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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*

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A B S T R A C T

We estimated the influence of human disturbance and environmental factors on territory establishment in common ringed plovers *Charadrius hiaticula* and Eurasian oystercatchers *Haematopus ostralegus*, to inform the conservation of these species. We examined a 212 km stretch of coastline in the United Kingdom in 2003, mapping all breeding pairs of both study species, as well as the environmental characteristics of beaches and locations of visitors on the beach, the latter measured by filming from a light aircraft. Of the 1,003 200m sections of beach surveyed, 183 contained ringed plover territories (267 breeding pairs) and 117 contained oystercatcher territories (226 breeding pairs). 38,634 human visitors to the beach were mapped from three flights. Population densities of both ringed plovers and oystercatchers were lower in locations with high visitor numbers, even when accounting for the influence of the environmental characteristics of the beach. The two bird species showed similar rates of territory establishment at very low visitor rates, but oystercatchers showed a stronger negative response when visitor rates reached higher levels. Binary logistic regression models were used to identify areas where the birds would benefit most from 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 and Simmons (1983), and Ens and Underhill (2014).

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 and Herrera, 2012; Mallord et al., 2007; McGowan and Simons, 2006; Anderson, 1988; Gillett et al., 1975; Safina and Burger, 1983; Carney and Sydeman, 1999; Finney et al., 2005). 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). (Virzi, 2010) found that human disturbance influenced territory choice in American oystercatchers *Haematopus palliatus*.

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, 1984). Human recreation has also been shown to be associated with reduced breeding success in Eurasian and other oystercatcher species (Tjørve and Tjørve, 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 8400 pairs in 1984–4070 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 et al., 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 et al., 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 Eastern England in a single flight. This coastline hosts some of the UK's most popular tourist destinations, spans a wide variety of beach types and levels of use by tourists, and is also an important breeding area for both our study species, which establish breeding territories there during the spring and summer, when human visitor numbers are also relatively high. It is therefore an ideal study area to examine the way in which the density of human visitors affects the location of breeding territories.

Further to estimating the effects of habitat and disturbance on the location of ringed plover and oystercatcher territories, we show how models of these effects can be used in conjunction with site specific information to distinguish areas where management to reduce visitor numbers would be most likely to bring about increases in breeding populations of these bird species. Our study is particularly pertinent in view of proposals to improve visitor access to our study area as sections of the England Coastal Path, which aims to make the whole coastline of England accessible to walkers. Approximately half of the study coastline has been included since the fieldwork for this study was conducted, with the other half currently at the planning stage (Natural England, 2020).

2. Methods

2.1. Beach surveys to obtain breeding bird data

Our study area was composed of all habitats suitable for territory establishment by our study species along the coastline of Norfolk and Suffolk, UK. It was therefore restricted to sand and shingle beaches, amounting to 83% of the total coastline of these counties. This coast contains a number of protected sites of significant conservation value and is a nationally important breeding area for both species.

To obtain data on the location of bird territories, these habitats were walked between early April and mid-June, 2003; this time period was chosen on the basis of published information on the breeding behaviour of these species in the study area and elsewhere (Cramp and Simmons, 1983; Liley, 1999; Prater, 1974, 1976; Rooney and Eve, 1993). By this time individuals, even if

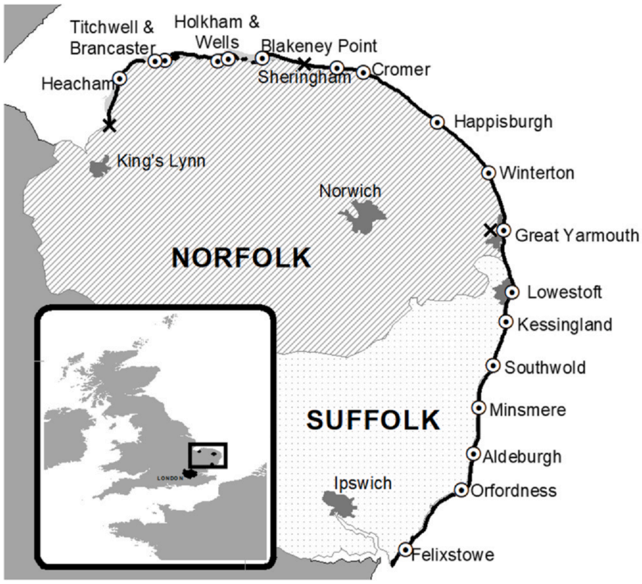

Fig. 1. Map of the study area, showing the coastline surveyed (black line), key locations, the start point of walked sections (black crosses) and (inset) the location of the study area within the UK.

not yet commencing nesting, would still exhibit behaviour indicative of territoriality; however, to minimise temporal bias, three starting points at approximately equal intervals along the coast were selected. Sections were then walked alternately from these points. Fig. 1 shows the coastline surveyed.

