Level of local human disturbance and feeding state determines escape behaviour in Eurasian Oystercatchers

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Abstract

Human disturbances may constitute a significant stressor for wildlife, especially where human recreational activities overlap with fitness-enhancing activities such as feeding. Disturbances cause an animal to flee from the perceived predation risk, using energy, rather than remaining and gaining energy. Such reactions are, however, context-dependent, as predicted by optimal escape theory: animals should only flee when the perceived risk of predation of remaining exceeds the risk of starvation of leaving. Animals may also learn that humans do not generally represent a predation risk after repeated false alarms and then learn to only respond when approached deliberately and closely. We tested the Flight Initiation Distance (FID; distance at which an approached animal begins escape) of feeding or roosting Eurasian Oystercatchers *Haematopus ostralegus* (oystercatchers) to a human (as a simulated predator) in areas with or without humans on beaches in south-east Scotland. We predicted roosting oystercatchers to respond earlier (greater FID) than feeding birds because the risk of starvation will be lower, and earlier on beaches where there were no humans at the start of the experiment because a human will then represent a more novel predator signal. As predicted, oystercatchers escaped at greater distances away from the perceived threat when feeding and in areas with humans. We found that escape distances decreased (greater tolerance of the perceived threat) as the number of people in an area increased, but people being present or not explained more of the variation in the data. The results show that oystercatchers habituate on a short timescale to non-lethal human presence and generally respond to perceived predation risk in accordance with the predictions of optimal escape theory.

Introduction

Wildlife generally responds to humans as they would do to a predator, making human disturbance an important source of perceived predation risk with significant fitness implications (Allan, Bailey, & Hill, 2020; Beale & Monaghan, 2004; Frid & Dill, 2002; Müllner, Eduard Linsenmair, & Wikelski, 2004). The impact of human-induced disturbances on wildlife has increased with increasing human population (Baker & Leberg, 2018). Therefore, the need to protect wildlife, especially in the areas where their fitness-enhancing activities overlap with recreational activities by humans, has also increased (Larson, Reed, Merenlender, & Crooks, 2016). This increased need makes the understanding of the escape behaviour of wildlife in response to non-lethal human activities crucial and relevant.

When initiating escape in response to an approaching potential predator, wildlife incur some fitness costs in terms of lost opportunities (e.g., leaving a profitable feeding patch) and energetic costs (e.g., energy used for locomotion) (Frid & Dill, 2002; Lagos et al., 2009). Optimal escape theory proposes that an animal should employ the economic principle of optimisation of trade-offs when approached by a potential predator by initiating escape at a distance where the cost of staying exceeds the benefit of staying (Cooper & Frederick, 2007; Ydenberg & Dill, 1986). Flight initiation distance (FID), the distance at which an approached individual initiates escape in response to a potential predator, can then be used to quantify the risk that an organism is willing to take given the costs and the benefits associated with each predator-prey encounter (Møller & Liang, 2013; Sol et al., 2018; Stankowich & Blumstein, 2005). Any factor that affects the starvation/predation risk trade-off will then affect FID. For example, factors relating to the animal's state (e.g., body condition) and environment (e.g., distance to protective cover or being among a large flock so that risk is diluted) will influence the costs and the benefits of escape and therefore affect the FID of an organism (Allan et al., 2020; Braimoh et al., 2018; Cooper, 2007; Stankowich & Blumstein, 2005; Zaman, Rakha, Wrensford, & Zhu, 2020). Therefore, the activity of the individuals at the time of each approach should influence the risks that individuals are willing to take during encounters with potential predators. For example, individuals feeding in a potentially food-rich area and at a time when food is likely more available should be expected to take more risk than roosting individuals (Lagos et al., 2009; Mbise et al., 2020).

