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The hidden cost of disturbance: Eurasian Oystercatchers (*Haematopus ostralegus*) avoid a disturbed roost site during the tourist season

HENK-JAN VAN DER KOLK,*[1,2,3] BRUNO J. ENS,[2,4] KEES OOSTERBEEK,[4] EELKE JONGEJANS[1,2,5] & MARTIJN VAN DE POL[1,2,6]

[1]*Department of Animal Ecology, Netherlands Institute of Ecology, Wageningen, The Netherlands*
[2]*Centre for Avian Population Studies, Wageningen, The Netherlands*
[3]*Dutch Bryological and Lichenological Society, Utrecht, The Netherlands*
[4]*Sovon Dutch Centre for Field Ornithology, Sovon-Texel, Den Burg, The Netherlands*
[5]*Animal Ecology and Physiology, Radboud University, Nijmegen, The Netherlands*
[6]*College of Science and Engineering, James Cook University, Townsville, Australia*

Disturbance may impact individual birds and ultimately bird populations. If animals avoid disturbed sites this may prevent them from being disturbed directly but may also negatively impact their movement patterns and energy budgets. Avoidance is, however, challenging to study, because it requires following individuals over large spatial scales in order to compare their movement rates between sites in relation to spatiotemporal variation in disturbance intensity. We studied how 48 GPS-tracked non-breeding Eurasian Oystercatchers *Haematopus ostralegus* used two neighbouring roost sites in the Wadden Sea. One roost site is highly influenced by seasonal recreational disturbance whereas the other is an undisturbed sandbar. We analysed roost choice and the probability of moving away from the disturbed roost site with regard to a seasonal recreation activity index, weekends and night-time. Oystercatchers often chose to roost on the undisturbed site, even if they were foraging closer to the disturbed roost. The probability that Oystercatchers chose to roost on the disturbed site was negatively correlated with the recreation activity index and was lowest in the tourist season (summer and early autumn), indicating that birds used the site less often when recreation levels were high. Furthermore, the probability that birds moved away from the disturbed site during high tide was positively correlated with the recreation activity index. The choice to roost on the undisturbed site implies that birds must fly an additional 8 km during one high-tide period, which equates to 3.4% of daily energy expenditure of an average Oystercatcher. Our study tentatively suggests that the costs of avoidance may outweigh the energetic cost of direct flight responses and hence that avoidance of disturbed sites requires more attention in future disturbance impact studies. Nature managers should evaluate whether high-quality undisturbed roosting sites are available near foraging sites, and in our case closing of a section of the disturbed site during high tides in the tourist season may mitigate much disturbance impact.

Keywords: avoidance, energy expenditure, recreation, shorebirds, tourism, Wadden Sea.

Minimizing the impacts of disturbance on wildlife is a major challenge for nature managers (Monz *et al.* 2013). Disturbance by human activities can negatively impact wildlife by increasing energy expenditure and altering behavioural patterns, which may ultimately decrease fitness or lower carrying capacity (Platteeuw & Henkens 1997, Gaynor *et al.* 2018). Most noticeably, disturbance causes animals to elicit flight responses, resulting

*Corresponding author.
Email: henk-jan@blwg.nl
Twitter: @hjvdkolk

in additional energy expenditure and loss of foraging time (Platteeuw & Henkens 1997, Frid & Dill 2002). However, animals may also change their space use in response to the presence of human activities. For example, animals may avoid human infrastructure or increase their home range on days with more human activities (Benítez-López *et al.* 2010, Perona *et al.* 2019). If animals change their space use and avoid human activities, this may prevent them from being directly disturbed. However, there may be other costs associated with changing space use, including increased commuting distances, avoidance of preferred or high-quality feeding areas, and increased competitor densities (Fernández-Juricic & Tellería 2000, Bautista *et al.* 2004, Rutten *et al.* 2010) causing faster depletion of food at undisturbed sites. All of these costs caused by changes in space use may contribute to increased energetic costs and lower intake. It is, however, challenging to study avoidance of disturbed sites because it requires that individuals are followed over large spatial scales to compare their movement rates between sites in relation to spatiotemporal variation in disturbance intensity.

Shorebirds are an interesting case study to quantify the impacts of disturbance on space use, as they commute between foraging areas at low tide and roost sites at high tide. Therefore, it is essential for shorebirds that there is a network of roost sites that provides sufficient access to feeding sites (Dias *et al.* 2006). At the same time, the coastal habitats inhabited by shorebirds worldwide are often also used for many human activities (Davidson & Rothwell 1993, Wallace 2016). The presence of human disturbances can prevent shorebirds from using certain roosting or feeding sites (Burton *et al.* 1996, McCrary & Pierson 2000, Meager *et al.* 2012, Navedo & Herrera 2012, Burger & Niles 2013, Drever *et al.* 2016). For example, numbers of shorebirds were shown to be lower in the presence of high levels of recreational activities (e.g. walkers and birdwatchers) (Kirby *et al.* 1993, McCrary & Pierson 2000, Burger & Niles 2013) and local declines in shorebird numbers over time have been associated with increased recreational activities (Mitchell *et al.* 1988, Burton *et al.* 1996). Reduced use of disturbed sites could be a result of birds being frequently (e.g. every morning or every high-tide period) disturbed, as a result of which they temporarily move to other areas, meaning that on average a lower number of birds can be observed. Alternatively, birds may completely avoid areas with a high level of disturbance, and so no longer reside there, even at times when levels of recreation are relatively low. It is, however, often difficult to quantify the impacts of disturbance on space use, given that space use under normal conditions is determined by a complex interaction of environmental variables such as weather and time of day (e.g. van Beest *et al.* 2012).

