bird territories we have assumed that any pairs changing nest location  
164 during the study period, e.g. as a result of failed breeding attempts, would have done so within their

165 original territory; however, it is possible that there may have been some cases of territory movement  
166 between beach sections

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## 169 *2.2 Beach characteristic data*

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171 During the bird surveys, the characteristics of the beach from the high water mark to the back of the  
172 beach (e.g. backing cliff, sea wall or sand dunes) were also recorded at 200m intervals. The following  
173 data were estimated by eye for each 200m section as percentage cover estimates: vegetation, tideline  
174 debris, sand (particles < 2 mm diameter), fine shingle (2-10 mm), medium shingle (10 - 50 mm), coarse  
175 shingle (50 - 200 mm) and rocks (>200 mm). In those areas where access was restricted (described in  
176 the previous section) beach characteristic data were collected immediately before or immediately  
177 after the breeding season. The geographical coordinates of the approximate centroid of each 200m  
178 section were also recorded. This enabled us to map the data in a Geographical Information System  
179 (GIS) (ArcView 3.2, Esri Inc), and use Ordnance Survey data and aerial photographs to calculate the  
180 following additional variables for each section: the presence or absence of dunes, cliffs and human  
181 populated areas, the width, in metres, of the beach to mean high water and to mean low water (at  
182 spring tides), and the width of the beach between high and low water.

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## 185 *2.3 Data on visitor numbers*

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187 To map the locations of human visitors on the beach, the coastlines of Norfolk and Suffolk were  
188 filmed, from an altitude of approximately 150m, using a Canon XL1 digital video camera, from a  
189 Cessna 152 light aircraft, on three separate occasions – Saturday 12th April, Saturday 21st June and  
190 Sunday 24th August 2003. All three surveys took place on sunny days between 12:30 and 16:00,

191 when the tide was at approximately mid phase. Our aim was to film on several occasions when a  
192 large number of visitors could be counted, to reduce the effect of stochasticity on our index of visitor  
193 numbers, and taking into account the fact that the way in which beach visitors distributed  
194 themselves along the beach was largely dependent on distance to access points rather than the time  
195 of year (Tratalos et al., 2013). The tide needed to be at approximately mid phase as some beaches  
196 would be so narrow as to deter visitors at high tide and others would be so wide at low tide that  
197 counting of all visitors would not have been possible. We therefore added the date in August, even  
198 though chicks of our study species would be less vulnerable to disturbance by that point, as flights  
199 needed to be planned in advance and weekends with a reliable forecast of warm sunny weather,  
200 and with the tide at mid phase, were very few during spring and early summer of the study period.  
201 Based on our observations of human activity across the study area, we believe that human  
202 disturbance due to a range of human behaviours (walking, picnicking, sunbathing, kite surfing etc.)  
203 would be covered by our choice of three sunny weekend afternoons during the spring and summer.  
204 The entire area of the beach was filmed, which in the case of very wide beaches involved filming the  
205 foreshore and rear of the beach in separate passes.  
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207 The April flight covered 164.8 km, consisting of the entire Norfolk coast and as far south as Minsmere  
208 RSPB reserve in Suffolk; the June flight covered 198 km, consisting of the entire Norfolk coast and  
209 along the Suffolk coast as far as Orfordness; and the August flight covered 211 km, consisting of the  
210 whole of both the Norfolk and Suffolk coastlines, with the exception of a 1 km section at Holkham in  
211 North Norfolk (see Fig. 1). The locations of all visitors to the beach shown on the videos were manually  
212 digitised using georeferenced aerial photos in the GIS, to map human visitors in their correct location.  
213 Data derived from these videos are also described and analysed in Coombes et al. (2009a, 2009b) and  
214 in Tratalos et al. (2013).

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1 216 Because none of the three videos individually covered the entire study area, but they did do so when  
2 217 they were combined, an estimate of the total numbers of visitors for each 200m beach section across  
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4 218 the three filming periods was calculated, extrapolating on the assumption that the number of visitors  
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7 219 between the three periods would differ by a constant factor throughout the entire coastline. In these  
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9 220 extrapolations, beach sections missing data for the April flight were calculated by multiplying the  
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11 221 August data by the ratio between the mean values for August and April across sections captured on  
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13 222 both those flight dates, and those sections missing data for June or August were likewise calculated  
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15 223 using same approach on the mean values for August and June across sections captured in both of  
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17 224 those months. These data were then then divided by their mean value across all sections, resulting in  
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19 225 a visitor index with a mean of 1.  
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#### 26 27 28 228 *2.4 GIS data processing and statistical analysis*

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33 230 ArcView 3.2 and ArcMap 10.6 were used for GIS processing. The number of people, ringed plover and  
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35 231 oystercatcher territories falling within each of the 200m sections was calculated and matched to the  
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37 232 beach characteristic data for each section in the GIS. The degree of collinearity was measured i)  
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39 233 amongst the number of human visitors per section for each of the three flights and ii) amongst the  
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41 234 beach characteristic and visitor index variables, using Pearson correlation for the former (r) and  
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43 235 Spearman Rank correlation (Rs) for the latter.  
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49 237 The statistical analyses were done in SAS 9.4. Binary logistic regression (Hosmer et al., 2013) was used  
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51 238 to assess the relationship between the presence or absence of ringed plover and oystercatcher  
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53 239 territories in each 200m section of beach and the number of visitors on the beach observed in the  
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55 240 videos, first in simple logistic models and then in multivariable models including the beach  
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2 242 characteristic data as additional predictor variables. In cases where two or more variables were highly  
3 correlated with one another we choose the one that resulted in the greatest reduction in the AIC.

