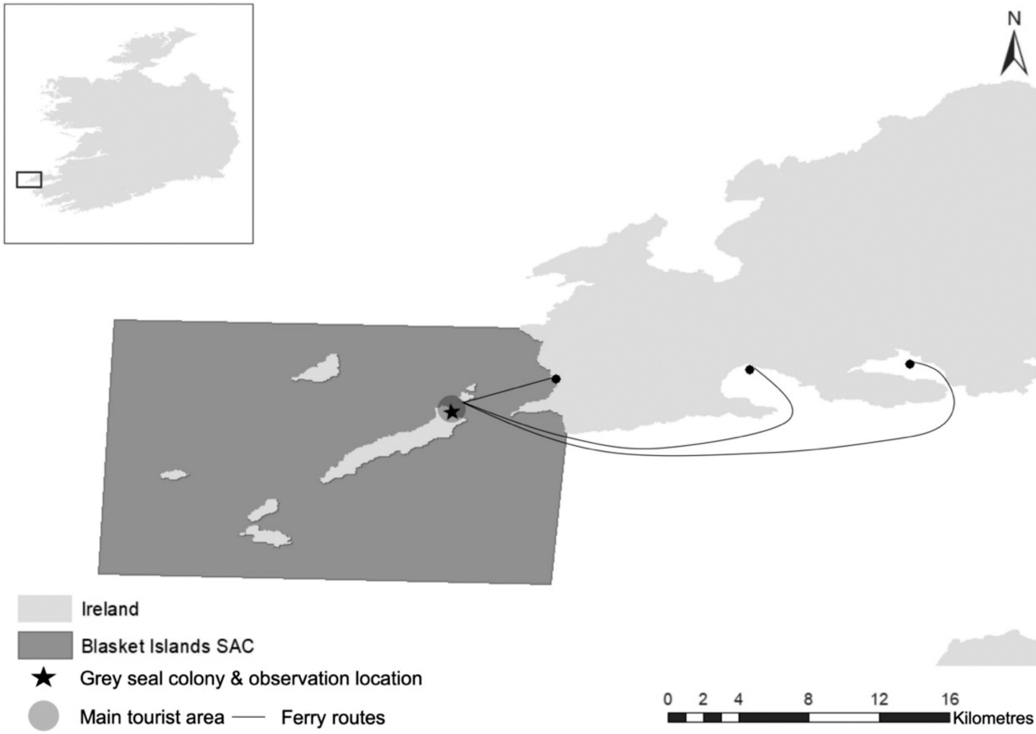

Figure 1. Grey seal (*Halichoerus grypus*) colony and observation location in White Strand Beach; main area occupied by tourism and ferry routes to the main island in the Blasket Islands Special Area of Conservation (SAC), Co. Kerry, Ireland.

pups hauled out on the beach (National Parks & Wildlife Service [NPWS], 2014). Different sites around the islands are used by grey seals throughout the year (NPWS, 2014), with Beginish and the Great Blasket containing the highest pup numbers during the breeding season—from late September to December but peaking during September and October (Cronin et al., 2007). Although pups have previously been seen on White Strand Beach, no pups were observed during the current study, although pups were observed in adjacent small sandy coves and inlets, as well as on the other surrounding islands. The area had an estimated population size of *ca*. 1,099 to 1,413 (15.09% of the total Irish population) with 314 pups born in 2011 (Ó Cadhla et al., 2013).

During the last few years, from April to October, this location has been increasingly subject to tourism activity. The tourist season overlaps with the early part of the breeding season, which is the most sensitive time in terms of potential impacts of disturbances. Tourists access the island by boat, which is located 4 km offshore. There are three main ferry routes to the island (Figure 1), with companies operating daily throughout the tourist season. Ten different tour vessels were observed in the area during the study period with up to five different tour vessels recorded in the same day. Each tour vessel arrived at the small dock, located at approximately 350 m from the colony, several times per day. Furthermore, before and/or after landing, ferries also passed by the colony as part of the tour at a distance as close as 100 m. Additionally, there is a hostel on the island in operation during the tourist season from which people can approach the colony at any time of the day. Currently, there are no warning signs for the public or measures to control people accessing areas that large numbers of animals are using.

Data Collection

Preliminary observations were carried out on 6 September 2018 to develop an ethogram of grey seal behaviour for use in the present study (Table 1; adapted from Haller et al., 1996; Granquist & Sigurjonsdottir, 2014). Grey seal behaviour was recorded using a variation of classic scan sampling techniques (Altmann, 1974), recording the colony located in White Strand Beach at irregular intervals or when specific events (i.e., tourism activities) took place. Behavioural sampling was conducted during two consecutive years—from

Table 1. Ethogram containing mutually exclusive behavioural patterns recorded for grey seals (*Halichoerus grypus*) hauled out on the beach, their descriptions, and the average proportion of seals ± SD engaged in each behaviour during the preliminary observations (adapted from Haller et al., 1996; Granquist & Sigurjonsdottir, 2014)

Behaviour	Subtype	Description	% seals
Rest		Seal still, lying on the beach with head down or up with eyes closed	67.72 ± 13.91
Vigilance		Seal still, lifting the head or with head up, eyes open and alert, occasionally moving its head from side to side	17.74 ± 14.44
Comfort		Seal performing different movements, including scratching, weight shifting, stretching, and rolling in one location	9.34 ± 2.23
Locomotion		Seal changing location but not rushing into the water or apparently approaching another seal, including movements on the beach, going outside the water, or going towards the water	2.32 ± 1.47
Flush		Seal quickly entering the water	0.31 ± 0.75
Mating		Male and female seals having physical contact with each other and adopting copulatory position	1.41 ± 0.98
Interaction male-male	Approach	Male seal moving towards another male seal	0.13 ± 0.32
	Chase	Male seal moving towards another male that is escaping	
	Escape	Male seal moving away from another male that is chasing him	
	Aggressive/ fighting	Male seals displaying agonistic behaviour, including threat position, roaring, and/or neck extended or having physical contact with each other	
Other interactions		Same interactions as above but regardless of the sex of the individuals (not two males) or when sex is unknown	1.04 ± 1.26

7 September to 3 October 2018 (8 d) and from 23 April to 19 September 2019 (20 d). Disturbances were already recorded during the first day of sampling (7 September 2018). Therefore, samples recorded on 8 September 2018 were used as a control since no anthropogenic disturbances (i.e., vessels or tourists) took place during the entire day. Unfortunately, since days without disturbances were not common over the course of the study, control data only represent a low proportion of the total samples, a factor that should be improved in future similar studies. Fieldwork was carried out when environmental conditions allowed access to the island and behavioural recording to take place. Fieldwork was carried out during six different trips to the island, with each trip lasting between 3 and 7 d (2 trips in 2018 and 4 trips in 2019). The study period covered part of the pre-breeding, breeding, and pupping seasons, and tourism activity was still occurring during both years.