Ordinarily, the risk perceived by animals and the associated human disturbance effects should increase as the number of humans in an area increase (Beale & Monaghan, 2004), but habituation or tolerance to non-lethal human presence may cause a waning of responses to humans, thereby resulting in a decline of sensitivity (shorter FID) as the number of people in an area increase (Mikula, 2014; Webb & Blumstein, 2005). Many studies have shown the behavioural waning of responsiveness by wildlife to repeated, non-lethal stimuli over time (Cavalli, Baladrón, Isacch, Biondi, & Bó, 2018; Gazagne et al., 2020; Raderschall, Magrath, & Hemmi, 2011; Rankin et al., 2009; Whittaker & Knight, 1998). Wildlife are therefore expected to be more habituated to humans in sites with greater human use (Mbise et al., 2020; Rodriguez-Prieto, Fernández-Juricic, Martín, & Regis, 2009; Webb & Blumstein, 2005). By learning to habituate to frequent non-threatening human activities, wildlife may be able to reduce the costs associated with fleeing from humans and thereby use areas of high human use (Blumstein, 2016; Knight, 2009; Shen et al., 2020).

An individual's level of habituation at any given time should be related to the sum of all its previous non-lethal exposures to humans (Cavalli et al., 2018; Knight, 2009). However, while the overall previous experiences of an individual to non-lethal human disturbance should count (Blumstein, 2016; Eason, Sherman, Rankin, & Coleman, 2006), the sensitivity of an organism to the first non-threatening person in its vicinity on a short timescale would be expected to be stronger than for the subsequent additional humans coming into its vicinity. This is because, on a short spatiotemporal scale, individuals in areas where there have been humans present in a non-predatory way are likely to regard another human as similarly non-threatening even if they approach. But a new human appearing in an area where there are no other humans represents an unknown threat. Therefore, when determining the presence or degree of habituation of organisms to levels of non-lethal human disturbance, the presence or absence of humans may be more important than the absolute number of people using an area.

We tested the responses of Eurasian Oystercatchers *Haematopus ostralegus* (oystercatchers) to a human-simulated predator in sites where their activities overlap with human recreational activities along the sandy beaches of south-east Scotland (St Andrews and Crail, Fife). Oystercatchers, like most shorebirds utilising coastal habitats, feed predominantly at low tide (Burger, 2018; Fonseca, Basso, Serrano, & Navedo, 2017). We assumed that individuals roosting during low tide would have foraged and met their energy budgets, whereas feeding individuals still required energy. Hence, we predicted that roosting oystercatchers approached by a human-simulated predator during the period of low tide would escape sooner (i.e., longer FIDs) than feeding oystercatchers. We also predicted that oystercatchers tested in areas where humans were already present before the start of the test would be less wary of humans (i.e., shorter FIDs) compared with oystercatchers tested in areas where humans were absent at the start of the approach. We anticipated FID to be negatively correlated with the number of people in an area (Mikula, 2014), but tested whether the presence or absence of humans was a better predictor of FID rather than absolute number. Potential confounding factors which may affect the foraging profitability of the beaches used by the oystercatchers (habitat type, tide height and time of day) and the risks a predator represents (distance that a predator starts its approach, group size, presence of other species, and distance to nearest neighbour) which have been previously shown to influence FIDs of wildlife in other studies (e.g., Blumstein 2003; Tatte et al. 2018; Mayer et al. 2019), were also recorded and controlled for in the analysis.

Methods
Field methods
The model species in this study is the Eurasian Oystercatcher *Haematopus ostralegus* (oystercatchers). This study was carried out in four sandy beaches (Crail, Kingsbarns, East Sands and West Sands) fringed by rocks between St. Andrews and Crail, Fife, Scotland. Rocky shores used as roosting sites by shorebirds were usually available up to 300 meters away from the shore at low tide. Crail beach is about 6 km from Kingsbarns which is about 11km from East Sands which is located about 3 km from West Sands. All four beaches receive visitors regularly with people often walking, picnicking, and with children playing. Dogs off the leash are allowed on all four beaches.

Only one observer (BA) conducted the experiment by walking through the sites looking for oystercatchers occurring singly or in groups, by eye and through a pair of binoculars (8 x 42 mm) between 08–24 April 2017. All observations were made on the feeding/roosting grounds of the species, hence, none of the individuals tested were nesting. Also, none were with chicks at the time of the approach (chicks appear in June). Once the focal species was sighted, the date and time of observation, the sighting distance (distance at which the observer first sighted the focal bird, measured as the distance between the observer's position and that of the focal bird) were recorded. The site (Crail, Kingsbarns, East Sands or West Sands), habitat type (Rocky, Sandy or Mixed) and group size within a 10-meter radius of focal bird (Fernández-Juricic, Jimenez, & Lucas, 2001) (recorded as the number of oystercatchers, number of other birds and the total number of birds) were noted. The flock type (as either a single species flock or a mixed-species flock), the activity of the focal birds (feeding, preening or roosting) and the distance between a focal bird and its nearest neighbours (estimated by eye as the distance between a focal bird and the nearest oystercatcher to it) were recorded at the start of each observation.