High-tide roost choice of shorebirds is probably determined by the energetic costs of commuting and the roost site characteristics (Rogers 2003, Rogers *et al.* 2006a, 2006b). From an energetic perspective it is best to minimize the flight distance between feeding sites and roosting sites. Shorebirds are therefore expected to roost on the site that is closest to their feeding grounds (Rogers *et al.* 2006a). Roost site characteristics, however, may make birds choose to roost on more distant sites. First, variation in microclimate among roost sites can influence the high-tide roost choice of shorebirds. For example, on windy days shorebirds may prefer sheltered sites (Peters & Otis 2007) and in warm regions shorebirds may prefer to roost on wet substrates to reduce heat stress during daytime (Rogers *et al.* 2006a). Secondly, shorebirds may choose to fly farther to roosts where the predation risk is lower (Piersma *et al.* 1993, 2006, Rogers *et al.* 2006a, Rosa *et al.* 2006, Conklin *et al.* 2008). In a similar way, because birds perceive danger from the presence of human activities (Frid & Dill 2002), the presence of human disturbance sources may prevent birds from choosing their optimal roosting sites. Studying human disturbance is especially important because the frequency of human activities can affect how strongly birds respond to disturbance and may result in redistribution of birds such that only the most tolerant individuals stay in the most disturbed sites (e.g. Webb & Blumstein 2005). A few studies have investigated roost use by shorebirds in relation to disturbance intensity. For example, Short-billed Dowitchers *Limnodromus griseus* avoid roosts with high boat activity nearby (Peters & Otis 2007). In other studies, no impacts of disturbance were found on roost site selection of Dunlins *Calidris alpina* and Whimbrels *Numenius phaeopus* (Conklin *et al.* 2008, Johnston-González & Abril 2019). No study has yet focused on how roost choice is related to recreational disturbance that varies throughout the year, and in general studies focusing on roost choice of shorebirds are lacking for the Wadden Sea area.

Eurasian Oystercatchers *Haematopus ostralegus* (hereafter Oystercatchers) winter in large numbers in the Wadden Sea, where they face numerous human activities. The population of Oystercatchers in the Wadden Sea has declined over the last few decades and disturbance is one of the potential drivers that has been insufficiently studied (van de Pol *et al.* 2014). In a previous study, we visually observed how often birds were disturbed at five high-tide roost sites (van der Kolk *et al.* 2020a) that were influenced by either military aircraft or recreational disturbance, but could not analyse whether birds were less likely to roost on these sites when disturbances occurred more frequently. On one roost site ('Westerseveld') on the Wadden island Vlieland, we noticed that Oystercatchers were scarce in summer and early autumn, even though by the beginning of August most Oystercatchers have returned to the Wadden Sea from their breeding grounds. The roost location at Westerseveld is accessible for walkers, who disturb roosting birds on average 0.26 times per hour (van der Kolk *et al.* 2020a). In other seasons, when birds were present at Westerseveld at the start of the high tide, we observed that upon disturbance birds often flew to Richel, a deserted sandbar that is located 4 km eastwards and is protected by bird wardens. Based on these observations, we hypothesized that Oystercatchers avoid roosting at Westerseveld during periods when most tourists are present on the island (i.e. in summer and early autumn), and instead directly fly to Richel at the start of the high-tide period, even though this roost is farther away from their feeding grounds. Additionally, levels of recreation at Westerseveld are higher on weekends compared with weekdays, and recreation occurs mostly during daytime. Since time of day and day of the week were previously shown to affect space use by birds (Conklin & Colwell 2007, Perona *et al.* 2019), we expected that Oystercatchers would also avoid Westerseveld more at weekends and during daytime. There are no other frequently used high-tide roost sites in the vicinity, meaning that these two sites provide a simple and powerful case study to compare roost choice between a disturbed and undisturbed roost location.