The general approach was that data collection—including recordings of behaviour, number of grey seals hauled-out, disturbance type, and environmental conditions—was carried out throughout the day. Early morning observations were conducted at an average sampling interval of 47 min and began when no anthropogenic disturbances of any kind were present (generally between 0600 and 1030 h) nor had taken place since the end of the previous day (i.e., boats had not yet returned to the island and tourists had not visited the beach since the previous evening). Observations of the grey seal colony under tourism activity conditions mainly took place from 1030 to 1700 h. Scans were conducted every time a vessel was approaching, whenever it changed distance category (Table 2), or when walking tourists were observed on the beach. Each scan was recorded under one single disturbance category, except on two occasions (0.44% of the samples) when tourists were on the beach while a vessel was approaching (samples were coded as disturbance level 6). Scans were also conducted at an average sampling frequency of 1 h 33 min after disturbances had taken place (Table 2) to assess whether there were changes in the behaviour and the abundance of seals hauled-out over time. Sampling timing could not be standardized as it depended on environmental conditions (e.g., absence of precipitation) and logistic issues when arriving/leaving the island. Therefore, we tried to ensure that the timing for data collection early in the morning and the interval following disturbances was as random as possible to reduce the possibility of bias. A Poisson GLMM with a logarithmic link function was used to assess when disturbance would revert to 0 after a disturbance took place.

A total of 451 (2018: n = 78; 2019: n = 373) behavioural samples of the grey seal colony were conducted across 28 d in 2018 (8 d) and 2019 (20 d). There was an average effort of 9.8 ± 6.7 and 18.7 ± 10.4 samples recorded per day in 2018 and 2019, respectively.

Table 2. Categories for different disturbance levels due to ecotourism assigned to different circumstances

Disturbance level	Disturbance type
Control	No disturbance: Samples recorded during an entire day on which no disturbances took place
0	No disturbance: During the morning before disturbances or at least 3 h after disturbances took place
1	Vessels approaching the island at a distance of 1 to 1.5 km from the colony
2	Vessels approaching the island at a distance of 750 to 1,000 m from the colony
3	Vessels approaching the island at a distance of 500 to 750 m from the colony
4	Vessels approaching the island at a distance of 250 to 500 m from the colony
5	Vessels passing along the beach occupied by the seals at a distance < 250 m from the colony
6	Tourists walking on the beach occupied by the seals at a distance < 100 m from the colony
After disturbances	Immediately after disturbances end, up to 3 h after disturbances had taken place

After arriving at the study site, a camera (Canon 77D, 100-400 mm Sigma lens or Nikon Coolpix P900 on Manfrotto 128 RC tripods) was set up on the top of the cliff surrounding the beach at a distance far enough to avoid disturbances but adequate to record the colony (on average 100 m). Vessels approaching the island were spotted using Opticron 10 × 42 binoculars, and distance to the colony at the start of the scan sample was recorded using a laser rangefinder (Leica Rangemaster 900, 7 × 24). Samples were only recorded when vessels were approaching or travelling parallel to the beach and not when vessels were moving away from the colony. If a vessel changed distance category after scanning the colony, this was recorded with the colony then scanned a second time. Recordings were carried out by scanning the colony from one end to the other using one of the cameras listed above.

Similar methodology has been widely used previously in pinniped behavioural studies focussed on assessing anthropogenic disturbances caused by tourism on various pinniped species (Boren et al., 2002; van Polanen Petel et al., 2008; Granquist & Sigurjonsdottir, 2014; Cowling et al., 2015; Back et al., 2018). Video files were backed up and coded at the end of each day for subsequent statistical analysis. For each sample recorded, all the grey seals hauled out on the beach were counted to extract abundance data, and each seal was assigned a single behavioural category following the ethogram previously generated: rest, vigilance, comfort, locomotion, flush, mating, and other interactions (detailed in Table 1). Afterwards, the percentage of seals displaying each behaviour was calculated for each sample. The level of disturbance experienced by the colony during each recording was classified on a scale ranging from 0 to 6 (lowest to highest level of disturbance, respectively) as defined in Table 2. Whenever tourists were at a distance within 100 m from the colony, they were recorded as being on the beach. Vessels passing by or approaching the colony were classified into four categories: (1) small ferries, (2) small vessels, (3) slow-approaching rigid inflatable boats (RIBs), and (4) fast-approaching RIBs. Small ferries and vessels were always recorded as approaching the colony at a constant speed; RIBs that were at a constant speed or that slowed down when passing by or approaching the colony were classified as slow-approaching; and RIBs that increased speed when passing by or approaching the colony were classified as fast-approaching.

Environmental conditions, such as precipitation, wind speed and direction, cloud cover, and temperature, were obtained for each observation from the online weather service provided by the Norwegian Meteorological Institute and the Norwegian Broadcasting Corporation (https://www.yr.no/place/Ireland/Munster/Great_Blasket_Island). Tidal phase was determined from the tide and current prediction software *WXTide32* (Hopper, 2000) and categorised into slack low, ebb, slack high, and flood (following O'Brien, 2013). The variables time of day (categorised into morning, afternoon, and evening), date, and season (pre-breeding and breeding) were also recorded. Season was defined as pre-breeding when no pups nor mating behaviour had been observed yet on the island. A breeding category started to be assigned when pups and/or mating behaviour were observed on the island and until the end of the fieldwork for that year as fieldwork finished while the breeding and pupping seasons were still taking place during both years. Seal counts were as accurate as possible and carried out by the same person. However, to minimise potential errors, each video file was analysed three times when a large number of seals were lying on the beach (> 300) and/or the spacing between them was reduced (37% of the samples). In this case, the average abundance of individuals counted was used for subsequent analysis.

Statistical Analysis

Data analysis was carried out using the statistical *RStudio* package, Version 3.6.2 (R Core Team, 2019). Due to the high variation in grey seal numbers hauled-out between samples (from 0 to 1,145 with an average of 267 ± 249 seals), behavioural data recorded were converted into proportions to allow for later comparison and analysis. The abundance of seals recorded was presented as the number of individuals hauled-out during each sample.

To assess the effect of different explanatory variables on the vigilance, flushing, and resting behaviours, and on the abundance of grey seals hauled-out, a Generalised Linear Mixed Models (GLMMs) approach utilising a Laplace approximation was applied using the package 'lme4' (Bates et al., 2015). Since proportion data ranging from 0 to 1 were modelled as a function of the covariates when assessing the seal's behaviour, three binomial GLMMs (which can be used for proportional data; Zuur et al., 2009) for each response variable (i.e., proportion of grey seals displaying vigilance, flushing, and resting behaviours) were fitted with a logistic link function. The explanatory variables initially included in the binomial models as fixed effects were the continuous variables group size (number of seals hauled out on the beach), wind speed, cloud cover, and temperature as well as the factors season, level of disturbance (Table 2), wind direction, tidal state, time of day, and vessel type. Due to the high correlation between level of disturbance and time of day, two different sets of GLMMs were fitted for each response variable (Acevedo-Gutiérrez & Cendejas-Zarelli, 2011): the first one focussed on assessing the influence of level of disturbance, and the second one focussed on the effects of season and time of day. The rest of the covariates were included in the initial model for both sets. A third model was fitted separately for each behaviour to assess the expression of vigilance, flushing, and resting behaviours of grey seals as a function of vessel type. This model included group size, time of day, and wind speed as continuous variables and vessel type, level of disturbance, and tidal state as factors.

The absolute abundance of grey seals hauled out on the beach was modelled using a Poisson GLMM with a logarithmic link function. The explanatory variables initially included in the Poisson model as fixed effects were the continuous variables wind speed, temperature, and cloud cover, as well as the factors season, level of disturbance (Table 2), wind direction, tidal state, and time of day.