The start distance (the distance at which approach was initiated by the observer towards the focal oystercatcher measured as the distance between the observer and the focal bird at the point when the observer commenced intentional and direct advancement towards the focal bird (Blumstein, 2003)), was recorded. The observer approached the focal bird directly at an average walking speed of about ~ 0.5 ms-1 (Blumstein, 2003; Braimoh et al., 2018), keeping a gaze at the focal bird and stopped as soon as the focal bird began to escape (Blumstein, Fernández-juricic, Zollner, & Garity, 2005). FID was measured as the distance between the position where the observer stopped and the point where the focal bird was when it started to escape in resonse to the observer (Ydenberg & Dill, 1986). All distance measurements, except that of the nearest neighbour, were taken in meters using a laser range finder (Nikon Laser-550; Nikon, Tokyo, Japan with a measuring range of 10 – 500 meters). Data collection was alternated among the four sites (Webb & Blumstein, 2005).

The index for human disturbance was recorded in two formats: scored as 0 when no humans present, and 1 when at least one person was sighted within approximately 150 m of the focal bird. The second measure of human disturbance was a count of the number of people using the area of the beach within approximately 150 m of the focal bird at the start of each observation. Most parts of the beach were usually flooded at high tide, making it logistically difficult to access the beach on foot. Hence the data were collected at the low tide period, except for two observations made at about the time of high tide. We extracted the predicted time of low tide and the predicted low tide height for each observation from the FifeWeather.co.uk at the following website http://www.fifeweather.co.uk/index.php/tide-predictions. The time of observation and the expected time of low tide were converted to a continuous numeric scale using the formula (hour+(minutes/60).

Data analysis
The data collected were analysed using general linear mixed effect models with a normal error distribution in R statistical package using the lme4, lme, lmertest and MuMIn libraries (R Core Team, 2019).

The total number of birds was correlated with the number of other birds (β = 0.17, p = 0.028) and the number of oystercatchers (β = 0.98, p = 0.001) but not with flock type (β = – 0.02, p = 0.79). Hence only the total number of birds and flock type were retained as the measures of group size in further analysis. 'Mixed' under the habitat categorisation had only 5 data points as compared with 104 and 56 for 'rocky' and 'sandy', respectively. 'Mixed' was therefore not included for further analysis due to this small sample size. Similarly, the activity category 'preening' had far fewer observations (6) compared with feeding (93) and 'roosting' (66) and was thus not included in further analysis due to its small sample size.

The hypotheses were tested using a full mixed effect model: lme (FID ~ time of observation (numeric) + predicted tide height (numeric) + predicted time of low tide (numeric) + site (factor of four levels) + human presence (factor of two levels) + activity (factor of two levels) + habitat type (factor of two levels) + sighting distance (numeric) + start distance (numeric) + total group size (numeric) + flock type (factor of two levels) + distance from nearest neighbour (numeric) + (1|day of observation). We included the day of observation (factor of 11 levels) as a random variable.

A backwards elimination method, as recommended by Crawley (2005) was used to eliminate non-significant variables by first removing the variables with the highest p-values. We repeated the procedure until we attained the simplest model (the model where all variables included were significant). Finally, the best model was selected using AIC, as the model with the lowest AIC value. All plots showed that the residuals from the models we present were normally distributed with even variance across the range of FIDs. The full, simplest, and smallest AIC models are presented to demonstrate that model simplification did not change the overall biological significance of the results. We show the mean values of variables as the range (mean ± 1SE).

To examine which human disturbance measure better explained the escape behaviour of the oystercatchers tested in this study, FID was included in the models above as either a binary function of human presence (two-level factor: present versus absent) or the absolute number of humans (continuous variable). The performance of the models in term of the R-squared (amount of explained variance) and the Akaike's Information Criterion (AIC) were compared. The variable type within the model with the consistently greater R-squared value and least AIC was considered as the better performing measure of human disturbance.