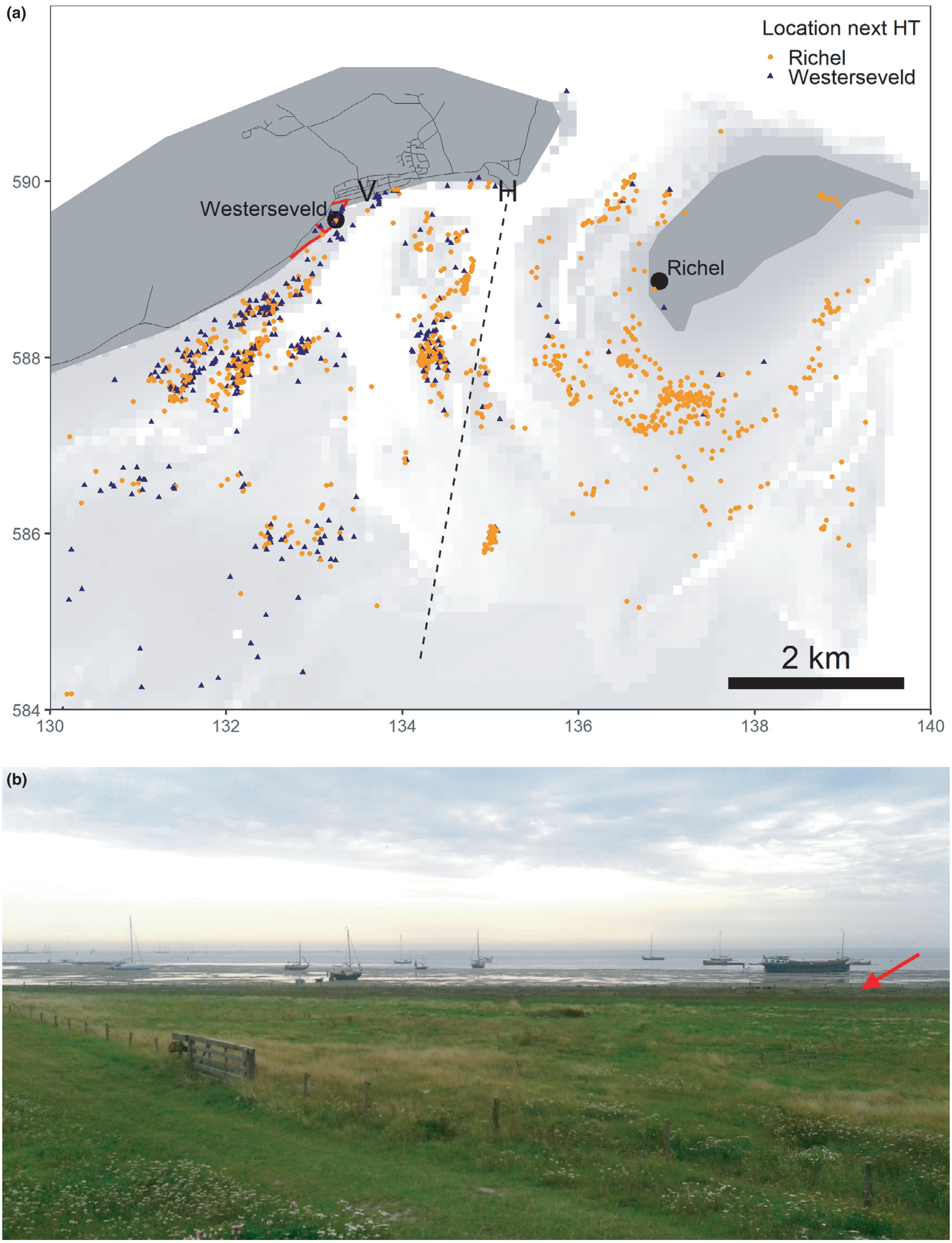
In this study, we use data from 2016 to 2020 on 48 GPS-tracked non-breeding Oystercatchers to quantify (1) the probability that Oystercatchers chose to roost on Westerseveld over Richel and (2) the probability that Oystercatchers move away from Westerseveld during high tide. We quantified whether these variables were explained by three proxies of the amount of human disturbance: (1) time of the day (daytime versus night-time), (2) day of the week (weekday versus weekend) and (3) an index of how recreational activity varies throughout the year, derived from boat activity in the Wadden Sea. We predicted that birds avoided the Westerseveld roost during the tourist season (summer and adjacent months when the recreation activity index is high), and if avoidance acts on shorter timescales, also during daytime and weekends.

METHODS

Study system

The Oystercatcher is a long-lived shorebird that breeds in coastal areas in northwest Europe and winters in large numbers in tidal estuaries around the North Sea such as the Wadden Sea. During low tide, birds forage on shellfish on mussel beds and other intertidal mudflats. During high tide, birds roost in flocks on elevated sandflats, saltmarshes, polders, dunes and dikes. Typically, high-tide roosts are located within a few kilometres from the foraging areas (Bakker *et al.* 2021).

Our study focuses on the Wadden island Vlieland and the sandflat Richel in the Western Wadden Sea (Fig. 1). The island counts around 1150 inhabitants but is annually visited by 150 000 tourists. Adjacent to the only village on the island, a field enclosed by a low dike is used as a high-tide roost by Oystercatchers (Westerseveld, Fig. 1). Recreational disturbance is common, especially by walkers (sometimes with their dogs) who are allowed to walk over the dike and thereby disturb roosting birds, causing Oystercatchers to fly up on average 0.26 times per daylight hour (van der Kolk *et al.* 2020a). Richel is a protected deserted sandflat for which access is denied to tourists and boats. There are no other sites within a range of 7 km that are frequently used as a high-tide roost by Oystercatchers. The nearest roost sites are at Kroonpolders (7 km southwest from Westerseveld), the Noordsvaarder on the island Terschelling (8 km north of Richel) and the island Griend (10 km southeast of Richel).


(a)
Location next HT
Richel
Westerseveld
Westerseveld
V
H
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2 km
590
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586
584
130
132
134
136
138
140
(b)

Figure 1. (a) Map of the study area, showing the locations of the high-tide roosts at Westerseveld and at Richel (n = 1488 locations of non-breeding Oystercatchers between December 2016 and July 2020). Points show locations of Oystercatchers during low tide (6 h before high tide) and their shape–colour combination indicates where they were roosting during the upcoming high tide (blue triangles: Westerseveld, orange circles: Richel), measured 3 h before high tide. The dashed line indicates the mid-point between Westerseveld and Richel. When birds minimize their flight distance, individuals west from the line are expected to roost on Westerseveld and individuals east from the line are expected to roost on Richel. Dark grey colour is land, light grey colours are sandflats that are exposed during low tide, white colour is sea and black lines are roads. The footpaths at Westerseveld are indicated by red lines. V = Village, H = Harbour. (b) Picture of Westerseveld and adjacent intertidal flats on 15 August 2017, where the red arrow points towards the dike that is often used as a high-tide roost by Oystercatchers. In summer, boats fall dry in a small area directly east of Westerseveld, but not on the mudflats used as foraging area by Oystercatchers southwest of Westerseveld.

Data collection

GPS tracking data

In total, 82 wintering (70 (sub)adults and 12 first winter) and 20 local breeding Oystercatchers were caught with mist-nets and nest cages on the Vliehors (53.236°N, 4.934°E) and equipped with colour-rings and 13.5-g solar-powered UvA-BiTS GPS trackers (size 61 × 25 × 10 mm) between December 2016 and December 2018. The trackers were attached with a 2-g wing loop harness and the total weight of the device was ~3% of the body weight of a 500-g Oystercatcher. The annual re-sighting rate based on colour-ring readings was 48.8% for the 82 individuals that were equipped with GPS trackers in winter, and lower (non-significantly, χ^2 test, $P = 0.214$) than the re-sighting rate of 57.5% for 134 individuals that were simultaneously caught but equipped with only colour-rings and no GPS tracker. Additional mortality due to deployment of the GPS tracker may occur mostly suddenly or shortly after the GPS tracker is equipped as the result of stress; birds that were observed in the field looked healthy and did not show abnormal behaviour (see box 1 in chapter 8 in van der Kolk (2021) for more details on potential device effects).