Each day, a different section of beach several kilometres in length was surveyed. The locations of all breeding pairs of ringed plovers and oystercatchers were recorded using a GPS (Global Positioning System), both on the outward and the return journey, to minimise the probability of pairs being missed. Breeding was determined on the basis of indications of the presence of a nest (a scrape with eggs, an incubating adult, an adult distraction display or the presence of young) or on territorial behaviour, which included slow wing beat butterfly flights in either species, as well as, in oystercatchers, piping displays in ground confrontations with neighbouring and intruding birds of the same species, alarm calling and mobbing and, in ringed plovers, agitated behaviour (e.g. head-bobbing), sometimes with breast 'puffing' and tail fanning (see Cramp and Simmons, 1983). Single birds were included if they behaved in a manner indicative of territoriality, as one adult of a pair might be absent if feeding elsewhere in cases where the feeding territory was not within the nesting territory, but flocks were not.

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

2.2. Beach characteristic data

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

2.3. Data on visitor numbers

To map the locations of human visitors on the beach, the coastlines of Norfolk and Suffolk were filmed, from an altitude of approximately 150 m, using a Canon XL1 digital video camera, from a Cessna 152 light aircraft, on three separate occasions – Saturday 12th April, Saturday 21st June and Sunday 24th August 2003. All three surveys took place on sunny days between 12:30 and 16:00, when the tide was at approximately mid phase. Our aim was to film on several occasions when a large number of visitors could be counted, to reduce the effect of stochasticity on our index of visitor numbers, and taking into account the fact that the way in which beach visitors distributed themselves along the beach was largely dependent on distance to access points rather than the time of year (Tratalos et al., 2013). The tide needed to be at approximately mid phase as some beaches would be so narrow as to deter visitors at high tide and others would be so wide at low tide that counting of all visitors would not have been possible. We therefore added the date in August, even though chicks of our study species would be less vulnerable to disturbance by that point, as flights needed to be planned in advance and weekends with a reliable forecast of warm sunny weather, and with the tide at mid phase, were very few during spring and early summer of the study period. Based on our observations of human activity across the study area, we believe that human disturbance due to a range of human behaviours (walking, picnicking, sunbathing, kite surfing etc.) would be covered by our choice of three sunny weekend afternoons during the spring and summer.

The entire area of the beach was filmed, which in the case of very wide beaches involved filming the foreshore and rear of the beach in separate passes.

The April flight covered 164.8 km, consisting of the entire Norfolk coast and as far south as Minsmere RSPB reserve in Suffolk; the June flight covered 198 km, consisting of the entire Norfolk coast and along the Suffolk coast as far as Orfordness; and the August flight covered 211 km, consisting of the whole of both the Norfolk and Suffolk coastlines, with the exception of a 1 km section at Holkham in North Norfolk (see Fig. 1). The locations of all visitors to the beach shown on the videos were manually digitised using georeferenced aerial photos in the GIS, to map human visitors in their correct location. Data derived from these videos are also described and analysed in Coombes et al. (2009a, 2009b) and in Tratalos et al. (2013).

Because none of the three videos individually covered the entire study area, but they did do so when they were combined, an estimate of the total numbers of visitors for each 200 m beach section across the three filming periods was calculated, extrapolating on the assumption that the number of visitors between the three periods would differ by a constant factor throughout the entire coastline. In these extrapolations, beach sections missing data for the April flight were calculated by multiplying the August data by the ratio between the mean values for August and April across sections captured on both those flight dates, and those sections missing data for June or August were likewise calculated using same approach on the mean values for August and June across sections captured in both of those months. These data were then divided by their mean value across all sections, resulting in a visitor index with a mean of 1.

2.4. GIS data processing and statistical analysis

ArcView 3.2 and ArcMap 10.6 were used for GIS processing. The number of people, ringed plover and oystercatcher territories falling within each of the 200 m sections was calculated and matched to the beach characteristic data for each section in the GIS. The degree of collinearity was measured (i) amongst the number of human visitors per section for each of the three flights and (ii) amongst the beach characteristic and visitor index variables, using Pearson correlation for the former (r) and Spearman Rank correlation (Rs) for the latter.

The statistical analyses were done in SAS 9.4. Binary logistic regression (Hosmer et al., 2013) was used to assess the relationship between the presence or absence of ringed plover and oystercatcher territories in each 200 m section of beach and the number of visitors on the beach observed in the videos, first in simple logistic models and then in multivariable models including the beach characteristic data as additional predictor variables. In cases where two or more variables were highly correlated with one another we choose the one that resulted in the greatest reduction in the AIC.