Results
We recorded 165 observations: 28 at Crail, 15 at East Sands, 61 at Kingsbarns and 50 at West Sands. Oystercatchers were sighted at a minimum distance of 57.5 m and a maximum distance of 239 m with a mean of 101.72±2.14. Start distance ranged from 53–165 m (93.75±1.74). FID ranged from 18 m – 68 m (43.81±0.86). The number of people using a site at the time of observation ranged from 0 to 50 (7.64±0.94).

The simplest of the models explaining the variability in the FID of oystercatchers retained human presence and activity. However, the simplest model was not the model with the smallest AIC. The model with the smallest AIC retained site, human presence, habitat, and activity (See Table 1). The difference between the AIC of the simplest model was, however, less than 2 (change in

AIC = 1.49). FID was significantly higher in the areas without humans than those with humans at the start of the experiment (Table 1, Figure 1). FID was significantly smaller when oystercatchers were feeding than when they were roosting (Table 1, Figure 1). Although the FID of oystercatchers significantly declined as the number of people in an area increased (Figure 2), human presence explained more of the variation (marginal R^2 = 0.32, overall R^2 = 0.37, AIC = 1121.7) in the data than the number of people (marginal R^2 = 0.28, overall R^2 = 0.31, AIC = 1131.9). FID also varied depending on the day of observation, with day accounting for up to 18% (overall R^2 of the simplest model, 0.48 – marginal R^2 of the best model, 0.30) of the variation in the FIDs of the tested oystercatchers (Table 1, section 1).

Discussion

The results confirmed theory and our predictions. We found that the distance at which oystercatchers escaped was significantly lower for feeding oystercatchers than roosting ones and when there were more people present. However, people being present or not explained more of the variation in the data than the absolute number of people, with oystercatchers exhibiting larger FIDs in areas without humans compared with those with humans at the start of the experiment.

The shorter FIDs exhibited by feeding oystercatchers compared with roosting ones at low tide that we observed in this study agrees with our prediction that roosting oystercatchers approached by a human-simulated predator during the period of low tide would take fewer risks by escaping sooner than feeding oystercatchers that will lose feeding time if they escape (Cooper & Frederick, 2007; Ydenberg & Dill, 1986). This is because, the prey on which shorebirds, including oystercatchers, feed in the intertidal zone of coastal habitats is presumably more exposed and accessible during low tide period (Burger, 2018; Fonseca et al., 2017; Schwemmer, Weiel, & Garthe, 2017). Hence, the observed responses of the oystercatchers in this study supports the optimal escape theory and is like the findings of some other studies. For example, in Degus (a small mammal) exhibited shorter FIDs when feeding in patches which had relatively higher abundance of food and in proximity to a burrow (Lagos et al., 2009). Also, feeding Rock Hyraxes *Procavia capensis johnstoni* and Bush Hyraxes *Hetero-hyrax brucei* were observed to respond with shorter FIDs compared with resting ones (Mbise et al., 2020). Alternatively, some shorebirds may have more safe roosting sites available to them at low tide than at high tide such that our result of early flights by roosting oystercatchers at low tide in response to the simulated human predator may be interpreted as being driven by the opportunities available to the birds' to easily relocate to alternative sites when disturbed. This explanation of potential ease of relocation to alternative safe sites at low tide but probably not at high tide suggests that the cost of escape by roosting birds occurring in their preferred roosting habitats may be higher at high tide when roosting sites are few than at low tide. For example, Semipalmated Sandpipers *Calidris pusilla* in Canada remained in flight over the ocean at high tide when perceived predation risk from Peregrine Falcons *Falco peregrinus* was higher and/or roosting sites were inundated (Dekker, Dekker, Christie, & Ydenberg, 2011). However, in our study system, roosting sites were widely available even at high tide, with oystercatchers utilising many different sites on different days. Moreover, oystercatchers are very rarely targeted by raptors in Eastern Scotland (Cresswell & Whitfield, 1994; Whitfield, 1985).