The GPS trackers measured GPS locations at least once per hour when the battery was sufficiently charged. Although all birds were caught on the Vliehors, on the western half of the island Vlieland, many individuals regularly moved eastwards to forage and to roost at Westerseveld or Richel (for effective sample sizes see Data analysis section). See van der Kolk *et al.* (2020b, 2020c) for more details on the GPS tracking data collection.

Environmental data

Timings of high tides were obtained from Rijkswaterstaat for Vlieland harbour, located between Westerseveld and Richel. Weather variables were obtained from the weather station of the Royal Netherlands Meteorological Institute (KNMI) on Vlieland.

Recreation activity index

Most disturbance at Westerseveld is caused by walkers (van der Kolk *et al.* 2020a). To obtain an index of overall levels of disturbance we derived a recreation activity index from boat activity. Boat activity is a good proxy for the amount of recreation activity because many tourists arrive on Vlieland via passenger boats and smaller boats often reside in front of Westerseveld (Fig. 1). We used the monthly number of sailing ships (international Automatic Identification System (AIS) code 36), pleasure crafts (i.e. pleasure crafts for personal use, international AIS code 37) and passenger ships (AIS codes 60–69, excluding regular ferries) tracked with AIS in the Wadden Sea in 2015 as a proxy for the amount of recreation (Fig. 2; data provided in fig. 3.1 in Meijles *et al.* 2019, see also Meijles *et al.* 2021). Data from 2015 were used because this was the only year for which tracks in all months were available (Meijles *et al.* 2019). The total number of boat tracks per month (i.e. one unique boat could be included multiple times) was z-transformed in order to obtain a 'recreation activity index'. We transformed the number of boat tracks to ease interpretation of the other factors in the statistical models, and to highlight that the absolute number of boat tracks is in itself meaningless, but rather should be interpreted as a relative measure of how the intensity of tourism fluctuates throughout the year. The recreation activity index was low in winter (minimum −1.06 in February) and highest in summer (maximum 1.74 in August). Boat activity data were available on a monthly basis, so the recreation activity index could be used to detect seasonal patterns in space use, but not for more fine-scaled (intra-weekly or

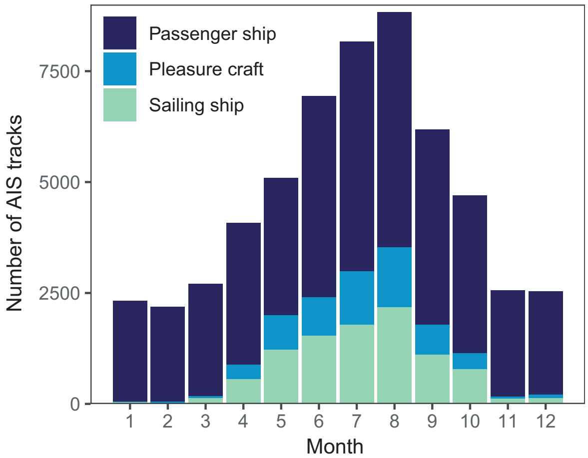

Figure 2. Cumulative monthly number of Automatic Identification System (AIS) boat tracks of passenger ships (AIS codes 60–69), pleasure craft (AIS code 37) and sailing ships (AIS code 36) in the Dutch Wadden Sea in 2015. Modified from figure 3.1 of Meijles *et al.* (2019). Data for all months were only provided for 2015 and not for other years.

intra-daily) patterns of space use. The recreation activity index was highly correlated with the average monthly number of overnight stays in the province of Friesland between 2012 and 2019 (n = 12 months, $R^2 = 0.934$, data from Statistics Netherlands (CBS) StatLine; see Fig. S1). Vlieland and three other Wadden islands are tourist hotspots in the province of Friesland. This provides confidence that the recreation activity index accurately describes how levels of tourism and recreation fluctuate throughout the year.

Data analysis

The purpose of the analysis was to study the probability that individuals would roost on Westerseveld (as opposed to Richel) and the probability that birds would leave Westerseveld during high tide (presumably due to disturbance), with respect to the time of day (daytime versus night-time), day of the week (weekday versus weekend) and the recreation activity index as a proxy for varying recreational activity throughout the year. All analyses were perfomed in R version 4.0.4 (R Core Team, 2021) and binary logistic mixed effects models were fitted using the *glmer* function of the *lme4* package (Bates *et al.* 2015).

We first selected for each bird and each high-tide period the GPS location 6 h before the peak of high tide (i.e. around low tide) as a measure of the foraging location. We then selected GPS locations in hourly intervals from 3 h before to 3 h after high tide (giving a total of seven GPS locations per individual per high-tide period). We chose this timespan because in our study area one tidal period (i.e. from one high tide to the next high tide) takes 12.4 h. Oystercatchers typically forage for 4–6 h around the moment of low tide and rest for a minimum of 6 h (i.e. from at least 3 h before to 3 h after high tide) at a roost (van der Kolk *et al.* 2020c). For each GPS location, we determined whether a bird was at Westerseveld, at Richel or at another location. We only retained data from high tides where birds visited Westerseveld or Richel. As birds were captured on the Vliehors (on roosts 10 km or more to the west of Westerseveld) and mostly roosted elsewhere, only 3.2% (~1650 out of ~51 600) of all bird – high tide combinations were included in this study. If birds roosted at Westerseveld or Richel, however, there was a 79% chance they also used one of these two roosts in the next high-tide period.