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7 244 In these models, the three beach width variables were log transformed, on the assumption that the  
8 attractiveness to the birds of each extra metre of beach could be expected to decline as the overall  
9 245 beach width increased. For distance to high water we added 1 before transformation to avoid  
10 calculation over zero values in a small number of beach sections (N = 21). The visitor index was also  
11 246 recalculated using a square root transformation for the number of visitors in each section, in order to  
12 247 examine whether our study species were more sensitive to increases in disturbance when visitor  
13 248 numbers were relatively low (the existence of zero values meant that a direct log transformation could  
14 249 not be used for these data). Our general approach was to use forward stepwise procedures to build  
15 250 up a model using environmental variables only, to then examine the effect of incorporating visitor  
16 251 numbers and finally to check that these models were stable if environmental variables which had  
17 252 previously been rejected were reintroduced. We were careful to make sure that no important beach  
18 253 characteristics were missing, to ensure that any association found with visitor numbers was not due  
19 254 to collinearity with a missing environmental variable.  
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41 258 For both the ringed plover and oystercatcher models, the predicted values from the models were  
42 259 calculated for all 200m beach sections after setting visitors numbers to zero, to examine the  
43 260 predicated effect that a removal of visitors would have on territory establishment in each section of  
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### 47 264 **3. Results**

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#### 49 266 *3.1 Summary of data sets and simple logistic regressions*

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2 268 38,634 visitors on the beach were mapped from the three flights: 1,593 in April, 11,466 in June and  
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4 269 25,575 in August. There were pronounced peaks in visitor numbers at intervals along the coastline,  
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7 270 with 19 of the 1,003 beach sections experiencing over 10 times the average number of visitors and  
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9 271 231 sections hosting none; visitors per beach section were strongly correlated between all three  
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11 272 filming episodes ( $r$ : April vs. June: 0.68; April vs. August: 0.62; June vs. August: 0.83). The mean number  
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13 273 of visitors for each flight equated to c. 9.7 people per kilometre in April, 58.9 in June and 121.2 in  
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15 274 August. These figures corresponded closely to those for the average number of people per c. 200m  
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17 275 section from the extrapolated data used to calculate the normalised visitor index (39.1 people per  
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19 276 200m section across the three dates).  
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26 278 The predictor variables for the statistical analyses, consisting of the visitor index and the beach  
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28 279 characteristic data for each section, were generally not strongly correlated with one another, except  
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30 280 in cases where they measured proportions of the same entity (e.g.  $R_s = -0.95$  for sand vs medium  
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32 281 shingle). The only other cases of  $r$  lower than -0.40 or higher than 0.40 were % vegetation on beach  
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34 282 vs. distance to high water (0.44) and dunes vs. % medium shingle ( $R_s = -0.41$ ) and % sand ( $R_s = 0.41$ ).  
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36 283 The visitor index was generally only weakly correlated with the other dependent variables, with the  
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38 284 most notable correlates being the presence of human populated areas at the back of the beach ( $R_s =$   
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40 285 0.45), % vegetation on the beach ( $R_s = -0.36$ ), % sand ( $R_s = 0.27$ ), and % medium shingle ( $R_s = -0.27$ ).  
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43 286 A correlogram of these variables can be found in the supplementary material.  
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49 288 183 beach sections contained ringed plover territories (266 breeding pairs), and 117 contained  
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51 289 oystercatcher territories (223 pairs). Occupation of territories was associated with lower than average  
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53 290 visitor numbers, for both ringed plovers and oystercatchers (ringed plovers: mean visitor index for  
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55 291 occupied sections: 0.30, for unoccupied sections: 1.16; oystercatchers: for occupied sections: 0.13, for  
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57 292 unoccupied sections: 1.11).  
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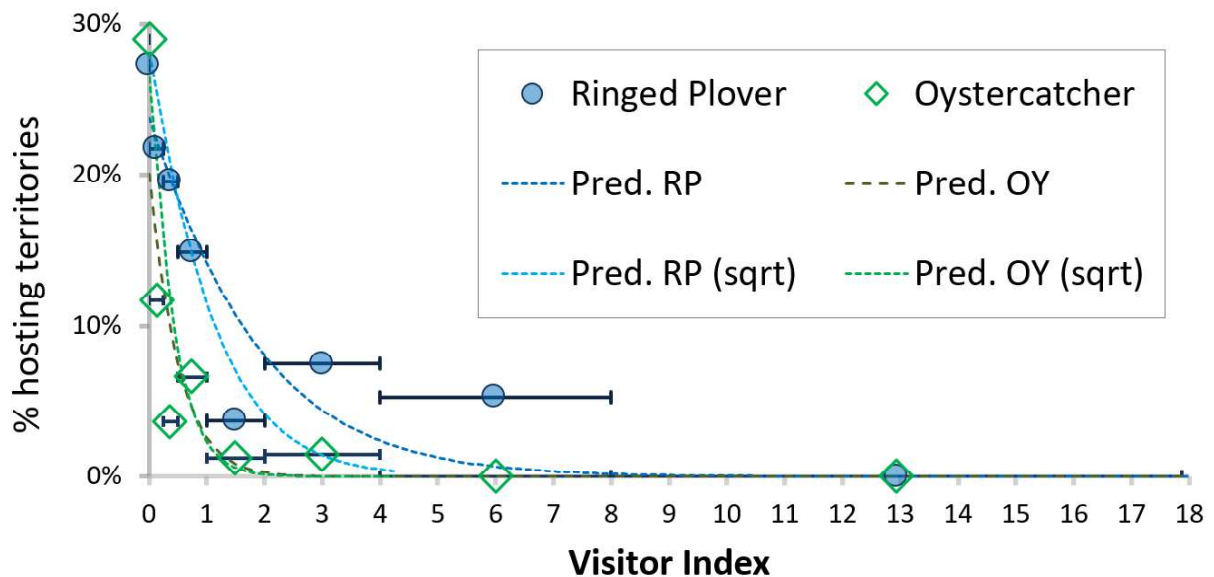
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The functional form of the relationship between visitors and presence/absence of bird territories differed between the species. Where no visitors were recorded, there was approximately the same probability that a 200m section would be occupied by a ringed plover (27.3%) as by an oystercatcher (29.0%) territory. However, oystercatchers showed a more sensitive response to increasing visitor numbers. Between the lowest non-zero visitor index (0.026) and 1 (i.e. between 2.6% of the mean number of visitors per section and the mean number), 19.7% of sections were occupied by ringed plovers and 8.5 % by oystercatchers; at visitor indices between 1 and 4 (i.e. between the mean number of visitors per section and four times the mean number), 5.4% were occupied by ringed plovers but only 1.4 % by oystercatchers, whereas 5.3% had ringed plover territories at visitor indices between 4 and 8, but none had oystercatchers. At higher visitor numbers (index  $\geq 8$ ) neither species had established territories (Fig. 2). No oystercatcher territories occurred in the 91 sections of beach with a visitor index  $> 2.8$  and no ringed plover territories in the 49 sections with a visitor index  $> 5.5$ .