To account for potential pseudoreplication among samples, scans were nested into sampling days and included as random intercepts in all the above models. Backwards model selection was applied: nonsignificant variables were dropped one at a time using the drop1 function, and models were compared based on the Akaike Information Criterion (AIC) and the *anova* function. Together with the assessment of multicollinearity and overdispersion, model validation was conducted by visual exploration of residual plots following Zuur et al. (2010) and Zuur & Ieno (2016).

Results

Overall Behaviour of Grey Seals Hauled-out

Grey seals were most commonly recorded displaying resting (66.8 ± 22.3%) and vigilance (20.1 ± 17.2%) behaviours. Due to their prevalence, an increase in vigilance would often lead to a decrease in resting and vice versa. These behaviours were followed by comfort movements (6.7 ± 4.2%), flushing into the water (3.5 ± 12.5%), locomotion (1.8 ± 4.5%), and interactions, including fighting, approaching, and mating (1.1 ± 2.2%).

Effect of Disturbance Level

The selected GLMMs fitted to model the proportion of grey seals displaying vigilance, flushing, and resting behaviours included level of disturbance due to ecotourism activities and tidal state as common covariates (Supplementary Appendix I, Equations 1, 2, and 3; supplementary appendices are available in the "Supplemental Material" section of the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147). Wind speed was also included in the models assessing the proportion of individuals vigilant and flushing, group size when assessing vigilance and resting, and cloud cover when assessing the proportion of resting individuals. The nested random factors scan and sampling day were included in all the models.

Level of disturbance had a strong influence on all the behaviours assessed. The proportion of grey seals displaying vigilance behaviour increased significantly with higher disturbance levels, showing the highest response under disturbance levels 4, 5, and 6 (Figure 2A; Table 3). Average proportion (± SD) displaying vigilance behaviour was 16.5 ± 10.0, 25.8 ± 14.8, and 30.6 ± 19.4% of grey seals, respectively. The proportion of seals flushing into the water was strongly influenced by disturbance levels 5 and 6 (Table 3), leading to a significant increase of seals entering the water (3.8 ± 9.2 and 8.5 ± 20.5% of seals flushing, respectively). Conversely, disturbance levels 5 and 6 led to a reduction in the proportion of seals resting (Figure 3A; Table 3), with 61.7 ± 20.6 and 52.4 ± 26.4% of seals resting under disturbance levels 5 and 6, respectively. The proportion of seals vigilant after disturbances had taken place was significantly different from the proportion of seals under undisturbed conditions (i.e., control data; Figure 2A; Table 3).

Tidal state was also a significant factor, with a lower proportion of grey seals vigilant during ebb and slack low tide conditions (Figure 2B; Table 3)

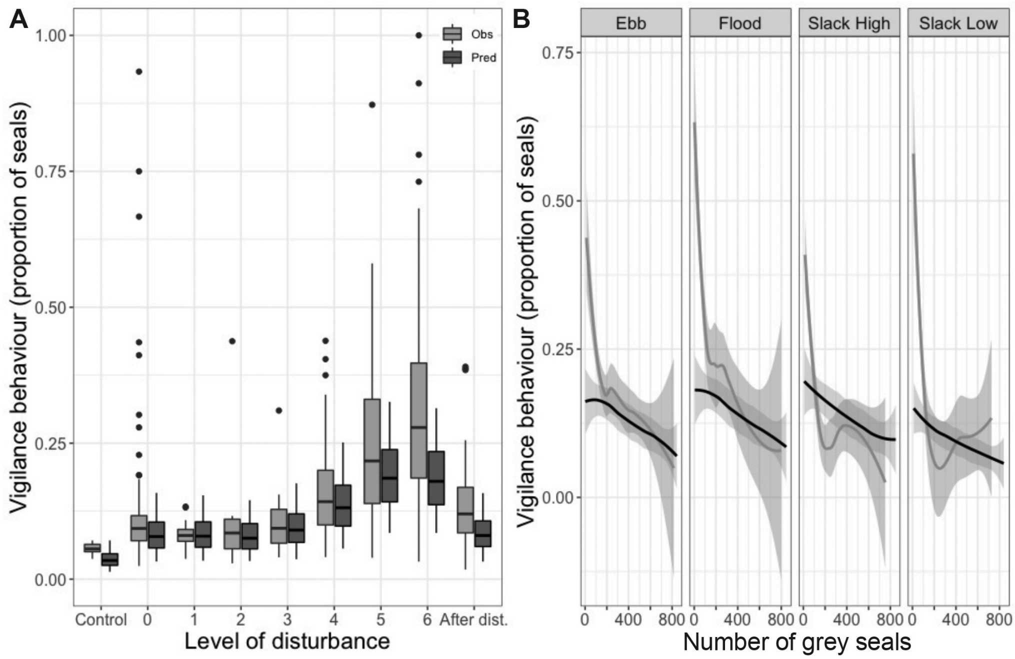

Figure 2. (A) Observed (grey) and predicted from the selected model (dark grey) proportion of grey seals displaying vigilance behaviour vs level of disturbance; and (B) observed (grey line) and predicted from the selected model (black line) proportion of grey seals displaying vigilance behaviour vs number of seals hauled-out for each tidal state.

Table 3. Significant results for the most supported GLMM assessing the proportion of grey seals displaying vigilance, flushing, and resting behaviours in response to level of disturbance and tidal state. Group size was also included for vigilance and resting behaviours and cloud cover for resting.

Predictor variables	Vigilance behaviour				Flushing behaviour				Resting behaviour			
	Est	SE	*z*	*p*	Est	SE	*z*	*p*	Est	SE	*z*	*p*
Intercept	-2.68	0.46	-5.87	< 0.001	-9.97	1.55	-6.43	< 0.001	1.23	0.48	2.55	0.01
Disturbance level*												
0	0.87	0.40	2.17	< 0.05	--	--	--	--	--	--	--	--
1	0.89	0.42	2.09	< 0.05	--	--	--	--	--	--	--	--
3	1.04	0.43	2.40	< 0.05	--	--	--	--	--	--	--	--
4	1.46	0.41	3.57	< 0.001	--	--	--	--	--	--	--	--
5	1.88	0.40	4.65	< 0.001	3.81	1.46	2.62	< 0.01	-0.90	0.45	-1.99	< 0.05
6	1.85	0.40	4.58	< 0.001	4.04	1.45	2.79	< 0.01	-1.06	0.45	-2.33	< 0.05
After disturbance	0.93	0.41	2.24	< 0.05	--	--	--	--	--	--	--	--
Tidal state*												
Slack low	-0.37	0.09	-4.28	< 0.001	--	--	--	-	0.36	0.11	3.28	0.001
Flood	--	--	--	--	1.24	0.40	3.06	< 0.01	--	--	--	--
Slack high	--	--	--	--	1.46	0.50	2.93	< 0.01	--	--	--	--
Group size	-1.59e-03	2.05e-04	-7.78	< 0.001	--	--	--	--	1.75e-03	2.52e-04	6.93	< 0.001
Cloud cover	--	--	--	--	--	--	--	--	-0.01	1.86e-03	-3.41	< 0.001

*Control data was the reference category for disturbance level and ebb for tidal state.