We derived two binary response variables for our analysis. First, for the subset of bird – high tide combinations in which birds roosted either on Westerseveld or on Richel, we derived whether birds chose to roost on Westerseveld as opposed to Richel 3 h before the peak of high tide. This time is early in the high-tide period so the probability that birds were already disturbed by then was relatively low. The location at this time can therefore be interpreted as roost site choice unaffected by disturbance during high tide itself that may cause displacement to another roost. Secondly, for the subset of bird – high tide combinations in which birds chose to roost at Westerseveld 3 h before the peak of high tide, we derived whether birds had moved away or were still present at Westerseveld 2 h after the high-tide peak. We measured the probability of having moved away at 2 h after the peak of high tide instead of 3 h after the peak because some birds returned from Richel to Westerseveld at the end of the high-tide period before foraging on nearby intertidal mudflats (see Results). Sample sizes were 1488 bird – high tide combinations from 48 individuals (range 1–328 observations per bird) and 998 unique high-tide periods for the initial roost choice and 411 bird – high tide combinations from 36 individuals (range 1–120 observations per bird) and 305 unique high-tide periods for the probability of moving away from Westerseveld during high tide. Data from 56 individuals with GPS trackers were not used because they never roosted on Westerseveld or Richel.

Both variables were used as the response variable in a binary logistic mixed effects model using bird individual as a random intercept to account for individual consistency in roost site choice. Day of the week (weekday or weekend), time of day (proportion of night, calculated as the proportion of the high-tide period between sunset and sunrise) and recreation activity index were added as explanatory variables. Two-way interactions were included between time of day and day of the week and between time of day and recreation activity index, because we expected an effect of weekend and recreation index during daytime but not during night-time. Wind speed was added as confounding variable, because we observed in the field that on windy days Oystercatchers tended to roost more on Westerseveld, probably because it is sheltered (by a dune) compared with the open sandflat of Richel. Windspeed was *z*-standardized before analysis. In the model for the initial roost choice, the distance between foraging location and roost sites was included as an additional explanatory variable. This distance variable was calculated by the distance from the foraging location (6 h before high tide) to Richel minus the distance from the foraging location to Westerseveld. As a result, if this value was negative, birds were foraging closer to Richel than to Westerseveld, and were expected to roost on Richel if they aimed to minimize flight distance. The interpretation of the results would not change when using a different timing for the reference position of the foraging location, i.e. 5 h or 4 h before high tide instead of 6 h before high tide (see Fig. S2).

RESULTS

The spatial position of a bird's feeding ground significantly predicted which roost site they chose ($P < 0.0001$; Table 1, Fig. 3a). However, although birds that foraged closest to Richel had a 95.2% probability of also roosting at Richel, birds that foraged closest to Westerseveld only had a 41.5% probability of roosting at Westerseveld (Fig. 3a). As predicted under the avoidance hypothesis, a bird's initial choice to roost at Westerseveld (measured 3 h before high tide) was significantly negatively correlated with the recreation activity index

Table 1. Binomial mixed effects model predicting whether Oystercatchers initially choose to roost on the more frequently disturbed site Westerseveld (WV; 1) or on Richel (RI; 0), based on their location 3 h before high tide. Night is the proportion of the high tide between sunset and sunrise. Weekend reflects whether a tide was during the weekend or not. Distance to RI – distance to WV is a measure of relative proximity to WV of a bird's foraging location during low tide (high tide – 6 h). Windspeed was standardized before analysis. Sample size is 1488 bird – high tide combinations (from 48 bird individuals).

Predictor	Estimate	se	*P* value
Intercept	–1.15	0.26	< 0.0001
Night	–2.08	0.28	< 0.0001
Weekend	0.27	0.27	0.3171
Recreation activity index	–1.23	0.16	< 0.0001
Night * Recreation activity index	0.75	0.28	0.0078
Night * Weekend	0.00	0.42	0.9916
Distance to RI – distance to WV	0.54	0.05	< 0.0001
Windspeed	0.52	0.08	< 0.0001
$\sigma^2_{residuals}$	3.29		
σ^2_{BirdID}	1.19		
Marginal R^2	0.507		
Conditional R^2	0.637		

($P < 0.0001$; Table 1, Fig. 3b), and more strongly so during daytime than night-time (interaction night * recreation activity index: $P = 0.008$). It is important to note that the recreation activity index correlates strongly with season (Fig. 2). Specifically, in summer almost all birds chose to roost at Richel instead of Westerseveld, whereas in winter Westerseveld was more often used (Fig. 4). The time of day significantly affected roost choice, but contrary to our prediction on avoidance acting on shorter timescales, birds avoided roosting at Westerseveld more at night than during the day ($P < 0.0001$; Table 1). The probability that birds chose to roost on Westerseveld did not significantly differ between weekdays and weekend ($P = 0.317$; Fig. 3c), independent of whether high tide was during the day or at night-time. During windy high tides, birds were more likely to roost at Westerseveld ($P < 0.0001$; Table 1).