Our finding that FID decreased as the number of people using an area increased, or in areas with humans compared with those without humans, may have reflected some level of habituation to frequent exposure to non-lethal human activities. This is because animals in areas with high human presence and/or use are known to decrease their sensitivity to humans (Blumstein, 2016; Mikula, 2014; Webb & Blumstein, 2005). By continuing their activities despite the presence of the humans in their vicinity before the approach and reducing sensitivity to a human-simulated predator (shorter FIDs) in the areas with humans, the oystercatchers may have been able to reduce the impact of human disturbance to a certain degree. Similarly, a different population of oystercatchers at the Exe estuary, south-west England, were able to reduce the amount of time lost to disturbance through habituation by exhibiting shorter FIDs in sites with high levels of human presence (Urfi, Goss-Custard, & Durell, 1996). This suggests that behavioural flexibility by birds, including habituation, to the changing conditions in their environment, in this case, increased non-lethal human presence, could be one of the ways by which the negative impacts of human disturbance on wildlife may be minimised, thereby enhancing the likelihood that humans and wildlife could co-use an area. This idea of the minimised impact of non-lethal human disturbance through behavioural flexibility may, however, depend on factors such as species (Blumstein et al., 2005; Braimoh et al., 2018), personality (Allan et al., 2020; Strong, Weladji, Holand, Røed, & Nieminen, 2017), life-history traits (Møller, 2014; Oteyza, Mouton, & Martin, 2021), time of the season (Mikula, Díaz, Albrecht, et al., 2018), and the life-cycle stage (Beale & Monaghan, 2004; Mikula, Díaz, Møller, et al., 2018; Tratalos et al., 2021; Verhulst, Oosterbeek, & Ens, 2001) of the animals involved. Conversely, threatening human activities such as hunting may cause animals to become sensitised and respond with longer FIDs (Sreekar, Goodale, & Harrison, 2015; Tarakini, Crosmary, Fritz, & Mundy, 2014). It is also likely that very sensitive individuals have already moved to areas with lower levels to no human disturbances and were therefore not available for inclusion in the study (Bejder, Samuels, Whitehead, & Gales, 2006), as birds may have selected sites and be distributed based on the levels of human disturbance they can tolerate (Tratalos et al., 2021; Webb & Blumstein, 2005).

Our finding that human presence (quantified as present versus absent) in an area explained more variation in the responses of oystercatchers to the human-simulated predator than the absolute number of people suggests that while the number of people using an area is important, the fact that humans are present at all or not on a small spatiotemporal scale is even more important. When the physical presence of human is zero, the first person to enter (changing the human presence status from 'absent' to 'present') may be expected to constitute a stronger stimulus compared with the additional humans that increase the number of people in that space. This is because the first person to appear might be considered and responded to as a significant threat by the approached individual to minimise the chances of making fatal mistakes. However, when the first human does not inflict harm and the additional humans that arrive continue to not focus on them in a threatening way per se, the strength of the stimuli of the subsequent additional humans to arrive may likely diminish. Human disturbance studies generally quantify human disturbance on a point scale of the number of people residing or using the entire site either daily, weekly, annually, or multi-year basis, but the current study used a finer spatial scale around each focal bird and so provides insight into how oystercatchers responded to short-changes in the

physical presence (humans present versus absent) and the absolute number of people in an area. The number of people using an area in time and space is likely to be dynamic, causing some sections or the entire site to either spatially or temporally be without the physical presence of humans or experience a reduced or increased number of people at different times (Corsini, Marrot, & Szulkin, 2019; Webb & Blumstein, 2005). Correspondingly, individuals using these spaces should be selected to adapt by making small spatiotemporal adjustments in their responses to humans based on their perception of the physical presence, the number and overall behaviour of the humans in the area at any given space and time (Beale & Monaghan, 2004; McGowan, Patel, Stroh, & Blumstein, 2014; Moøller & Tryjanowski, 2014). For example, Hansen & Aanes (2015) noted that habituation to non-lethal human disturbance in animals depends on their risk perception and suggested that habituation in the ungulates they studied may operate on small spatiotemporal scales through individual learning mechanisms on the scale of days or weeks. The ability to carefully monitor the physical presence and behaviours of potential predators to correctly assess the small scale spatiotemporal changes in human disturbances may contribute to an individual's ability to learn to ignore, habituate or sensitise to different local levels and types of human disturbance which may eventually improve its fitness (Smith-Castro & Rodewald, 2010; Sreekar et al., 2015; Sreekar & Quader, 2013).