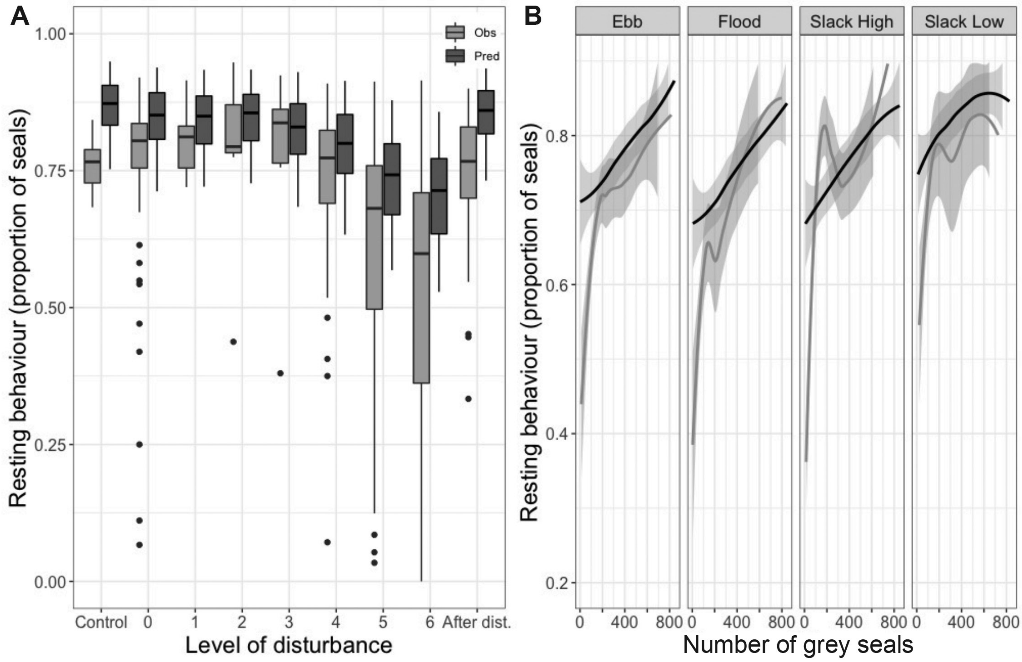

Figure 3. (A) Observed (grey) and predicted from the selected model (dark grey) proportion of grey seals resting vs level of disturbance; and (B) observed (grey) and predicted from the selected model (black) proportion of grey seals resting vs number of seals hauled-out for each tidal state.

and a significantly higher proportion of seals flushing under high tide conditions (Table 3). In contrast to the proportion of vigilant seals, resting increased significantly under ebb and slack low tide conditions (Figure 3B; Table 3). Seal group size also showed a significant influence, with an inverse relationship between the proportion of vigilant seals and group size (Figure 2B; Table 3) and, therefore, an increase in the proportion of seals resting with a higher number of individuals hauled-out (Figure 3B; Table 3). The proportion of seals resting decreased with higher cloud cover (Table 3).

Effect of Time of Day

Due to the strong correlation between disturbance level and time of day, a second set of GLMMs were fitted to assess the proportion of grey seals vigilant, flushing, and resting as a function of time of day as a common covariate for all the models. Season was also included when assessing vigilance and flushing, wind direction when assessing vigilance and resting, and cloud cover and group size when assessing vigilance. Time of day was a significant factor, with lower levels of vigilance during the morning and evening times and lower levels of flushing behaviour during the morning (Table 4). Conversely, a higher proportion of seals were resting during the morning. Wind from the west, northwest, and southwest resulted in a higher proportion of seals displaying vigilance and, therefore, in a lower proportion of seals resting (Table 4). Season also had a significant effect, with a higher proportion of seals vigilant during the pre-breeding season.

Effect of Type of Vessel

GLMMs were also fitted to assess the vigilance, flushing, and resting behaviours of grey seals hauled out on the beach as a function of vessel type. Fast-approaching RIBs showed the strongest effect on the proportion of seals displaying vigilance, flushing, and resting behaviours, with an increase in vigilance and flushing among seals, and a decrease in resting behaviour (Table 5). Slow-approaching RIBs also showed an effect on vigilance and resting behaviours. The proportion of vigilant seals increased significantly when vessels approached at a distance of 500 m from the colony (disturbance level 4), showing the highest response when vessels passed along the colony at a distance closer than 250 m (disturbance level 5; Table 5). The proportion of resting seals significantly decreased under disturbance level 5 conditions.

Since the conditions after disturbances had taken place did not seem to strongly influence the vigilance, flushing, and resting behaviours of grey seals in comparison with conditions of no

Table 4. Significant results for the most supported GLMM assessing the proportion of grey seals displaying vigilance, flushing, and resting behaviours in response to time of day. Season was also included for vigilance behaviour, and cloud cover, wind direction, and group size for vigilance and resting behaviours.

	Vigilance behaviour				Flushing behaviour				Resting behaviour			
Predictor variables	Est	SE	*z*	*p*	Est	SE	*z*	*p*	Est	SE	*z*	*p*
Intercept	-1.44	0.18	-8.06	< 0.001	-6.15	0.50	-12.27	< 0.001	0.61	0.18	3.36	< 0.001
Time*												
Evening	-0.43	0.14	-3.05	< 0.01	--	--	--	--	--	--	--	--
Morning	-0.26	0.09	-2.84	< 0.01	-1.47	0.38	-3.90	< 0.001	0.41	0.11	3.82	< 0.001
Season*					--	--	--	--	--	--	--	--
Pre-breeding	0.28	0.14	1.97	< 0.05	--	--	--	--	--	--	--	--
Cloud cover	0.01	1.68e-03	3.15	< 0.01	--	--	--	--	-5.58e-03	1.75e-03	-3.19	0.001
Wind direction*												
Northwest	0.47	0.22	2.10	< 0.05		--	--	--	-0.53	0.24	-2.19	< 0.05
Southwest	0.48	0.23	2.08	< 0.05					-0.58	0.25	-2.31	< 0.05
West	0.81	0.24	3.39	0.001	--	--	--	--	-0.74	0.26	-2.81	< 0.01
Group size	-2.70e-03	2.22e-04	-12.16	< 0.001	--	--	--	--	2.49e-03	2.49e-04	9.99	< 0.001

*Afternoon was the reference category for time of day, breeding for season, and east for wind direction.

Table 5. Significant results for the most supported GLMM assessing the proportion of grey seals displaying vigilance, flushing, and resting behaviours in response to vessel type and group size. Level of disturbance and tide conditions were also included as covariates when assessing vigilance and resting behaviours.

	Vigilance behaviour				Flushing behaviour				Resting behaviour			
Predictor variables	Est	SE	*z*	*p*	Est	SE	*z*	*p*	Est	SE	*z*	*p*
Intercept	-1.37	0.70	-1.97	< 0.05	-1.97	2.49	-0.79	n.s.	0.20	0.79	0.25	n.s.
Vessel type*												
Slow-appr. RIB	0.71	0.31	2.29	< 0.05	--	--	--	--	-0.75	0.37	-2.04	< 0.05
Fast-appr. RIB	0.75	0.30	2.46	< 0.05	2.60	1.24	2.09	< 0.05	-0.85	0.36	-2.36	< 0.05
Disturbance level*												
4	0.49	0.22	2.26	< 0.05	--	--	--	--	--	--	--	--
5	0.94	0.22	4.34	< 0.001	--	--	--	--	-0.52	0.26	-1.99	< 0.05
Tidal state*												
Slack high	-	--	--	--	--	--	--	--	-1.03	0.35	-2.91	< 0.01
Slack low	-0.30	0.15	-2.02	< 0.05	--	--	--	--	--	--	--	--
Group size	-7.07e-04	3.60e-04	-1.96	< 0.05	-2.75e-03	1.26e-03	-2.18	< 0.05	--	--	--	--

*Small vessel was the reference level for vessel type, 1 was the reference level for disturbance level, and ebb was the reference category for tidal state.