In these models, the three beach width variables were log transformed, on the assumption that the attractiveness to the birds of each extra metre of beach could be expected to decline as the overall beach width increased. For distance to high water we added 1 before transformation to avoid calculation over zero values in a small number of beach sections ($N = 21$). The visitor index was also recalculated using a square root transformation for the number of visitors in each section, in order to examine whether our study species were more sensitive to increases in disturbance when visitor numbers were relatively low (the existence of zero values meant that a direct log transformation could not be used for these data). Our general approach was to use forward stepwise procedures to build up a model using environmental variables only, to then examine the effect of incorporating visitor numbers and finally to check that these models were stable if environmental variables which had previously been rejected were reintroduced. We were careful to make sure that no important beach characteristics were missing, to ensure that any association found with visitor numbers was not due to collinearity with a missing environmental variable.

For both the ringed plover and oystercatcher models, the predicted values from the models were calculated for all 200 m beach sections after setting visitors numbers to zero, to examine the predicated effect that a removal of visitors would have on territory establishment in each section of beach.

3. Results

3.1. Summary of data sets and simple logistic regressions

38,634 visitors on the beach were mapped from the three flights: 1593 in April, 11,466 in June and 25,575 in August. There were pronounced peaks in visitor numbers at intervals along the coastline, with 19 of the 1003 beach sections experiencing over 10 times the average number of visitors and 231 sections hosting none; visitors per beach section were strongly correlated between all three filming episodes (r: April vs. June: 0.68; April vs. August: 0.62; June vs. August: 0.83). The mean number of visitors for each flight equated to c. 9.7 people per kilometre in April, 58.9 in June and 121.2 in August. These figures corresponded closely to those for the average number of people per *c.* 200 m section from the extrapolated data used to calculate the normalised visitor index (39.1 people per 200 m section across the three dates).

The predictor variables for the statistical analyses, consisting of the visitor index and the beach characteristic data for each section, were generally not strongly correlated with one another, except in cases where they measured proportions of the same entity (e.g. Rs = −0.95 for sand vs medium shingle). The only other cases of r lower than −0.40 or higher than 0.40 were % vegetation on beach vs. distance to high water (0.44) and dunes vs. % medium shingle (Rs = −0.41) and % sand (Rs = 0.41). The visitor index was generally only weakly correlated with the other dependent variables, with the most notable correlates being the presence of human populated areas at the back of the beach (Rs = 0.45), % vegetation on the beach (Rs = −0.36), % sand (Rs = 0.27), and % medium shingle (Rs = −0.27). A correlogram of these variables can be found in the supplementary material.

183 beach sections contained ringed plover territories (266 breeding pairs), and 117 contained oystercatcher territories (223 pairs). Occupation of territories was associated with lower than average visitor numbers, for both ringed plovers and oystercatchers (ringed plovers: mean visitor index for occupied sections: 0.30, for unoccupied sections: 1.16; oystercatchers: for occupied sections: 0.13, for unoccupied sections: 1.11).

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 200 m 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 >= 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.

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

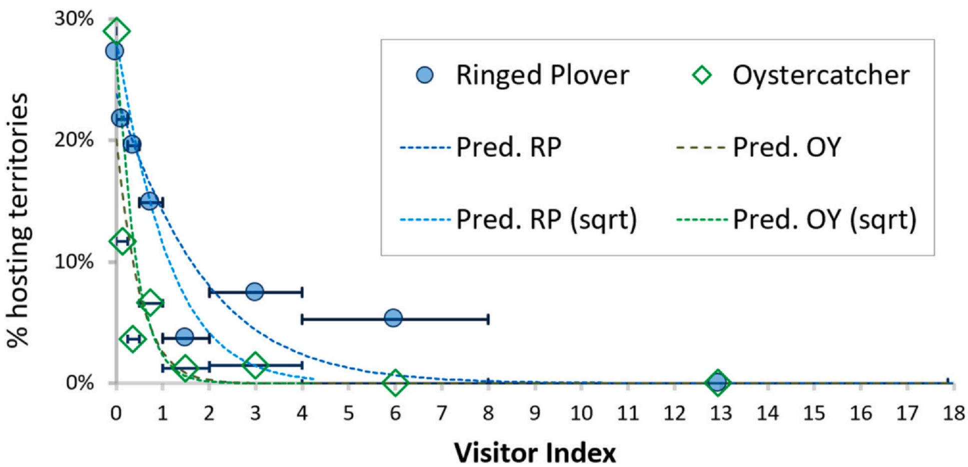

Fig. 2. Percentage of 200 m beach sections hosting Ringed Plover and Oystercatcher territories at different values of the visitor index. Bars indicate the range of values for the visitor index over which the percentages were calculated. These ranges double in width after the first two, and were as follows: 0 (containing 234,200 m 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.