**Figure 2. Percentage of 200m beach sections hosting Ringed Plover and Oystercatcher territories at different values of the visitor index. Bars indicate the range of values for the visitor index over which the percentages were calculated. These ranges double in width after the first two, and were as follows: 0 (containing 234 200m sections), 0-0.25 (299), 0.25-0.5 (138), 0.5-1 (121), 1-2 (81), 2-4 (67), 4-8 (38) and 8-17.9 (28). Predicted values from univariable logistic regressions, using untransformed and square root transformed (sqrt) visitor data are shown for each species: RP = ringed plover, OY = oystercatcher.**

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2 317 In simple logistic regression models, presence of territories was for both species negatively correlated  
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4 318 with visitor numbers, reducing the AIC of an intercept only model from 724.6 to 652.4 for  
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6 319 oystercatchers and from 955.0 to 911.7 for ringed plovers. Using the square root transformation of  
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9 320 the visitor index considerably reduced the AIC value for the oystercatcher model (AIC = 628.1), but  
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11 321 resulted in a much smaller, but still significant, reduction for ringed plovers (AIC = 907.2). Predicted  
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13 322 values from these models are shown in Fig.2.

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18 324 *3.2 Multivariable logistic regressions – ringed plover*  
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23 326 For both species, the square root version of the visitor index continued to be a highly significant ( $p <$   
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25 327 0.01) predictor of presence of a territory in multivariable models that included the beach characteristic  
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27 328 data as predictor variables.

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32 330 For ringed plovers, presence of a territory was, in these multivariable models, significantly positively  
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34 331 correlated with dunes at the back of the beach and distance to low water. Distance to low water varied  
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36 332 considerably between locations and its distribution was highly skewed, but using the natural log of  
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38 333 these data produced a distribution that approximated to normal. Using this transformation improved  
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40 334 the fit of the models, with AIC values reduced by approximately 16.5.

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45 336 Adding further variables to these multivariable ringed plover models had little impact on the overall  
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47 337 fit or the statistical significance of the original variables. The inclusion of % fine shingle and % tideline  
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49 338 debris resulted in a slightly better fit (see Table 1a) but the reduction in AIC of the model was much  
50  
51 339 lower than for presence of dunes, distance to low water and the visitor index (see Table 1a: AIC  
52  
53 340 Change). Similar results were obtained if untransformed data were used for the visitor index, although  
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341 tideline debris was no longer significant (0.065 > 0.041) and the AIC of the overall model increased  
 342 (778.3 < 784.7).

343  
 344 The visitor index (square root version) carried an odds ratio of 0.286, indicating that the probability of  
 345 a 200m section of beach hosting a ringed plover territory was reduced by more than two thirds each  
 346 time there was an increase in the square root of number of people in the beach section equal to the  
 347 mean. This odds ratio was similar to that when using this visitor index as the sole predictor (0.334),  
 348 and it was 0.489 in a model equivalent to that shown in Table 1a but using untransformed visitor data,  
 349 also indicating a strong negative relationship.

350  
 351 **Table 1. Logistic regressions for presence/absence of ringed plover (a, top) and**  
 352 **oystercatcher (b, bottom) territories, using data from 200m sections of beach on the**  
 353 **Norfolk and Suffolk coast (N = 1003). LN = Natural log transformation; dist. = distance**  
 354 **(metres), P/A = presence/ absence. CL = 95 % Wald Confidence Limits. P = p-value based on**  
 355 **Chi-Square test statistic. AIC Change shows the increase in the AIC of the model if the**  
 356 **variable is removed. G denotes the likelihood ratio test for the model.**

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**a) Ringed Plover**

Parameter	Coefficient	Standard Error	Odds Ratio (+/- 95 % CL)	P	AIC Change
Intercept	-4.5967	0.5256		<.0001	
LN dist. to low water	0.5671	0.0999	1.763 (1.450-2.144)	<.0001	31.1
P/A Dunes	1.4337	0.1886	4.194 (2.898-6.071)	<.0001	57.4
% fine shingle	0.0195	0.0075	1.020 (1.005-1.035)	0.0093	4.5
% tide line debris	0.0606	0.0296	1.062 (1.003-1.126)	0.0408	2.1
Sq. root visitor index	-1.2515	0.2106	0.286 (0.189-0.432)	<.0001	48.9
<b>G: 186.7 p &lt;.0001    AIC: 778.3 (model with intercept only: 955.0)    Area under ROC Curve: 0.794</b>					