Table 6. Significant results for the selected GLMM assessing the number of grey seals hauled-out in response to level of disturbance, tidal state, time of day, wind speed, and direction

Predictor variables	Est	SE	*t*	*p*
Intercept	4.72	0.81	5.85	< 0.001
Disturbance level*				
4	-0.55	0.21	-2.61	< 0.01
5	-0.54	0.19	-2.91	< 0.01
6	-0.59	0.17	-3.37	< 0.001
After disturbance	-0.99	0.23	-4.35	< 0.001
Tidal state*				
Flood	-0.68	0.16	-4.28	< 0.001
Slack high	-1.04	0.18	-5.88	< 0.001
Slack low	0.45	0.16	2.91	< 0.01
Time*				
Evening	0.82	0.21	3.86	< 0.001
Morning	0.85	0.15	5.88	< 0.001
Wind speed	0.15	0.06	2.43	< 0.05
Wind direction*				
North	-1.77	0.83	-2.14	< 0.05

*0 was the reference category for disturbance level, ebb for tidal state, afternoon for time of day, and east for wind direction.

anthropogenic disturbances (Table 3), this was not explored in further detail. Results showed that behavioural samples recorded from 4 h after disturbances were not significantly different from the pre-disturbance conditions (Supplementary Appendix II, Table A); therefore, a disturbance level of 0 was assigned to these samples.

Effects of Ecotourism Activities on the Number of Grey Seals Hauled-out

The highest single abundance estimate of grey seals hauled-out was 1,145 individuals. The highest average group size was 546 ± 243 seals under disturbance level 1. This was followed by (in decreasing order) disturbance level 3: 418 ± 234; disturbance level 0: 412 ± 288; control data: 366 ± 124; disturbance level 4: 333 ± 271; disturbance level 5: 238 ± 166; after disturbances conditions: 228 ± 167; disturbance level 2: 209 ± 178; and disturbance level 6: 183 ± 197 seals.

The GLMM fitted to assess the number of grey seals hauled-out (Supplementary Appendix I, Equation 4), as a function of level of disturbance, season, tidal state, cloud cover, time of day, wind speed, and direction, showed a strong influence of disturbance levels 4, 5, 6, and after disturbances, leading to a reduction in the number of seals. Time of day also showed a strong influence, with a significantly higher number of seals hauled out during the morning and the evening time (Table 6); and the number of seals decreased significantly under flood and slack high tide conditions (Table 6). Wind speed showed a significant effect, and a lower number of seals were hauled-out with wind from the north.

Discussion

Our findings show that the grey seal colony in the Blasket Islands SAC was affected by ecotourism activities, especially by the presence of tourists on the beach and vessels passing along the colony. Approaching vessels at a distance between 250 and 500 m also resulted in a significant effect. These activities led to a reduction in the abundance of seals hauled-out, an increase in the proportion of individuals vigilant and rapidly entering the water, and a reduction in the proportion of resting individuals.

Several studies that focussed on the abundance of pinniped species at haulout sites and their behavioural responses to anthropogenic activities also identified the presence of pedestrians in the vicinity of the colonies together with approaching vessels as the main causes of disturbances (e.g., Jansen et al., 2010; Andersen et al., 2012; Granquist & Sigurjonsdottir, 2014; Pavez et al., 2014; Cowling et al., 2015; Mathews et al., 2016; Osterrieder et al., 2017; Back et al., 2018; Corral et al., 2018). In similar studies, the presence of walking tourists in the vicinity of fur seals reported a response distance of 30 m (Boren et al., 2002), while harbour seals responded at between 50 and 260 m (Andersen et al., 2012; Osinga et al., 2012). Studies have also assessed the response distances of pinnipeds to approaching vessels. Australian sea lions (*Neophoca cinerea*) responded at a short distance of 15 m (Osterrieder et al., 2017), while other studies variously reported Australian fur seals (*Arctocephalus pusillus*) were significantly disturbed by approaching vessels between 25 and 75 m (Back et al., 2018), or identified 30 m as the significant response distance (Boren et al., 2002; Cowling et al., 2015). In contrast, previous studies reported harbour seals responded to vessels at a much longer range of between 100 and 830 m (Johnson & Acevedo-Gutiérrez, 2007; Jansen et al., 2010, 2014; Andersen et al., 2012; Young et al., 2014; Matthews et al., 2016), similar to the 500 m identified in this study. This wide scope in response distances might suggest interspecific differences in behavioural responses and/or the effect of approaching pattern (i.e., speed, noise, and vessel type; Andersen et al., 2012). Therefore, both species and the site-specific factors must be considered when devising conservation and management plans (Cowling et al., 2015).

Time of day showed a significant effect in our study, with a lower display of vigilance and flushing behaviour and a higher proportion of grey seals resting during the morning and evening time. These times also correspond with larger numbers of seals hauled-out. However, as tourism activities took place mainly from 1030 to 1700 h (categorized as "afternoon"), caution must be taken when interpreting these results as this might be due to or partially explained by disturbances. Northwest, west, and southwest wind resulted in a significant increase in the proportion of seals vigilant and a decrease in resting. Seals would be relatively sheltered from west and southwest wind due to the morphology of the site. However, this result could be explained by the seals detecting human smell (Fogden, 1971) due to the presence of tourists on top of the cliff surrounding the beach where seals haul out.

Tidal state also played an important role as grey seals were less vigilant and rested more under ebb and slack low tide conditions, a higher proportion of them flushed into the water under flood and slack high tide conditions, and a higher abundance of them were hauled-out under low tide conditions, similar to Acevedo-Gutiérrez & Cendejas-Zarelli (2011). Since the beach was only partially covered during high tide conditions and provided enough space for the seals to haul out, this relationship between seal behaviour and abundance with tidal state might be partially explained by food availability in the area (Patterson & Acevedo-Gutiérrez, 2008). The combination of disturbances and the waves breaking on the shore could explain the increase in vigilant and flushing seals observed during slack high and flood tide conditions.

As predicted, our study confirmed an inverse relationship between group size and vigilance behaviour. This effect of group size, known as the many-eyes hypothesis (Rieucau & Martin, 2008), has been demonstrated in other pinnipeds (Cowling et al., 2015), as well as several other species such as starlings (*Sturnus vulgaris*; Powell, 1974) and antelopes (*Damaliscus pygargus* and *Aepyceros melampus*; Dalerum et al., 2008).