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

a) Ringed Plover

Parameter	Coefficient	Standard error	Odds ratio (+/− 95% CL)	P	AIC change
Intercept	-4.5967	0.5256		<0.0001	
LN dist. to low water	0.5671	0.0999	1.763 (1.450–2.144)	<0.0001	31.1
P/A Dunes	1.4337	0.1886	4.194 (2.898–6.071)	<0.0001	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)	<0.0001	48.9

G: 186.7 p < 0.0001 **AIC:** 778.3 (model with intercept only: 955.0) **Area under ROC Curve:** 0.794

b) Oystercatcher

Parameter	Coefficient	Standard error	Odds ratio (+/− 95% CL)	P	AIC change
Intercept	-7.7079	0.9203		<0.0001	
LN dist. to high water	0.6274	0.1444	1.873 (1.411–2.485)	<0.0001	18.6
LN dist. high to low water	0.7065	0.0930	2.027 (1.689–2.432)	<0.0001	66.7
% fine & med. shingle	0.0162	0.0041	1.016 (1.008–1.025)	<0.0001	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)	<0.0001	66.0

G:188.2 p < 0.0001 **AIC**: 546.4 (model with intercept only: 724.6) **Area under ROC Curve**: 0.862

3.2. Multivariable logistic regressions – ringed plover

For both species, the square root version of the visitor index continued to be a highly significant ($p < 0.01$) predictor of presence of a territory in multivariable models that included the beach characteristic data as predictor variables.

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

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

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

3.3. Multivariable logistic regressions – oystercatcher

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

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

Plots of the key data sets used in these analyses- the visitor index, distance to high water, distance to low water, presence of dunes, and presence of oystercatcher and ringed plover territories, are shown for each 200 beach section in Fig. 3. These plots

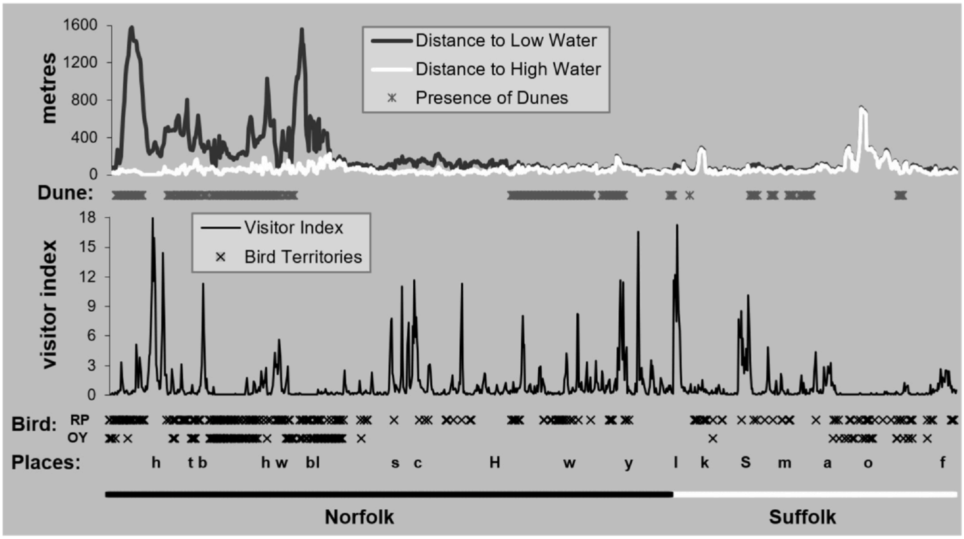

Fig. 3. Data for 200 m beach sections (N = 1003), measured from the north western to south eastern extremities of the coastline studied. The following are shown, from top to bottom: distance from the back of the beach to high and low water (thick black and thick white lines, respectively), presence of 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).

show how the apparent preference of both species for wide areas of beach backed by dune with low levels of human disturbance, as is revealed in the logistic regression models, is demonstrated across the study area.