Overall, our results agree with the predictions of the optimal escape theory where prey monitor the behaviour of potential predators and initiate escape when their perceived risk or cost of staying exceeds the benefit of staying during a prey-predator encounter (Cooper & Frederick, 2007; Cooper & Blumstein, 2013; Ydenberg & Dill, 1986). Our results also show that although the number of people in an area is important, the fact that humans are present at all could be more important than the number of humans, and that organisms may habituate to humans in areas with increased levels of non-lethal human presence. This suggests that animals may be able to reduce the impacts of human disturbance to certain extents through behavioural flexibility, potentially allowing the co-existence of wildlife and humans. However, it is likely that very sensitive individuals may avoid areas of high human presence completely by choosing sites with far less, or even no human disturbance. If this is the case, sites that are more disturbed may end up containing less-sensitive individuals while very sensitive individuals may be constrained in the number of spaces available to them. This would potentially have demographic implications as well as selection acting to promote accurate assessment and discounting of non-lethal disturbance, given the increasing human population, recreational activities, and the conversion of pristine habitats to human-dominated landscapes through urbanisation (Baker & Leberg, 2018; Larson et al., 2016). The time scale of this adjustment will be faster for species with greater individual behavioural flexibility but species where a large proportion of the population are excluded from profitable areas are likely to show detrimental population effects. But to distinguish the relative importance of individual behavioural flexibility versus more sensitive individuals being excluded from profitable areas, further work using a marked population with repeated measures from the same individuals using different sites would be necessary.

Ethical Statement

The field protocols used in this study did not handle or relocate any of the focal birds. No permits or licences were required to access any of the four sites visited, or to approach wild birds during the non-breeding season. The project complied with the UK legislation under the Animals (Scientific Procedures) Act 1986 Amendment Regulations (SI 2012/3039). The disturbance caused to the birds was small and brief and not different to those caused by the regular visitors frequenting the sites.

Data Statement

The data and the RMD file of the analysis supporting the results of this study can be found here.

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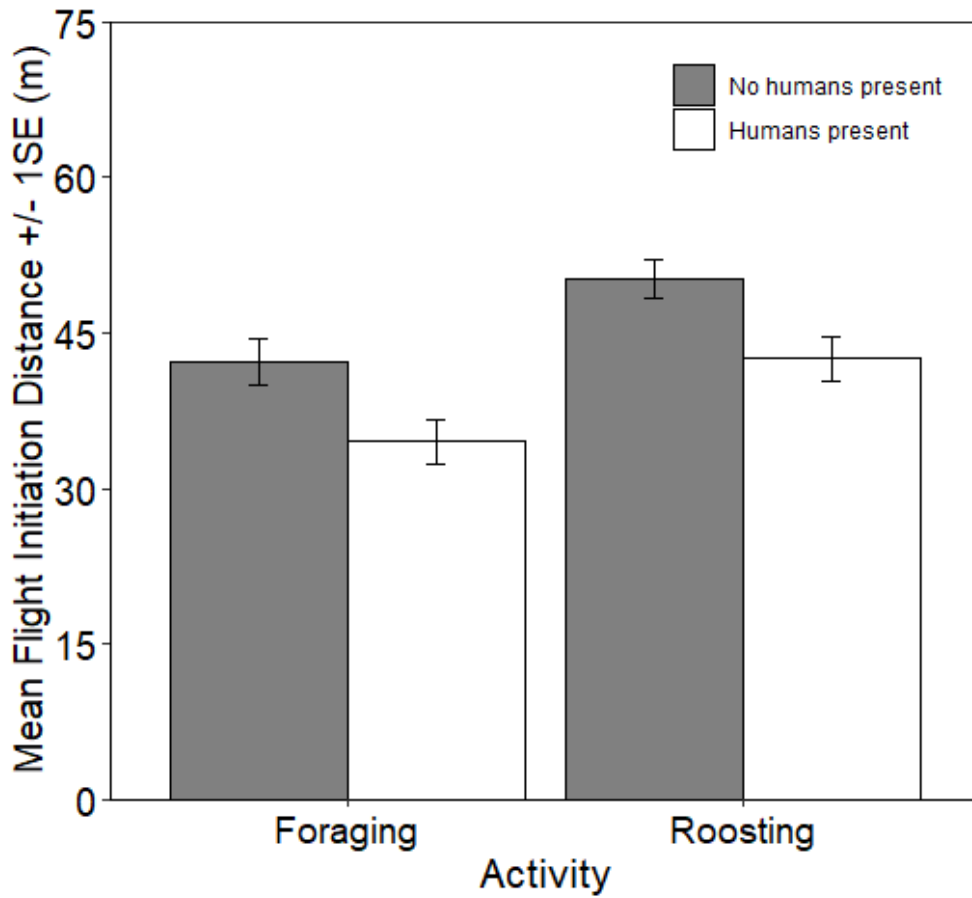
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Table 1: Mixed effect models testing the relationship between flight initiation distance and explanatory variables in Eurasian Oystercatchers from five beaches between St. Andrews and Crail, Fife. The full model (A), the model with the smallest AIC (B), and the simplest model (C) are shown in sections 1 (human disturbance entered as present versus absent) and 2 (human disturbance entered as the number of people). The day of observation was entered into the models as a random variable. Sample size = 154.