**b) Oystercatcher**

Parameter	Coefficient	Standard Error	Odds Ratio (+/- 95 % CL)	P	AIC Change
Intercept	-7.7079	0.9203		<.0001	
LN dist. to high water	0.6274	0.1444	1.873 (1.411-2.485)	<.0001	18.6
LN dist. high to low water	0.7065	0.0930	2.027 (1.689-2.432)	<.0001	66.7
% fine & med. shingle	0.0162	0.0041	1.016 (1.008-1.025)	<.0001	14.7
P/A Dunes	0.5844	0.2630	1.794 (1.071-3.004)	0.0263	2.9
Sq. root visitor index	-2.4972	0.3919	0.082 (0.038-0.177)	<.0001	66.0
<b>G:188.2 p &lt;.0001    AIC: 546.4 (model with intercept only: 724.6)    Area under ROC Curve: 0.862</b>					

358 3.3 Multivariable logistic regressions – oystercatcher

359

360 For oystercatchers, width of the beach to high water, distance from high to low water and the visitor  
361 index were most strongly associated with territory location (based on changes in model fit as  
362 measured by the AIC) (Table 1b). Natural log transformations improved the normality of both these  
363 beach width variables and produced better-fitting models. The visitor index again gave a considerably  
364 better fit when square root transformed. % fine and % medium shingle were both found to be  
365 significantly correlated with the presence of a territory, and further improvements in AICs were  
366 achieved in models incorporating these data as a single variable (fine + medium shingle), which was  
367 not the case for ringed plovers. Presence of dunes at the back of the beach was also statistically  
368 significant, although it resulted in only a small improvement in the AIC. No other variables were  
369 statistically significant when added to a model incorporating these predictors (Table 1b).

370

371 The square root transformed visitor index carried an odds ratio of 0.082, which was similar to the  
372 model where it was used as the sole predictor variable (0.066). It was 0.149 in a model equivalent to  
373 the final selected model but using untransformed visitor data. These results indicated an even stronger  
374 negative relationship with visitor numbers than was the case for the ringed plover models.

375

376 Plots of the key data sets used in these analyses- the visitor index, distance to high water, distance to  
377 low water, presence of dunes, and presence of oystercatcher and ringed plover territories, are shown  
378 for each 200 beach section in Fig. 3. These plots show how the apparent preference of both species  
379 for wide areas of beach backed by dune with low levels of human disturbance, as is revealed in the  
380 logistic regression models, is demonstrated across the study area.

381

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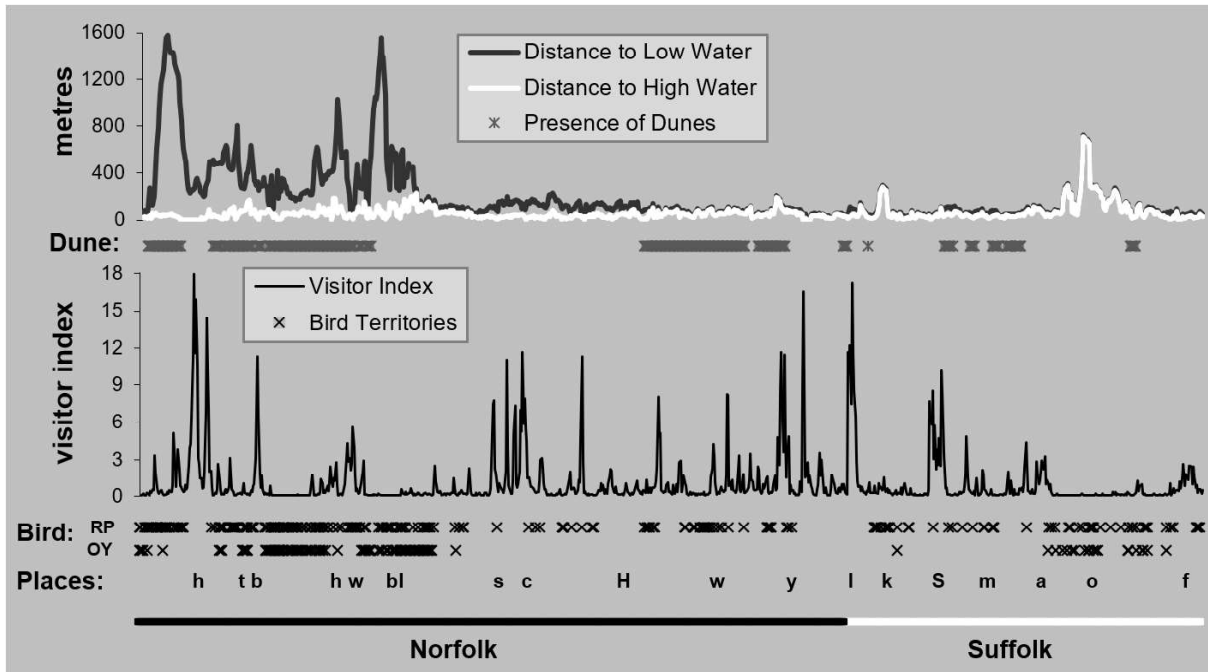