Birds that initially roosted at Westerseveld often moved away during high tide (Fig. 4), possibly as a result of disturbance. Specifically, 37.7% of birds present at Westerseveld 3 h before high tide had left the roost 2 h after high tide (Fig. 4). The probability of displacement was significantly positively related to the recreation activity index ($P = 0.016$; Table 2, Fig. 5a), indicating that birds

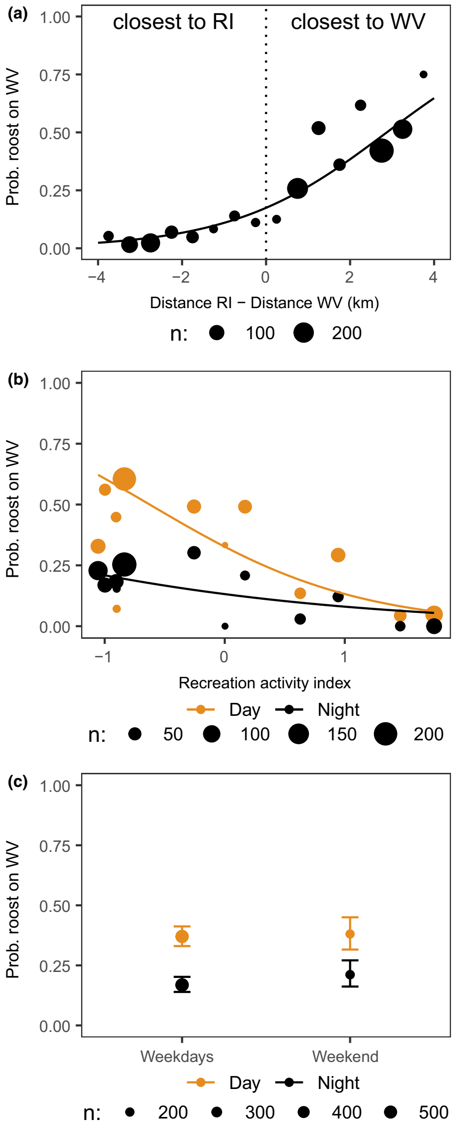

Figure 3. (a) Relationship between the foraging location of a bird 6 h before high tide and the probability of choosing to roost at Westerseveld (opposed to Richel) 3 h before high tide. The foraging location is expressed as the distance from the foraging location from Richel (RI) minus the distance from the foraging location to Westerseveld (WV), meaning that negative values indicate birds were closest to Richel and positive values indicate birds were closest to Westerseveld. (b) Relationship between recreation activity index and the probability that birds choose to roost on Westerseveld 3 h before high tide during daytime high tides and night-time high tides. (c) Probability that birds choose to roost at Westerseveld 3 h before high tide during either weekdays and weekends and daytime and night-time high tides (±95% confidence interval). In (b), each point represents data from 1 month. The point size indicates the sample size (number of bird – high tide combinations). All plots show the raw uncorrected data with model fits as lines in (a) and (b); see Table 1 for statistical significance.

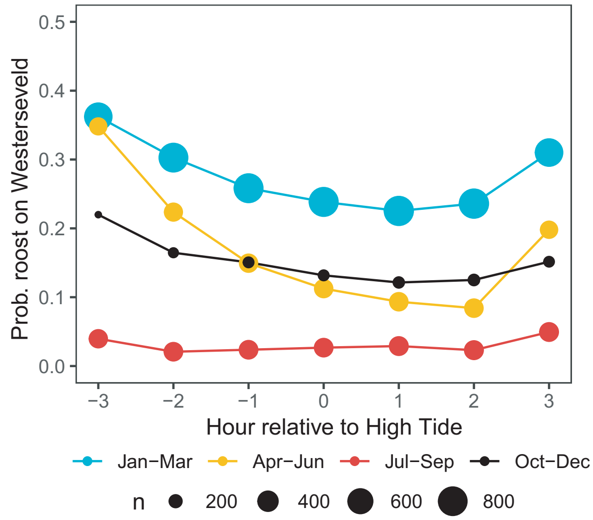

Figure 4. Relative proportion of GPS-tagged Oystercatchers roosting at Westerseveld (i.e. birds at Westerseveld divided by the total number of birds at Westerseveld and Richel) in relation to different timings relative to high tide for each of the four seasons.

moved away during high tide more often in months with high levels of recreation. The relationship between displacement probability and recreation activity index did not significantly differ between daytime and night-time high tides ($P = 0.510$; Table 2). In general, birds were more likely to displace during night-time high tides ($P = 0.0003$; Table 2), but displacement did not differ between weekdays and weekends ($P = 0.400$; Table 2, Fig. 5b). After moving away from Westerseveld, 47% of birds returned to Westerseveld between 2 and 3 h after high tide, shortly before the start of the low-tide foraging period (Fig. 4). During windy high tides birds were less likely to move away from Westerseveld ($P < 0.0001$, Table 2), as expected because Westerseveld is more sheltered as a result of its vicinity to dunes.

DISCUSSION

Factors determining roost choice of Oystercatchers

Our study shows that the probability of Oystercatchers roosting on Westerseveld is related to an index of recreation activity. The most likely explanation of why birds avoid roosting on

Table 2. Binomial mixed effects model predicting whether Oystercatchers moved away from Westerseveld during high tide after they initially chose to roost there 3 h before high tide. See Table 1 for an explanation of the explanatory variables. Sample size is 411 bird – high tide combinationss (from 36 bird individuals).

Predictor	Estimate	se	*P* value
Intercept	–0.03	0.35	0.9337
Night	3.42	0.94	0.0003
Weekend	–0.31	0.37	0.4002
Recreation activity index	0.71	0.30	0.0160
Night * Recreation activity index	–0.62	0.94	0.5100
Night * Weekend	0.16	0.92	0.8623
Windspeed	–1.08	0.16	< 0.0001
$\sigma^2_{residuals}$	3.29		
σ^2_{BirdID}	0.92		
Marginal R^2	0.423		
Conditional R^2	0.549		

Westerseveld in the months when the recreation activity index is high is the large number of tourists present on the island, who also frequently walk by the roost site. The GPS data are supported by our previous observations in the field that even when birds choose to roost at Westerseveld, they are often disturbed and then fly off to Richel (van der Kolk *et al.* 2020a). The high probability that birds will be disturbed eventually during high tide on Westerseveld may be the reason why Oystercatchers often choose to fly to Richel immediately at the start of the high-tide period and avoid roosting on this frequently disturbed site, especially during summer when levels of recreational disturbance are high.