Section 1	A: (marginal R2 = 0.35, overall R2 = 0.35, AIC = 1131.86)				B: (marginal R2 = 0.32, overall R2 = 0.37, AIC = 1121.68)				C: (marginal R2 = 0.30, overall R2 = 0.48, AIC = 1123.17)			
	Estimates	SE	t	p	Estimates	SE	t	p	Estimates	SE	t	p
(Intercept)	40.76	5.38	7.57	**<0.001**	45.85	2.81	16.31	**<0.001**	45.65	2.22	20.54	**<0.001**
Time: observation	0.99	0.66	1.49	0.14								
Tide height	-1.34	2.93	-0.46	0.65								
Time: low tide	-0.13	0.48	-0.26	0.80								
Site: East Sands	-1.76	3.48	-0.51	0.61	-1.93	3.61	-0.53	0.60				
Site: Kingsbarns	-5.51	2.50	-2.20	**0.029**	-3.66	3.03	-1.21	0.23				
Site: West Sands	12.44	4.53	2.75	**0.021**	10.91	4.36	2.50	**0.031**				
Human: present	-8.17	2.00	-4.09	**<0.001**	-7.67	1.82	-4.20	**<0.001**	-7.57	1.71	-4.41	**<0.001**
Activity: roosting	8.34	1.79	4.65	**<0.001**	8.06	1.67	4.82	**<0.001**	8.29	1.61	5.16	**<0.001**
Habitat: sandy	-7.76	4.44	-1.75	0.083	-6.02	4.06	-1.48	0.14				
Sighting distance	-0.027	0.042	-0.65	0.52								
Starting distance	-0.021	0.056	-0.38	0.70								
Total group size	0.027	0.081	0.33	0.74								
Flock-type: mixed	-0.61	1.72	-0.35	0.72								
Nearest neighbour	0.26	0.23	1.15	0.25								
Section 2	A: (marginal R2 = 0.30, overall R2 = 0.33, AIC = 1142.36)				B: (marginal R2 = 0.28, overall R2 = 0.31, AIC = 1131.90)				C: (marginal R2 = 0.25, overall R2 = 0.39, AIC = 1137.52)			
(Intercept)	43.90	6.37	6.89	**<0.001**	42.46	2.56	16.57	**<0.001**	41.94	1.98	21.15	**<0.001**
Time: observation	-0.031	0.71	-0.04	0.97								
Tide height	1.84	3.49	0.53	0.60								
Time: low tide	-0.13	0.50	-0.27	0.79								
Site: East Sands	-2.36	4.17	-0.57	0.57	-1.80	3.67	-0.49	0.62				
Site: Kingsbarns	-3.84	3.22	-1.19	0.24	-3.03	2.89	-1.05	0.30				
Site: West Sands	12.81	5.17	2.48	**0.033**	15.07	4.59	3.28	**0.0083**				
Number of people	-0.22	0.095	-2.31	**0.022**	-0.24	0.088	-2.72	**0.0074**	-0.19	0.10	-1.93	0.056
Activity: roosting	8.60	1.83	4.69	**<0.001**	8.47	1.73	4.89	**<0.001**	9.19	1.67	5.50	**<0.001**
Habitat: sandy	-8.86	4.58	-1.93	0.055	-9.93	4.15	-2.39	**0.018**				
Sighting distance	-0.021	0.043	-0.48	0.63								
Starting distance	-0.00055	0.058	-0.01	0.99								
Total group size	0.061	0.083	0.74	0.46								
Flock-type: mixed	-2.26	1.72	-1.31	0.19								
Nearest neighbour	0.34	0.23	1.44	0.15								