Vessel type was also a significant factor. The presence of RIBs led to a higher proportion of grey seals becoming alert and entering the water in comparison with small vessels and ferries. Although individuals' behavioural response might also be influenced by previous experience as well as the conditions prior to disturbances, previous studies have also found vessel type to influence flushing behaviour in pinnipeds, with cruise ships and kayaks triggering the greater response in harbour seals (Young et al., 2014; Mathews et al., 2016) and power and tour vessels in sea lions (Osterrieder et al., 2017). We found that vessel speed did not affect vigilance and flushing behaviours, similar to Jansen et al. (2010) for harbour seals. However, Lozano & Hente (2014) found the vessel's wake to cause greater disturbance than the vessel itself, suggesting that vessel speed is a relevant factor that should be regulated.

Haulout sites are vital for pinniped species, including grey seals, as they allow them to rest, give birth, reproduce, and socially interact (Bonner, 1990; Lyons, 2004; Ó Cadhla et al., 2013). This study was carried out in the main haulout site for grey seals in the Blasket Islands SAC. Here, the strongest flushing response was observed when tourists were present on the beach and vessels were approaching at a distance closer than 500 m, resulting in more time spent at sea. Together with the increase in alertness and lower resting times, such disturbances might have adverse consequences for the fitness of this species, potentially via higher levels of stress, heart rate, and energetic expenditure (Jansen et al., 2010; Young et al., 2014; Karpovich et al., 2015; Back et al., 2018).

These consequences could be intensified during the breeding season. As capital breeders, grey seals undergo a period of high energetic demand while relying solely on stored fat reserves (Pomeroy et al., 1999; Shuert et al., 2020; Twiss et al., 2020). To optimise energy expenditure during this crucial period, grey seals must balance the time engaged in different activities, including nursing. There is a positive correlation between nursing time and body condition (Engelhard et al., 2002), which is known to determine grey seal pup survival during the first year of life (Hall et al., 2001). Recent work on lactating grey seals (Shuert et al., 2020) revealed how individual differences in stress management are a significant factor influencing the time spent resting vs vigilant and, hence, overall energy expenditure. Tourism activities might trigger an increase in stress levels (Karpovich et al., 2015), preventing an adequate balance between the time spent in different activities and also resulting in a higher energy expenditure, which ultimately could adversely affect the success of the offspring (Pomeroy et al., 1999).

Grey seal pups are born on land, and the first hour after giving birth is crucial for establishing a strong bond, which will allow the mother to recognise the pup by calls and olfactory cues (Fogden, 1971; McCulloch & Boness, 2000; Robinson et al., 2015, 2019). Mother–pup separation could increase inconsistent suckling and allosuckling (Fogden, 1971), adversely affecting the survival of the offspring (Robinson et al., 2015, 2019). Pups are unable to swim for the initial 18- to 21-d nursing period (Fogden, 1971; Pomeroy et al., 1999; Lyons, 2004), and this inability to follow the mother also makes them vulnerable to disturbances. Ecotourism activities might force the mothers to leave the beach where they have hauled out, impeding bonding and causing separation between mother and pup, ultimately leading to abandonment (Granquist & Sigurjonsdottir, 2014; Lozano & Hente, 2014; Karpovich et al., 2015; Mathews et al., 2016; Öqvist et al., 2018) and starvation, one of the main causes of pup mortality (Baker & Baker, 1988). Furthermore, the flushing behaviour of adult seals triggered by ecotourism activities could lead to physical injuries in pups (Back et al., 2018).

Grey seals show high site fidelity to their breeding haulout sites, returning to these sites to breed (Pomeroy et al., 2000; Sayer et al., 2018). White Strand Beach in the Great Blasket Island seems to be the preferred haulout site of this colony. Although White Strand Beach has been previously reported as a breeding site (NPWS, 2014), no pups were observed on the beach during the study period. The seals were found to use and breed on smaller islands located nearby and in more remote locations around the island such as in coves and small inlets. While inaccessible to tourists, these sites might be more exposed to storms, even getting completely flooded under high tide conditions (M. Pérez Tadeo, pers. obs.), which can lead to pup mortality.

Whether grey seals would habituate to tourism activities was beyond the scope of this study. However, as it was carried out across two consecutive years and different months, and tourism has been taking place for several years, habituation seems unlikely. Some authors reported habituation of fur, grey, and harbour seals subject to disturbances (Boren et al., 2002; Bishop et al., 2015; Cates & Acevedo-Gutiérrez, 2017). Apart from leading to an unnatural reaction that could adversely affect these species' survival in the long term (Boren et al., 2002; Bejder et al., 2009), other researchers found not only a lack of habituation (Andersen et al., 2012), but also an increase in pinnipeds' response after long-term exposure to tourism disturbances (Corral et al., 2018). Long-term human activities could ultimately result in habitat displacement, forcing them to search for areas that might present lower productivity (Becker et al., 2011) or be less suitable for resting and breeding than the Blasket Islands. Management actions are needed as tourism increases in the Blasket Islands SAC to ensure the welfare of this species and to avoid the displacement

Table 7. Recommendations aimed at avoiding grey seal disturbance due to ecotourism activities in the Blasket Islands SAC

Disturbance type	Recommendations from April to October (pre-breeding/breeding/mating seasons)
Vessels passing along the colony	Reduce speed when approaching the colony.
	Remain at least 250 m from the colony; markers should be in place so tour boats are aware of at what distance they should remain.
	Make guides on tour boats and on the island available for tourists and tour vessel operators to ensure compliance.
Walking tourists	Avoid the part of the beach occupied by the seals, remaining at a distance > 100 m from the colony.
	Avoid all kinds of interactions. Providing food, touching, or following the seals should be strictly forbidden.
	During breeding season, avoid using the beach. Seal-watching should only occur from the top of the cliff surrounding the beach.

of the colony as this is one of the most important breeding sites for grey seals in Ireland.

Based on the results of this study, recommendations on best practices aimed at avoiding grey seal disturbance due to ecotourism activities in the Blasket Islands SAC are presented in Table 7. Similar recommendations have been presented for different colonies where anthropogenic disturbances were also of concern. With special emphasis during breeding and nursing periods, these include reducing the speed and approaching distance of vessels to the colony; restricting access to the colony by land or sea; and providing signage, education, and public awareness as well as long-term monitoring programmes for different pinniped species such as grey and harbour seals (e.g., Curtin et al., 2009; Jansen et al., 2010; Granquist & Sigurjonsdottir, 2014; Lozano & Hente, 2014; Young et al., 2014; Granquist & Nilsson, 2016; Mathews et al., 2016; Cates & Acevedo-Gutiérrez, 2017).

Overall, these results confirm the urgent need to implement a code of conduct on best practices for ecotourism that is designed specifically for this particular area and species with the aim of minimising anthropogenic disturbances at a local scale. At a larger scale, this research provides reliable information to improve conservation plans for this species which are required to be devised under Natura 2000 designations across Europe (e.g., Habitats Directive 92/43/EEC; Birds Directive 2009/147/EC).