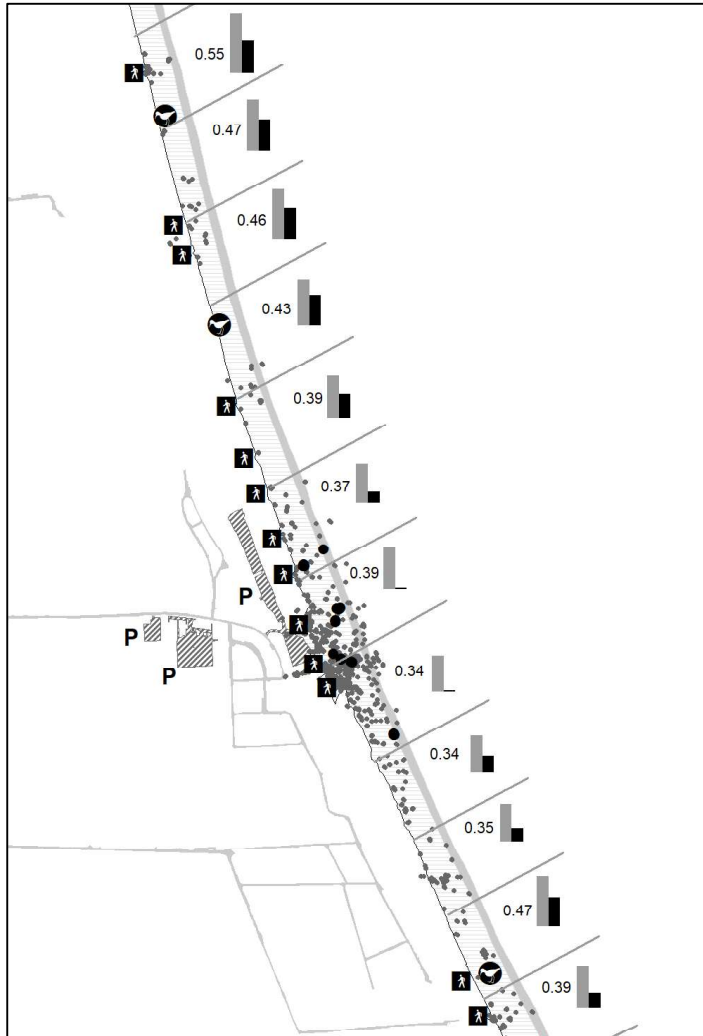
Figure 3. Data for 200m beach sections (N= 1003), measured from the north western to south eastern extremities of the coastline studied. The following are shown, from top to bottom: distance from the back of the beach to high and low water (thick black and thick white lines, respectively), presence of dunes at the back of the beach (grey crosses), index of visitor numbers and presence of ringed plover (RP) and oystercatcher (OY) territories on the beach (black crosses). 18 places on the Norfolk and Suffolk coasts are indicated as follows: h = Heacham, tb = Titchwell and Brancaster, hw = Holkham and Wells, bl = Blakeney Point, s = Sheringham, c = Cromer, H = Happisburgh, w = Winterton, y = Great Yarmouth, l = Lowestoft, k = Kessingland, S = Southwold, m = Minsmere, a = Aldeburgh, o = Orfordness, f = Felixstowe (see Fig. 1 for a map of these locations).

### 3.4 Predicted effects if visitor numbers were reduced to zero

Across the whole study area, the models shown in Table 1 predict that in the absence of visitors there would be an additional 90 beach sections where ringed plovers would establish territories and 96 where oystercatchers would do so (calculated on the basis of summing the predicted probabilities across all beach sections). For oystercatchers, there were 56 sections of beach where the predicted probability of presence of a territory differed by at least 0.3 between the model based on observed visitor numbers and the equivalent model with visitor numbers set to zero. There were 45 such sections in the case of the ringed plover model. An example is shown in Fig. 4, where two sections of



405 beach close to a beach entrance, itself close to a car park, present a very low probability of hosting a  
406 ringed plover territory given current visitor rates. However, if visitor number were reduced to zero,  
407 these probabilities would be predicted to increase to 34 % and 39%. A map showing these differences  
408 for the entire coastline can be found in the Supplementary Material.



409  
410 **Figure 4. Locations of breeding ringed plover territories on the beach at Winterton in Norfolk, UK,**  
411 **in relation to nearby roads, car parks, entrances to the beach and people on the beach recorded**  
412 **from aerial surveys. Grey dots on the beach indicate visitors recorded in July and August, larger**  
413 **black dots represent visitors in April. Data bars for each 200 m beach section show the probability**  
414 **predicted by the model (see table 1) that each 200 m section of beach would be occupied by a ringed**  
415 **plover territory, given the number of visitors recorded from the flights (black bars) and if visitor**  
416 **numbers were set to 0 (grey bars).**

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#### 417 4. Discussion

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419 These results indicate that human disturbance on beaches has a significant influence on the location  
420 of breeding territories of ringed plovers and oystercatchers at a regional scale, even when taking into  
421 account beach characteristics influencing territory location which may also be correlated with visitor  
422 numbers. Both species chose territories where the number of human visitors was relatively low, when  
423 considered both at the scale of the whole Norfolk and Suffolk coast, and locally within areas of this  
424 coastline. Although disturbance has been shown to affect roosting and feeding behaviour of  
425 oystercatchers, ringed plovers and other birds (Linssen et al, 2019, Collop et al., 2016, Carney &  
426 Sydeman, 1999, Glover et al., 2011, Klein et al., 1995, Tjørve & Tjørve, 2010, Martin et al., 2015,  
427 Navedo and Herrera, 2012, Stillman and Goss-Custard, 2002, Verhulst, 2001, Beale and Monaghan,  
428 2004 ) and nest distribution in some birds species across small study areas (Finney et al., 2005, Liley &  
429 Sutherland, 2006, Mallord et al., 2007), we believe this is the first study to demonstrate the influence  
430 of human disturbance on the location of breeding territories in coastal birds at a regional scale. These  
431 results are particularly concerning given the possibility that climate change may increase visitor  
432 numbers on UK beaches (Coombes et al., 2009a, Atzori et al., 2018). Fig. 2 suggests that territory  
433 distribution in oystercatchers is more severely impacted by visitor disturbance than in ringed plovers,  
434 and it is interesting that, although there were fewer pairs of oystercatchers (266 ringed plover pairs  
435 versus 223 oystercatcher pairs, a ratio of 1:0.84), the beach sections they chose to establish territories  
436 in were even more restricted (183 versus 117, a ratio of 1:0.64). This accords with the findings of a  
437 literature review by Blumstein et al. (2005), that larger bird species are more sensitive to human  
438 disturbance. This higher sensitivity to disturbance may explain the absence of oystercatcher territories  
439 across the middle section of our study area, where there were few stretches of coast with very low  
440 visitor numbers, although 50 of the 200m sections in this area contained ringed plover territories (Fig.  
441 4). It should also be noted that other beach characteristics which our models show to be important to

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2 442 both ringed plovers and oystercatchers, such as beach width and the presence of dunes, are often not  
3 443 favourable in this area (Fig. 4).