Figure 1: The predicted differences between the flight initiation distances of Eurasian Oystercatchers foraging and those roosting when approached directly by a simulated-human predator in the presence or absence of humans. The plot is from the model in Table1, Section 1B. Site was set at Kingsbarns, while habitat was set at rocky.
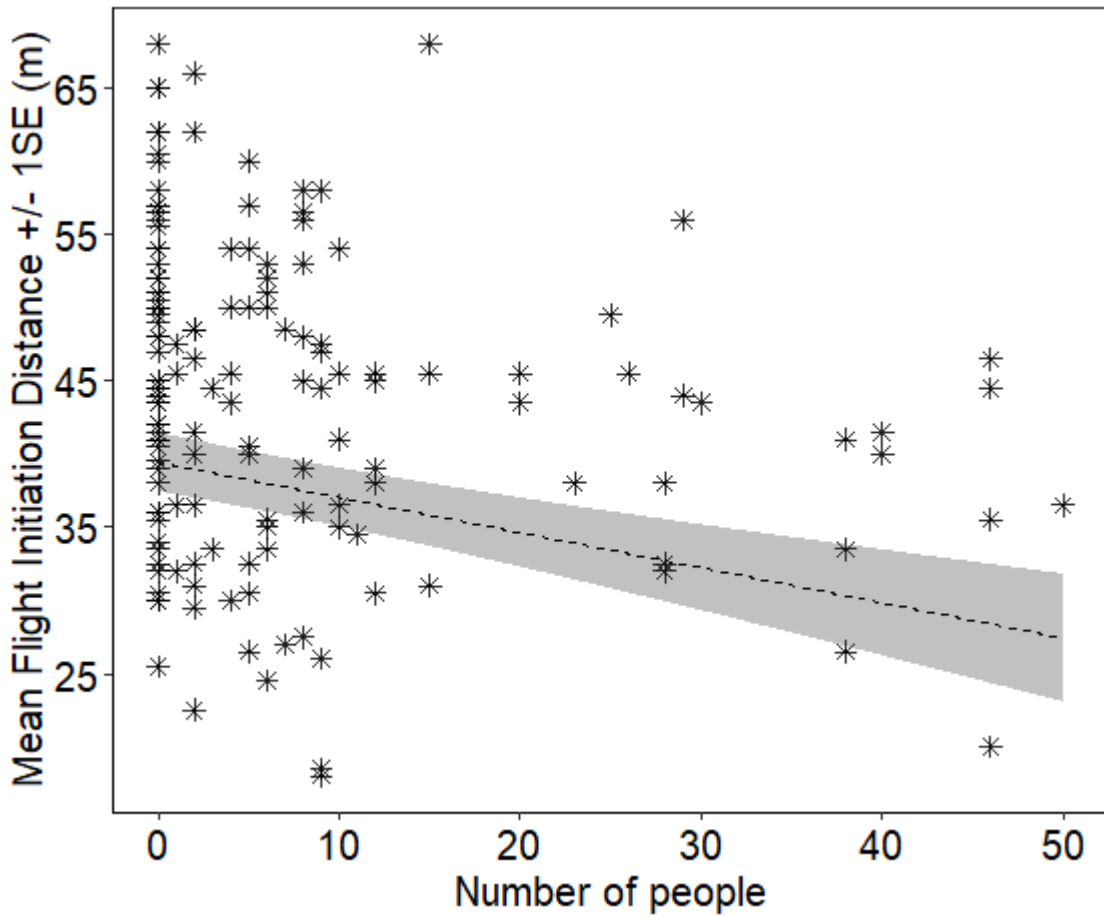
Figure 2: The predicted relationship between the flight initiation distances of Eurasian Oystercatchers and the number of people within their vicinity at the start of each experimental approach by a human-simulated predator in the sandy beaches of St Andrews to Crail, Scotland. The plot is from the model in Table1, Section 2B. Site was set at Kingsbarns, habitat was set at rocky, and activity set at foraging.