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Literature Cited

Acevedo-Gutiérrez, A., & Cendejas-Zarelli, S. (2011). Nocturnal haul-out patterns of harbor seals (*Phoca vitulina*) related to airborne noise levels in Bellingham, Washington, USA. *Aquatic Mammals*, *37*(2), 167-174. https://doi.org/10.1578/AM.37.2.2011.167

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*(3-4), 227-266. https://doi.org/10.1163/156853974X00534

Andersen, S. M., Teilmann, J., Dietz, R., Schmidt, N. M., & Miller, L. A. (2012). Behavioural responses of harbour seals to human-induced disturbances. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *22*(1), 113-121. https://doi.org/10.1002/aqc.1244

Back, J. J., Hoskins, A. J., Kirkwood, R., & Arnould, J. P. (2018). Behavioral responses of Australian fur seals to boat approaches at a breeding colony. *Nature Conservation*, *31*, 35-52. https://doi.org/10.3897/natureconservation.31.26263

Baker, J. R., & Baker, R. (1988). Effects of environment on grey seal (*Halichoerus grypus*) pup mortality: Studies on the Isle of May. *Journal of Zoology*, *216*(3), 529-537. https://doi.org/10.1111/j.1469-7998.1988.tb02449.x

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Gabor Grothendieck, B. D., Green, P., & Fox, J. (2015). Package 'lme4'. *Convergence*, *12*, 2.

Becker, B. H., Press, D. T., & Allen, S. G. (2011). Evidence for long-term displacement of breeding and pupping harbour seals by shellfish aquaculture over three decades. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *21*(3), 247-260. https://doi.org/10.1002/aqc.1181

Bejder, L., Samuels, A., Whitehead, H., Finn, H., & Allen, S. (2009). Impact assessment research: Use and misuse of habituation, sensitization and tolerance in describing wildlife responses to anthropogenic stimuli. *Marine Ecology Progress Series*, *395*, 177-185. https://doi.org/10.3354/meps07979

Bishop, A., Pomeroy, P., & Twiss, S. D. (2015). Breeding male grey seals exhibit similar activity budgets across varying exposures to human activity. *Marine Ecology Progress Series*, *527*, 247-259. https://doi.org/10.3354/meps11254

Bonner, W. N. (1990). *The natural history of seals*. Facts on File.

Boren, L. J., Gemmell, N. J., & Barton, K. J. (2002). Tourist disturbance on New Zealand fur seals (*Arctophalus forsteri*). *Australian Mammalogy*, *24*(1), 85-96. https://doi.org/10.1071/AM02085

Bowen, D. (2016). Grey seal. *Halichoerus grypus*. In International Union for Conservation of Nature (Ed.), *The IUCN red list of threatened species 2016: e.T9660A45226042*. https://www.iucnredlist.org/species/9660/45226042

Cates, K., & Acevedo-Gutiérrez, A. (2017). Harbor seal (*Phoca vitulina*) tolerance to vessels under different levels of boat traffic. *Aquatic Mammals*, *43*(2), 193-200. https://doi.org/10.1578/AM.43.2.2017.193

Corral, C. T., Szteren, D., & Cassini, M. H. (2018). Short- and long-term changes in the intensity of responses of pinnipeds to tourist approaches in Cabo Polonio, Uruguay. *Applied Animal Behaviour Science*, *201*, 111-116. https://doi.org/10.1016/j.applanim.2017.12.012

Cowling, M., Kirkwood, R., Boren, L., Sutherland, D., & Scarpaci, C. (2015). The effects of vessel approaches on the New Zealand fur seal (*Arctocephalus forsteri*) in the Bay of Plenty, New Zealand. *Marine Mammal Science*, *31*(2), 501-519. https://doi.org/10.1111/mms.12171

Cronin, M. A., Duck, C. D., & Ó Cadhla, O. (2007). Aerial surveying of grey seal breeding colonies on the Blasket Islands, Co. Kerry, the Inishkea Group, Co. Mayo and the Donegal Coast, Ireland. *Journal for Nature Conservation*, *15*(2), 73-83. https://doi.org/10.1016/j.jnc.2006.11.001

Cronin, M. A., Jessopp, M. J., & Del Villar, D. (2011). *Tracking grey seals on Ireland's continental shelf*. Report to National Parks & Wildlife Service, Department of Arts, Heritage and Gaeltacht, Dublin, Ireland.

Curtin, S., Richards, S., & Westcott, S. (2009). Tourism and grey seals in south Devon: Management strategies, voluntary controls and tourists' perceptions of disturbance. *Current Issues in Tourism*, *12*(1), 59-81. https://doi.org/10.1080/13683500802295663

Dalerum, F., Lange, H., Skarpe, C., Rooke, T., Inga, B., & Bateman, P. W. (2008). Foraging competition, vigilance and group size in two species of gregarious antelope. *African Journal of Wildlife Research*, *38*(2), 138-145. https://doi.org/10.3957/0379-4369-38.2.138

Engelhard, G. H., Baarspul, A. N., Broekman, M., Creuwels, J. C., & Reijnders, P. J. (2002). Human disturbance, nursing behaviour, and lactational pup growth in a declining southern elephant seal (*Mirounga leonina*) population. *Canadian Journal of Zoology*, *80*(11), 1876-1886. https://doi.org/10.1139/z02-174

Fogden, S. C. L. (1971). Mother-young behaviour at grey seal breeding beaches. *Journal of Zoology*, *164*(1), 61-92. https://doi.org/10.1111/j.1469-7998.1971.tb01298.x

Granquist, S. M., & Nilsson, P. Å. (2016). Who's watching whom?—An interdisciplinary approach to the study of seal-watching tourism in Iceland. *Journal of Cleaner Production*, *111*, 471-478. https://doi.org/10.1016/j.jclepro.2014.11.060

Granquist, S. M., & Sigurjonsdottir, H. (2014). The effect of land-based seal watching tourism on the haul-out behaviour of harbour seals (*Phoca vitulina*) in Iceland. *Applied Animal Behaviour Science*, *156*, 85-93. https://doi.org/10.1016/j.applanim.2014.04.004

Hall, A. J., McConnell, B. J., & Barker, R. J. (2001). Factors affecting first-year survival in grey seals and their implications for life history strategy. *Journal of Animal Ecology*, *70*(1), 138-149. https://doi.org/10.1111/j.1365-2656.2001.00468.x

Haller, M. A., Kovacs, K. M., & Hammill, M. O. (1996). Maternal behaviour and energy investment by grey seals (*Halichoerus grypus*) breeding on land-fast ice. *Canadian Journal of Zoology*, *74*(8), 1531-1541. https://doi.org/10.1139/z96-167

Hoover-Miller, A., Bishop, A., Prewitt, J., Conlon, S., Jezierski, C., & Armato, P. (2013). Efficacy of voluntary mitigation in reducing harbor seal disturbance. *The Journal of Wildlife Management*, *77*(4), 689-700. https://doi.org/10.1002/jwmg.510

Hopper, M. (2000). WXTide32*, Version 2.6*. www.wxtide32.com

Jansen, J. K., Boveng, P. L., Dahle, S. P., & Bengtson, J. L. (2010). Reaction of harbor seals to cruise ships. *The Journal of Wildlife Management*, *74*(6), 1186-1194. https://doi.org/10.1111/j.1937-2817.2010.tb01239.x

Jansen, J. K., Boveng, P. L., Ver Hoef, J. M., Dahle, S. P., & Bengtson, J. L. (2014). Natural and human effects on harbor seal abundance and spatial distribution in an Alaskan glacial fjord. *Marine Mammal Science*, *31*(1), 66-89. https://doi.org/10.1111/mms.12140

Jessopp, M., Cronin, M., & Hart, T. (2013). Habitat-mediated dive behavior in free-ranging grey seals. *PLOS ONE*, *8*(5), e63720. https://doi.org/10.1371/journal.pone.0063720