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

4. Discussion

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

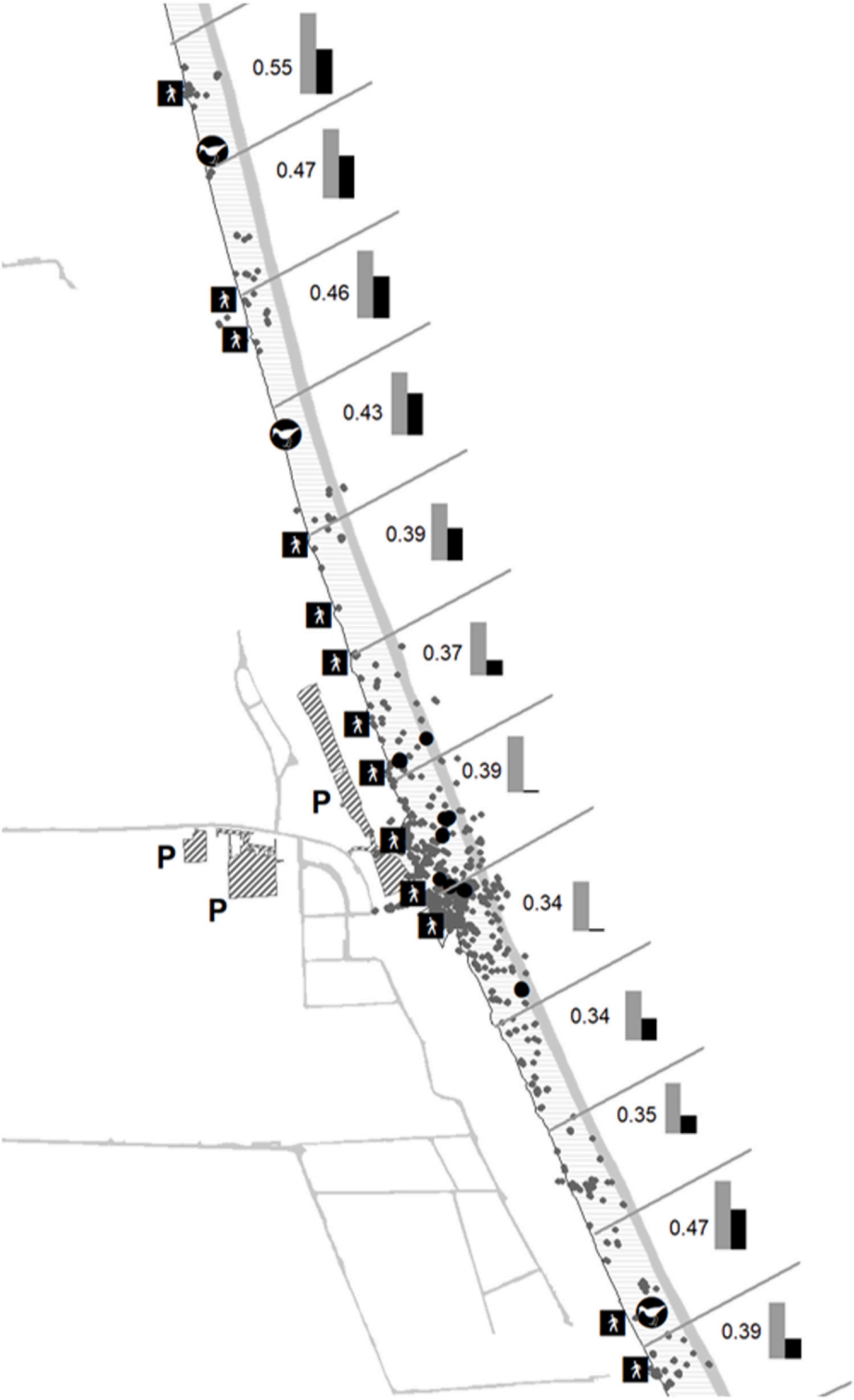

Fig. 4. Locations of breeding ringed plover territories on the beach at Winterton in Norfolk, UK, in relation to nearby roads, car parks, entrances to the beach and people on the beach recorded from aerial surveys. Grey dots on the beach indicate visitors recorded in July and August, larger black dots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

of the 200 m sections in this area contained ringed plover territories (Fig. 4). It should also be noted that other beach characteristics which our models show to be important to both ringed plovers and oystercatchers, such as beach width and the presence of dunes, are often not favourable in this area (Fig. 4).

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

We have shown that the likelihood of territory establishment in some sections of beach would often be much higher in the absence of human visitors than with them. Land managers should aim to restrict visitor numbers in these areas, for example, by repositioning paths or increasing the distance from beach entrances and car parks, which has been shown to have a major influence on visitor numbers along the coastline we examined in this study (Tratalos et al., 2013). Models of determinants of the number of visitors on a section of beach suggest that the presence of nearby amenities such as toilets, as well how close the beach is to housing, and the distance of the beach section from the nearest beach entrance, all have significant influences (Coombes et al., 2009b). This suggests that management of coastal areas should be directed towards controlling these factors in areas which are environmentally suitable for ringed plovers and oystercatchers in order to maximise the number of breeding territories of these birds. Alternative approaches might include the screening-off of some sections of beach through the erection of fences, banning activities such as dog walking and kite surfing, or putting in place exclusion zones.