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6 444 Aside from visitor numbers, for ringed plovers the strongest associations with territory distribution  
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8 445 were total beach width and presence or absence of dunes, with % fine shingle and % tideline debris  
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10 446 also influencing territory distribution (see Table 1). This suggests that they prefer gently shelving beach  
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12 447 profiles which allow a very wide intertidal range and provide opportunities for feeding, vegetation on  
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14 448 the beach providing cover for chicks to escape predators, and a shingle substrate which may allow  
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16 449 better crypsis for eggs; these findings are broadly in agreement with previous studies (Liley &  
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18 450 Sutherland (2006), Colwell et al., 2011, Lee et al, 2010, Grant et al., 2019). For Oystercatchers,  
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20 451 measures of beach width were again found to important drivers of territory distribution. Beach  
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22 452 substrate was also significant, as Grant et al. (2019) had found for American Oystercatchers  
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24 453 (Haematopus palliatus). For both species, improvements in model fit using log transformations for the  
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26 454 beach width variables suggested that the distribution of territories may partly reflect decreasing  
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28 455 marginal benefits of extra width i.e. wide beaches are preferred, but each extra metre of beach counts  
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30 456 less than the previous one.

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38 457 We have shown that the likelihood of territory establishment in some sections of beach would often  
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40 458 be much higher in the absence of human visitors than with them. Land managers should aim to restrict  
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42 459 visitor numbers in these areas, for example, by repositioning paths or increasing the distance from  
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44 460 beach entrances and car parks, which has been shown to have a major influence on visitor numbers  
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46 461 along the coastline we examined in this study (Tratalos et. al., 2013). Models of determinants of the  
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48 462 number of visitors on a section of beach suggest that the presence of nearby amenities such as toilets,  
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50 463 as well how close the beach is to housing, and the distance of the beach section from the nearest  
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52 464 beach entrance, all have significant influences (Coombes et al. ,2009b). This suggests that  
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54 465 management of coastal areas should be directed towards controlling these factors in areas which are  
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56 466 environmentally suitable for ringed plovers and oystercatchers in order to maximise the number of  
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1 467 breeding territories of these birds. Alternative approaches might include the screening-off of some  
2 468 sections of beach through the erection of fences, banning activities such as dog walking and kite  
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4 469 surfing, or putting in place exclusion zones.  
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8 470 Although the fieldwork for this study was conducted in 2003, in the intervening period this coastline  
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10 471 has for the most part been protected from development which would result in significant changes to  
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12 472 the distribution of human visitors over the beach. One exception to this is the planning of The English  
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14 473 coastal path, which is an ambitious project to make as much of the English coastline line accessible to  
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16 474 the public as possible (Natural England, 2020), and sections of this path have already been opened in  
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18 475 our study site, with further sections still in consultation (Natural England, 2020). We would encourage  
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20 476 planners of the path to use the results of our study to ensure the continued presence of breeding  
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22 477 oystercatchers and ringed plovers along this coastline.  
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30 479 Our study looks at the association between a measure of disturbance (the visitor index) and the  
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32 480 location of bird territories. However, we do not address the mechanisms that determine this  
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34 481 association. We therefore believe there is a need for more detailed, smaller scale studies to examine  
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36 482 how bird behaviour and survival varies according to the types of disturbance, the time of day and time  
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38 483 of year. Such studies could be used to inform management practices, which might restrict certain  
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40 484 activities to certain times of day or year. For example, dog walking and kite surfing might be banned  
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42 485 during periods when territory establishment or survivorship of chicks is most likely to be affected.  
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48 486  
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50 487 It may be possible to scale up the methodology used in this study to larger areas, such as the entire  
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52 488 UK coastline. Some of the environmental variables in the selected models could be calculated from  
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54 489 publicly available data (e.g. beach width). Further research would be needed to identify whether other  
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56 490 beach characteristics, such as beach composition or the presence of dunes, could be mapped over  
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58 491 large areas from remotely sensed information such as satellite imagery, aerial photography, or drones.  
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1 492 Estimation of visitor numbers might be possible using drones and auto processing of remote-sensing  
2 493 imagery. Thermal imaging on unmanned aerial vehicles (UAVs), or drones, can be highly effective for  
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4 494 surveying nesting birds, and might be used to extend the areal coverage of studies such as ours (Valle  
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6 495 and Scarton, 2019 a,b, Scholten et al, 2019). The use of models to estimate the distribution of beach  
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8 496 visitors (Coombes et al., 2009 a and b, Tratalos et al, 2013) might also provide suitable proxies to  
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10 497 determine those areas likely to experience high visitor numbers relative to others. This would enable  
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12 498 better targeting of areas suitable for management measures aimed at increasing breeding populations  
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14 499 of our study species, and, in combination with finer scale studies on the effect of environmental and  
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16 500 human factors on distribution and abundance, other coastal species.  
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## 22 502 **Acknowledgements**