We expected that birds may roost more often at night at Westerseveld, as levels of human disturbance are lower at that time of day. However, we found the opposite pattern and Oystercatchers avoided roosting at Westerseveld during nighttimes. Day–night patterns in roost choice have been linked to predation risk (Piersma *et al.* 2006, Rogers *et al.* 2006a). Possibly, Oystercatchers may perceive roosting at Westerseveld as being more dangerous at night, for example because of the presence of ground predators (e.g. feral cats), compared with the sandbar Richel where no ground predators occur. If this also causes Oystercatchers to move away from Westerseveld after sunset, this could explain why the probability of moving away from Westerseveld is higher at high tides that are (partly) during night-time.

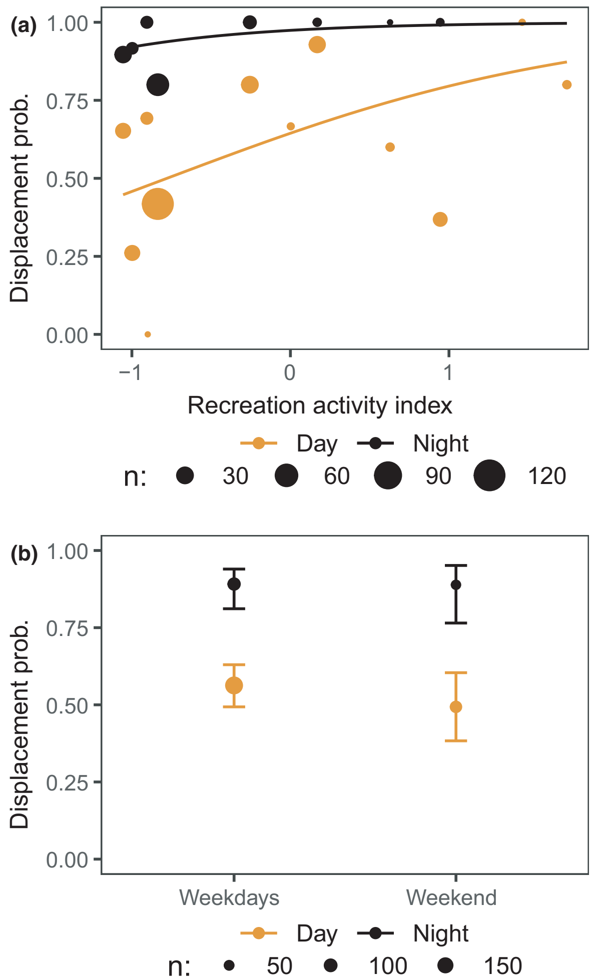

Figure 5. (a) Relationship between the recreation activity index and the probability that birds move away from Westerseveld during high tide for daytime and night-time high tides. (b) Probability that birds move away from Westerseveld during high tides during either weekdays and weekends and daytime and night-time high tides (± 95% confidence interval). In (a), each point represents data from 1 month. The point size indicates the sample size (number of bird – high tide combinations). Both plots show the raw uncorrected data with model fits as lines in (a); see Table 2 for statistical significance.

Some previous studies have shown how space use by animals is more severely affected during weekends than during weekdays (Bautista *et al.* 2004, Pirotta *et al.* 2018), but we did not find a 'weekend effect'. An explanation for the absence of such an effect is that most recreational disturbance is caused by tourists who generally stay on the island for multiple days or a whole week, as a result of which the intensity of recreational activities potentially does not vary much between weekdays and the weekend. Other factors, such as weather, may be more important than day of the week in determining whether or not tourists are present and cause disturbance at Westerseveld.

On windy high tides Oystercatchers were more likely to roost and stay on Westerseveld, possibly because on windy days there may be fewer tourists near the roost. An alternative explanation, however, is that the roost at Westerseveld is sheltered, especially in contrast to the open sandflat Richel. It was found in other studies as well that shorebirds preferred to roost on places sheltered by vegetation on windy high tides (e.g. in Dunlins, Handel & Gill 1992). Additionally, in our study area strong winds often co-occur with high water levels, which results in flooding of a large part of Richel, leaving little space for the birds to rest.

Our results should be interpreted with caution, because the recreation activity index is highly correlated with seasons, and there may be alternative explanations for why Oystercatchers avoid roosting at Westerseveld in summer. A first alternative explanation is that the presence of raptors at Richel and Westerseveld fluctuates among seasons. Specifically, Peregrine Falcons *Falco peregrinus* are more abundant at Richel in winter and Hobbies *Falco subbuteo* are migratory raptors breeding in summer near Westerseveld. If Oystercatchers perceive risk from these raptors, they may decide to adjust their behaviour accordingly (see e.g. Peters & Otis 2005) and may avoid Richel in winter and Westerseveld in summer. Secondly, differences in microclimate between roost sites may affect roost choice. Shorebirds have been shown to prefer to roost on cool and wet substrates in warm weather, probably to avoid heat stress (Rogers *et al.* 2006a). Indeed, in the warm summer months Oystercatchers may prefer to roost at Richel where it is easy to stand on wet substrates in or near the cool water, whereas at Westerseveld the presence of a dike prevents birds from roosting on a wet substrate. We did not include temperature as an explanatory factor in our model, because temperature is likely also to affect the level of recreation near the roost. Hence, it would be impossible to separate effects between microclimate and varying levels of recreation by adding temperature as an additional covariate. In general, the fact that recreational activity is confounded with other potential seasonal drivers of habitat selection (e.g. weather, predation pressure) is a challenge in studying avoidance of disturbed sites, as recreation exhibits clear seasonal patterns in most places (e.g. Peters & Otis 2005). Possibly, as a consequence, many studies have focused on avoidance over shorter timescales, such as between weekdays and weekend (Longshore *et al.* 2013), for which confounding with other temporal patterns is less likely. However, we stress that avoidance at seasonal timescales is from a biological perspective at least as important to understand and in need of more study.