Although the fieldwork for this study was conducted in 2003, in the intervening period this coastline has for the most part been protected from development which would result in significant changes to the distribution of human visitors over the beach. One exception to this is the planning of The English coastal path, which is an ambitious project to make as much of the English coastline line accessible to the public as possible (Natural England, 2020), and sections of this path have already been opened in our study site, with further sections still in consultation (Natural England, 2020). We would encourage planners of the path to use the results of our study to ensure the continued presence of breeding oystercatchers and ringed plovers along this coastline.

Our study looks at the association between a measure of disturbance (the visitor index) and the location of bird territories. However, we do not address the mechanisms that determine this association. We therefore believe there is a need for more detailed, smaller scale studies to examine how bird behaviour and survival varies according to the types of disturbance, the time of day and time of year. Such studies could be used to inform management practices, which might restrict certain activities to certain times of day or year. For example, dog walking and kite surfing might be banned during periods when territory establishment or survivorship of chicks is most likely to be affected.

It may be possible to scale up the methodology used in this study to larger areas, such as the entire UK coastline. Some of the environmental variables in the selected models could be calculated from publicly available data (e.g. beach width). Further research would be needed to identify whether other beach characteristics, such as beach composition or the presence of dunes, could be mapped over large areas from remotely sensed information such as satellite imagery, aerial photography, or drones. Estimation of visitor numbers might be possible using drones and auto processing of remote-sensing imagery. Thermal imaging on unmanned aerial vehicles (UAVs), or drones, can be highly effective for surveying nesting birds, and might be used to extend the areal coverage of studies such as ours (Valle and Scarton, 2019a, 2009b; Scholten et al., 2019). The use of models to estimate the distribution of beach visitors (Coombes et al., 2009a, 2009b; Tratalos et al., 2013) might also provide suitable proxies to determine those areas likely to experience high visitor numbers relative to others. This would enable better targeting of areas suitable for management measures aimed at increasing breeding populations of our study species, and, in combination with finer scale studies on the effect of environmental and human factors on distribution and abundance, other coastal species.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01640.