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24  
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28  
29 505 Trust and Landguard Bird Observatory for supplying some of the bird data (as described in the  
30  
31 506 methods section).  
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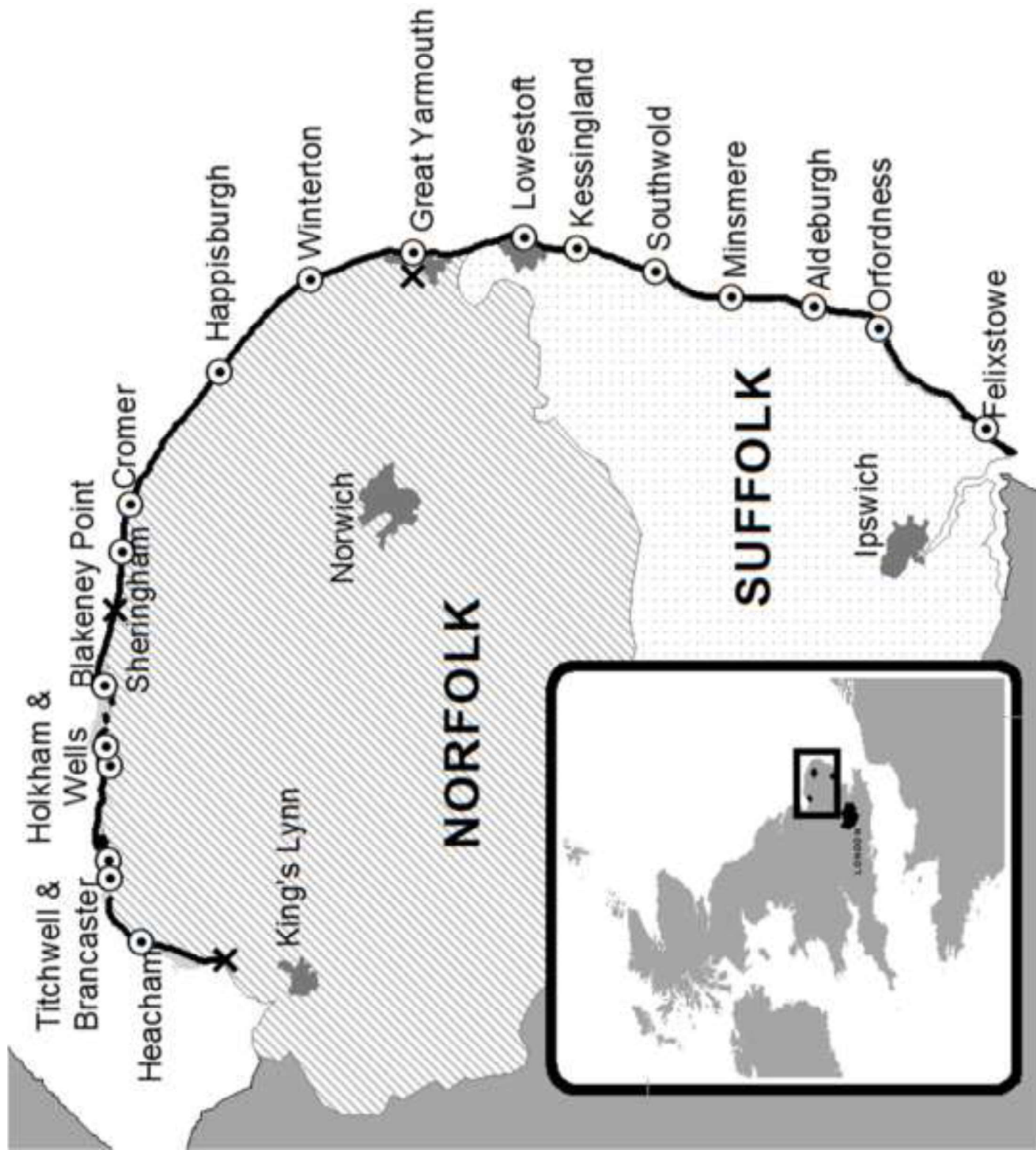
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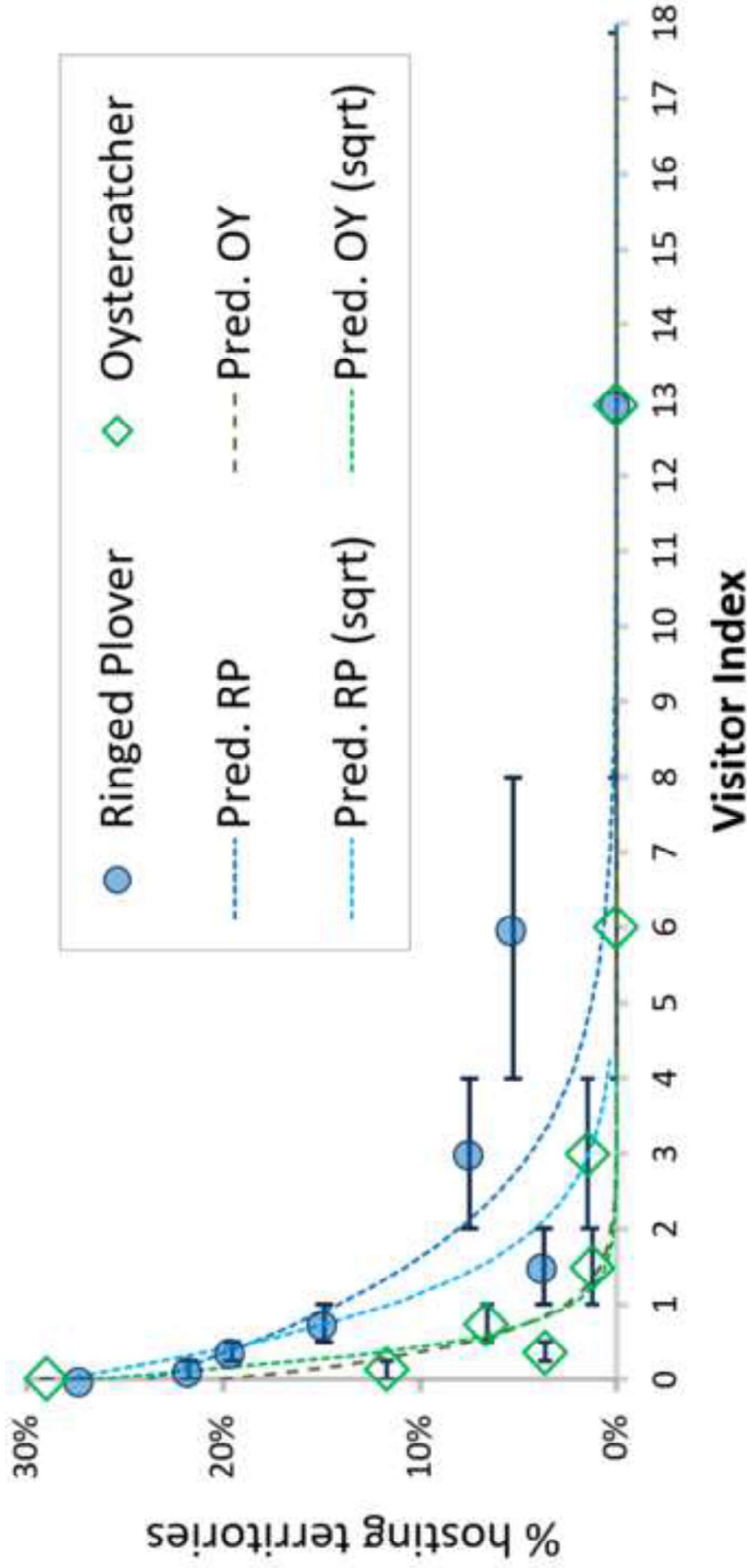
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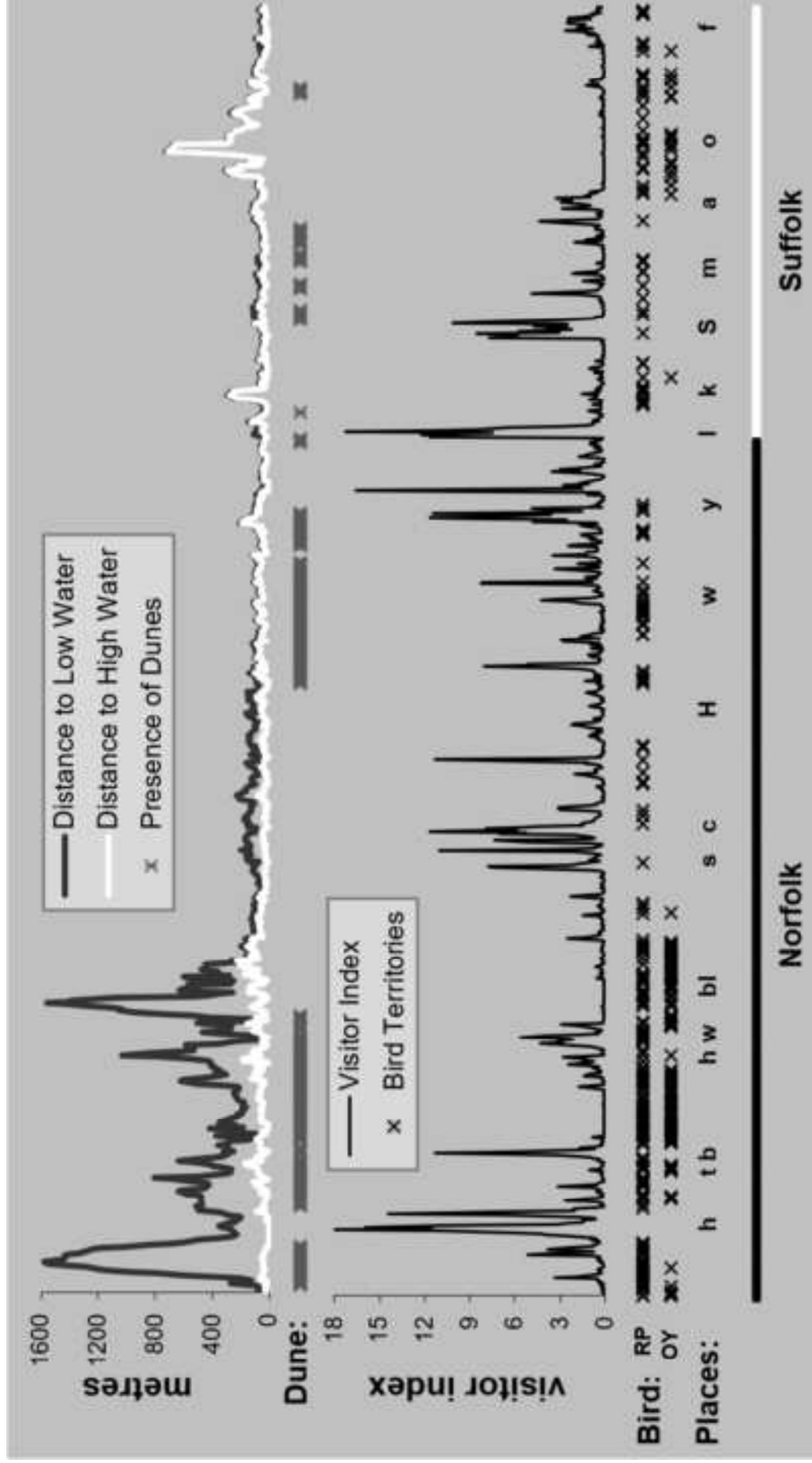
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