Implications of avoidance for energy expenditure

Birds that forage close to Westerseveld and roost at Richel must commute over larger distances which has a large impact on their energy expenditure. The extra flight distance amounts to 8 km (forth and back from Westerseveld to Richel) in a single high-tide period, and given that Oystercatchers have an average flight speed of 12 m s^{-1} (Linssen *et al.* 2019) and flight costs are 36 J s^{-1} (Pennycuick 2008), this amounts to a flight time of 11 min and an additional energy expenditure of 24 kJ. An Oystercatcher with a weight of 550 g has a daily energy expenditure of about 700 kJ (Zwarts *et al.* 1996), implying that roosting on Richel instead of roosting at Westerseveld increases daily energy expenditure by 3.4%. Given that Oystercatchers forage on average for around 9 h per day, to compensate Oystercatchers would have to lengthen their daily foraging time by 18 min. These costs of avoidance are about ten-fold the energetic costs of normal levels of disturbance due to aircraft, recreation and birds of prey at high-tide roost sites in our study area, which increased daily energy expenditure by 0.2–0.6% per high-tide period (van der Kolk *et al.* 2020a). Thus, the costs of avoidance can outweigh the more direct costs of disturbance, and while more studies are needed to determine whether this is a more general pattern, the ten-fold higher estimated costs of avoidance reported here do suggest that this indirect aspect of disturbance needs more attention.

There are three potential explanations of why birds choose to fly to Richel, even though the energetic costs are seemingly higher than if they were to stay at Westerseveld. First, birds may perceive danger and decide to avoid areas with high levels of recreation (Rösner *et al.* 2014). Secondly, in summer Westerseveld may be often so crowded with people that there is limited or no space for birds to roost. Thirdly, birds may have redistributed such that only the least sensitive birds roost at Westerseveld (Carrete & Tella 2013). If such redistribution occurs, the energetic costs of disturbance at Westerseveld may have been underestimated for more sensitive birds that now choose to roost at Richel.

Management implications of roost site avoidance

For shorebirds in coastal areas it is essential that high-quality foraging and roosting areas are available within close range of each other (Zharikov & Milton 2009). Preventing roost quality loss due to disturbance is a challenge for coastal management, as in many areas (like in the Wadden Sea) high levels of recreation can have a large disturbance impact, but at the same time nature recreation contributes to the general support for nature protection. Our study provides an example of a roost site that is underused during the months with highest levels of recreational activities, probably because of human disturbance. We encourage nature managers to ensure that undisturbed roosting sites are available within close range of high-quality foraging areas. BirdLife Netherlands already prioritizes the detection of underutilized roost sites in the Wadden Sea estuary and aims to improve the roost quality or create new disturbance-free roosts at such locations (van der Hut *et al.* 2014).

Specifically at our study site, closing off a section of the dike at Westerseveld for recreation during high tide (e.g. using a traffic light system) may result in shorebirds roosting more frequently at Westerseveld (meaning they have to fly shorter distances to their feeding grounds) and shorebirds being disturbed less often, especially in summer. If a section of the dike were to be closed for recreation, the number of roosting birds should be monitored frequently throughout the year, first in disturbed conditions (i.e. the current 'disturbed situation') and then throughout at least 1 year following closure of the dike for tourists (i.e. 'undisturbed condition'). A comparison of high-tide roost utilization between years with and without disturbance can then reveal whether our findings were indeed caused by high levels of disturbance. We also recommend that upcoming dike reinforcements can best be done in late summer when levels of recreational disturbance are already high.

Our case study focuses on only two roost sites and the lack of replication makes it difficult to generalize our findings, but also reflects the challenge of finding situations where avoidance can be studied (i.e. where animals have a clear choice between one disturbed and one undisturbed site). Nevertheless, we encourage future studies to include multiple roost and foraging sites with varying levels of human disturbance to understand the extent to which roost choice of shorebirds is influenced by the presence of human activities.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

AUTHOR CONTRIBUTION

Henk-Jan van der Kolk: Conceptualization (lead); Formal analysis (lead); Investigation (equal); Writing – original draft (lead). **Bruno Ens:** Conceptualization (supporting); Supervision (equal); Writing – review & editing (equal). **Kees Oosterbeek:** Investigation (equal). **Eelke Jongejans:** Conceptualization (supporting); Supervision (supporting); Writing – review & editing (equal). **Martijn van de Pol:** Conceptualization (supporting); Supervision (equal); Writing – original draft (supporting); Writing – review & editing (equal).

ETHICAL NOTE

Tagging of Oystercatchers was done under license of the Dutch Flora and Fauna Law (FF/75A/2013/038), the Natuurbeschermingswet (Province of Friesland, 801233) and approved by the Dutch Ethical Committee (Sovon AVD25002015200-001).

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Data Availability Statement

All oystercatcher GPS data are available in Movebank (https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1605802367). The data used in this study are available in Dryad (https://doi.org/10.5061/dryad.2z34tmpkq, data Chapter 7).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Correlation between boat tracks in the Wadden Sea in 2015 (used in our paper as recreation activity index) and the tourist overnight stays in the province of Friesland in the period 2012–19.

Figure S2. Relationship between the relative distance of the foraging location to the roosts Richel (RI) and Westerseveld (WV) and the probability that birds would choose to roost at Westerseveld (as opposed to roosting at Richel). The relationships are shown for choosing three different timings of the 'foraging location' at low tide.