References

Allen, A.M., Ens, B.J., van de Pol, M., van der Jeugd, H., Frauendorf, M., Oosterbeek, K., Jongejans, E., 2019. Seasonal survival and migratory connectivity of the Eurasian Oystercatcher revealed by citizen science. Auk 136, 1–17.
Anderson, D.W., 1988. In my experience: dose-response relationship between human disturbance and brown pelican breeding success. Wildl. Soc. Bull. 16, 339–345 1973-2006.
Atzori, R., Fyall, A., Miller, G., 2018. Tourist responses to climate change: potential impacts and adaptation in Florida's coastal destinations. Tour. Manag. 69, 12–22.
Beale, C.M., Monaghan, P., 2004. Behavioural responses to human disturbance: a matter of choice? Anim. Behav. 68, 1065–1069.
Blumstein, D.T., Fernández-Juricic, E., Zollner, P.A., Garity, S.C., 2005. Inter-specific variation in avian responses to human disturbance. J. Appl. Ecol. 42, 943–953.
Brown, A., Grice, P., 2005, Birds in England. T & AD Poyser, London.
Carney, K.M., Sydeman, W.J., 1999. A review of human disturbance effects on nesting colonial waterbirds. Waterbirds 22, 68–79.
Collop, C., Stillman, R.A., Garbutt, A., Yates, M.G., Rispin, E., Yates, T., 2016. Variability in the area, energy and time costs of wintering waders responding to disturbance. Ibis 158, 711–725.
Colwell, M.A., Meyer, J.J., Hardy, M.A., McAllister, S.E., Transou, A.N., Levalley, R.R., Dinsmore, S.J., 2011. Western Snowy Plovers Charadrius alexandrinus nivosus select nesting substrates that enhance egg crypsis and improve nest survival. Ibis 153, 303–311.
Conway, G.J., Austin, G.E., Handschuh, M., Drewitt, A.L., Burton, N.H.K., 2019. Breeding populations of Little Ringed Plover Charadrius dubius and Ringed Plover Charadrius hiaticula in the United Kingdom in 2007. Bird. Study 66, 22–31.
Coombes, E.G., Jones, A.P., 2010. Assessing the impact of climate change on visitor behaviour and habitat use at the coast: a UK case study. Glob. Environ. Change-Hum. Policy Dimens. 20, 303–313.
Coombes, E.G., Jones, A.P., Sutherland, W.J., 2009a. The implications of climate change on coastal visitor numbers: a regional analysis. J. Coast. Res. 25, 981–990.
Coombes, E.G., Jones, A.P., Bateman, I.J., Tratalos, J.A., Gill, J.A., Showler, D.A., Watkinson, Sutherland, W.J., 2009b. Spatial and temporal modeling of beach use: a case study of East Anglia, UK. Coast. Manag. 37, 94–115.
Cramp, S., Simmons, K.E.L., 1983. The Birds of the Western Palearctic Vol. III. Waders to Gulls. Oxford University Press, Oxford, UK.
Dwyer, J.F., 1988. Predicting daily use of urban forest recreation sites. Landsc. Urban Plan. 15, 127–138.
Eaton, M.A., Aebischer, N.J., Brown, A.F., Hearn, R.D., Lock, L., Musgrove, A.J., Noble, D.G., Stroud, D.A., Gregory, R.D., 2015. Birds of Conservation Concern 4: the population status of birds in the United Kingdom, Channel Islands and Isle of Man. Br. Birds 108, 708–746.
Ens, B.J., Underhill, L.G., 2014. Synthesis of oystercatcher conservation assessments: general lessons and recommendations. Int. Wader Stud. 20, 5–22.
Finney, S.K., Pearce-Higgins, J.W., Yalden, D.W., 2005. The effect of recreational disturbance on an upland breeding bird, the golden plover Pluvialis apricaria. Biol. Conserv. 121, 53–63.
Gillett, W.H., Hayward Jr., J.L., Stout, J.F., 1975. Effects of human activity on egg and chick mortality in a glaucous-winged gull colony. Condor 77, 492–499.
Glover, H.K., Weston, M.A., Maguire, G.S., Miller, K.K., Christie, B.A., 2011. Towards ecologically meaningful and socially acceptable buffers: Response distances of shorebirds in Victoria, Australia, to human disturbance. Landsc. Urban Plan. 103, 326–334.
Grant, D.M., Cohen, J.B., Stantial, M.L., Linhart, R.C., 2019. Substrate-level nest site selection of sympatric piping plovers (Charadrius melodus) and American oystercatchers (Haematopus palliatus) in New Jersey, USA. Waterbirds 42, 272–281.
Hockey, P., Kirwan, G.M., Boesman, P., 2020, Eurasian Oystercatcher (Haematopus ostralegus). 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.
Hosmer, D.W., Lemeshow, S., Strudivant, R.X., 2013. Applied Logistic Regression. John Wiley & Sons, New York.
IUCN, 2020, The IUCN Red List of Threatened Species. Version 2020–1. <https://www.iucnredlist.org/> (accessed 19 October 2020).
Klein, M.L., Humphrey, S.R., Percival, H.F., 1995. Effects of ecotourism on distribution of waterbirds in a wildlife refuge. Conserv. Biol. 9, 1454–1465.
Kubo, T., Uryu, S., Yamano, H., Tsuge, T., Yamakita, T., Shirayama, Y., 2020. Mobile phone network data reveal nationwide economic value of coastal tourism under climate change. Tour. Manag. 77, 104010.
Lee, W.S., Kwon, Y.S., Yoo, J.C., 2010. Egg survival is related to the colour matching of eggs to nest background in Black-tailed Gulls. J. Ornithol. 151, 765–770.
Liley, D., Sutherland, W.J., 2006. Predicting the consequences of human disturbance for Ringed Plovers Charadrius hiaticula: a game theory approach. Ibis 149, 82–94.
Liley, D., 1999, Predicting the Consequences of Human Disturbance, Predation and Sea Level Rise for Ringed Plover Populations. PhD Thesis, University of East Anglia.
Linssen, H., van de Pol, M., Allen, A.M., Jans, M., Ens, B.J., Krijgsveld, K.L., Frauendorf, M., van der Kolk, H.-J., 2019. Disturbance increases high tide travel distance of a roosting shorebird but only marginally affects daily energy expenditure. Avian Res. 10, 31.
Mallord, J.W., Dolman, P.M., Brown, A.F., Sutherland, W.J., 2007. Linking recreational disturbance to population size in a ground-nesting passerine. J. Appl. Ecol. 44, 185–195.
Martin, B., Delgado, S., de la Cruz, A., Tirado, S., Ferrer, M., 2015. Effects of human presence on the long-term trends of migrant and resident shorebirds: evidence of local population declines. Anim. Conserv. 18, 73–81.
McGowan, C.P., Simons, T.R., 2006. Effects of human recreation on the incubation behavior of American Oystercatchers. Wilson J. Ornithol. 4, 485–493.
Natural England, 2020, England Coastal Path – Stretch Progress, Provisional Timings and Stretches. <https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/926228/coastal-access-england-map.pdf> (accessed 19 October 2020).
Navedo, J.G., Herrera, A.G., 2012. Effects of recreational disturbance on tidal wetlands: supporting the importance of undisturbed roosting sites for waterbird conservation. J. Coast. Conserv. 16, 373–381.
Pienkowski, M.W., 1984. Breeding biology and population dynamics of ringed Plover Charadrius hiaticula in Britain and Greenland: nest predation as a possible factor limiting distribution and timing of breeding. J. Zool. Soc. Lond. 202, 83–114.
Prater, A.J., 1974. Breeding biology of the Ringed Plover Charadrius hiaticula. Proc. I. W. R. B. Wader Symp. Wars. 1973, 15–22.
Prater, A.J., 1976. Breeding Population of the Ringed Plover in Britain. Bird. Study 23, 156–161. https://doi.org/10.1080/00063657609476496
Rooney M.E.S. and Eve, V., 1993, The Number, Distribution and Breeding Success of the Ringed Plover in Norfolk 1993. Norfolk Coast Project / RSPB.
Safina, C., Burger, J., 1983. Effects of human disturbance on reproductive success in the black skimmer. Condor 85, 164–171.
Scholten, C.N., Kamphuis, A.J., Vredevoogd, K.J., Lee-Strydhorst, K.G., Atma, J.L., Shea, C.B., Lamberg, O.N., Proppe, D.S., 2019. Real-time thermal imagery from an unmanned aerial vehicle can locate ground nests of a grassland songbird at rates similar to traditional methods. Biol. Conserv. 233, 241–246.
Silva, J.S., Leal, M.M.V., Araújo, M.C.B., Barbosa, S.C.T., Costa, M.F., 2008. Spatial and temporal patterns of use of Boa Viagem Beach, Northeast Brazil. J. Coast. Res. 24, 79–86.
Stillman, R.A., Goss-Custard, J.D., 2002. Seasonal changes in the response of oystercatchers Haematopus ostralegus to human disturbance. J. Avian Biol. 33, 358–365.
Thies, L., Tomkovich, P., dos Remedios, N., Lislevand, T., Pinchuk, P., Wallander, J., Dänhardt, J., Þórisson, B., Blomqvist, D., Küpper, C., 2018. Population and subspecies differentiation in a high latitude breeding wader, the Common Ringed Plover Charadrius hiaticula. Ardea 106, 163–176.
Tjørve, K.M.C., Tjørve, E., 2010. Contrasting reaction to human disturbance in Eurasian Oystercatchers Haematopus ostralegus on the south coast of Norway. Wader Study Group Bull. 117, 62–63.

Tratalos, J.A., Sugden, R., Bateman, I.J., Gill, J.A., Jones, A.P., Showler, D.A., Sutherland, W.J., Watkinson, A.R., 2013. The conflict between conservation and recreation when visitors dislike crowding: a theoretical and empirical analysis of the spatial distribution of recreational beach users. Environ. Resour. Econ. 55, 447–465.

Valle, R.G., Scarton, F., 2019a. Drones improve effectiveness and reduce disturbance of censusing Common Redshanks Tringa totanus breeding on salt marshes. Ardea 107, 275–282.

Valle, R.G., Scarton, F., 2019b. Effectiveness, efficiency, and safety of censusing eurasian oystercatchers Haematopus ostralegus by unmanned aircraft. Mar. Ornithol. 47, 81–87.

van de Pol, M., Atkinson, P., Blew, J., Crowe, O., Delany, S., Duriez, O., Ens, B.J., Hälterlein, B., Hötker, H., Laursen, K., Oosterbeek, K., Petersen, A., Thorup, O., Tjørve, K., Triplet, P., Yésou, P., 2014. A global assessment of the conservation status of the nominate subspecies of Eurasian Oystercatcher Haematopus ostralegus ostralegus. Int. Wader Stud. 20, 47–61.

Verhulst, S., Oosterbeek, K., Ens, B.J., 2001. Experimental evidence for effects of human disturbance on foraging and parental care in oystercatchers. Biol. Conserv. 101, 375–380.

Virzi, T., 2010. The effect of human disturbance on the local distribution of American Oystercatchers breeding on barrier island beaches. Wader Study Group Bull. 117, 19–26.

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.

Woodward, I.D., Massimino, D., Hammond, M.J., Barber, L., Barimore, C., Harris, S.J., Leech, D.I., Noble, D.G., Walker, R.H., Baillie, S.R. & Robinson, R.A., 2020, BirdTrends 2020: trends in numbers, breeding success and survival for UK breeding birds. BTO Research Report 732. BTO, Thetford. <www.bto.org/birdtrends>.