Johnson, A., & Acevedo-Gutiérrez, A. (2007). Regulation compliance by vessels and disturbance of harbor seals. *Canadian Journal of Zoology*, *85*(2), 290-294. https://doi.org/10.1139/Z06-213

Karpovich, S. A., Skinner, J. P., Mondragon, J. E., & Blundell, G. M. (2015). Combined physiological and behavioral observations to assess the influence of vessel encounters on harbor seals in glacial fjords of southeast Alaska. *Journal of Experimental Marine Biology and Ecology*, *473*, 110-120. https://doi.org/10.1016/j.jembe.2015.07.016

Kovacs, K. M., & Innes, S. (1990). The impact of tourism on harp seals (*Phoca groenlandica*) in the Gulf of St. Lawrence, Canada. *Applied Animal Behaviour Science*, *26*(1-2), 15-26. https://doi.org/10.1016/0168-1591(90)90083-P

Larm, M., Elmhagen, B., Granquist, S. M., Brundin, E., & Angerbjörn, A. (2018). The role of wildlife tourism in conservation of endangered species: Implications of safari tourism for conservation of the Arctic fox in Sweden. *Human Dimensions of Wildlife*, *23*(3), 257-272. https://doi.org/10.1080/10871209.2017.1414336

Le Boeuf, B. J., & Campagna, C. (2013). Wildlife viewing spectacles: Best practices from elephant seal (*Mirounga* sp.) colonies. *Aquatic Mammals*, *39*(2), 132-146. https://doi.org/10.1578/AM.39.2.2013.132

Lozano, E., & Hente, M. (2014). *The effects of disturbances on harbor seals (*Phoca vitulina*) on a haul-out site off Yellow Island, Washington* (Student paper). Friday Harbor Laboratories, University of Washington. http://hdl.handle.net/1773/34627

Lyons, D. O. (2004). Summary of National Parks & Wildlife Service surveys for common (harbour) seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*), 1978 to 2003. *Irish Wildlife Manuals*, *13*. National Parks & Wildlife Service, Dublin, Ireland.

Mathews, E. A., Jemison, L. A., Pendleton, G. W., Blejwas, K. M., Hood, K. E., & Raum-Suryan, K. L. (2016). Haul-out patterns and effects of vessel disturbance on harbor seals (*Phoca vitulina*) on glacial ice in Tracy Arm, Alaska. *Fishery Bulletin*, *114*(2), 186-202. https://doi.org/10.7755/FB.114.2.6

McCulloch, S., & Boness, D. J. (2000). Mother–pup vocal recognition in the grey seal (*Halichoerus grypus*) of Sable Island, Nova Scotia, Canada. *Journal of Zoology*, *251*(4), 449-455. https://doi.org/10.1111/j.1469-7998.2000.tb00800.x

Morris, C. D., & Duck, C. D. (2019). Aerial thermal-imaging survey of seals in Ireland, 2017 to 2018. *Irish Wildlife Manuals*, *111*. National Parks & Wildlife Service, Department of Culture, Heritage and the Gaeltacht, Dublin, Ireland.

National Parks & Wildlife Service (NPWS). (2014). *Blasket Islands SAC*. National Parks & Wildlife Service, Dublin, Ireland. https://www.npws.ie/protected-sites/sac/002172

Ó Cadhla, O., Keena, T., Strong, D., Duck, C., & Hiby, L. (2013). Monitoring of the breeding population of grey seals in Ireland, 2009-2012. *Irish Wildlife Manuals*, *74*. National Parks & Wildlife Service, Department of Arts, Heritage and the Gaeltacht, Dublin, Ireland.

O'Brien, J. (2013). *Cetacean presence at the Ocean Energy Test Site Spiddal: As determined through land-based visual monitoring and static acoustic monitoring using PODs*. Report prepared for the Marine Institute.

Öqvist, E. L., Granquist, S. M., Burns, G. L., & Angerbjörn, A. (2018). Seal watching: An investigation of codes of conduct. *Tourism in Marine Environments*, *13*(1), 1-15. https://doi.org/10.3727/154427317X14964473293699

Osinga, N., Nussbaum, S. B., Brakefield, P. M., & de Haes, H. A. U. (2012). Response of common seals (*Phoca vitulina*) to human disturbances in the Dollard estuary of the Wadden Sea. *Mammalian Biology*, *77*, 281-287. https://doi.org/10.1016/j.mambio.2012.02.005

Osterrieder, S. K., Salgado Kent, C., & Robinson, R. W. (2017). Responses of Australian sea lions, *Neophoca cinerea*, to anthropogenic activities in the Perth metropolitan area, Western Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *27*(2), 414-435. https://doi.org/10.1002/aqc.2668

Patterson, J., & Acevedo-Gutiérrez, A. (2008). Tidal influence on the haul-out behavior of harbor seals (*Phoca vitulina*) at a site available at all tide levels. *Northwestern Naturalist*, *89*(1), 17-23. https://doi.org/10.1898/1051-1733(2008)89[17:TIOTHB]2.0.CO;2

Pavez, G., Muñoz, L., Barilari, F., & Sepúlveda, M. (2014). Variation in behavioral responses of the South American sea lion to tourism disturbance: Implications for tourism management. *Marine Mammal Science*, *31*(2), 427-439. https://doi.org/10.1111/mms.12159

Pavez, G., Muñoz, L., Inostroza, P., & Sepúlveda, M. (2011). Behavioral response of South American sea lion *Otaria flavescens* to tourist disturbance during the breeding season. *Revista de Biología Marina y Oceanografía*, *46*(2), 135-140. https://doi.org/10.4067/S0718-19572011000200004

Pomeroy, P. P., Twiss, S. D., & Redman, P. (2000). Philopatry, site fidelity and local kin associations within grey seal breeding colonies. *Ethology*, *106*(10), 899-919. https://doi.org/10.1046/j.1439-0310.2000.00610.x

Pomeroy, P. P., Fedak, M. A., Rothery, P., & Anderson, S. (1999). Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. *Journal of Animal Ecology*, *68*(2), 235-253. https://doi.org/10.1046/j.1365-2656.1999.00281.x

Powell, G. V. N. (1974). Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Animal Behaviour*, *22*(2), 501-505. https://doi.org/10.1016/S0003-3472(74)80049-7

R Core Team. (2019). R*: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org

Rieucau, G., & Martin, J. G. (2008). Many eyes or many ewes: Vigilance tactics in female bighorn sheep *Ovis canadensis* vary according to reproductive status. *Oikos*, *117*(4), 501-506. https://doi.org/10.1111/j.0030-1299.2008.16274.x

Robinson, K. J., Hazon, N., Twiss, S. D., & Pomeroy, P. P. (2019). High oxytocin infants gain more mass with no additional maternal energetic costs in wild grey seals (*Halichoerus grypus*). *Psychoneuroendocrinology*, *110*, 104423. https://doi.org/10.1016/j.psyneuen.2019.104423

Robinson, K. J., Twiss, S. D., Hazon, N., & Pomeroy, P. P. (2015). Maternal oxytocin is linked to close mother-infant proximity in grey seals (*Halichoerus grypus*). *PLOS ONE*, *10*(12), e0144577. https://doi.org/10.1371/journal.pone.0144577

Sayer, S., Allen, R., Hawkes, L. A., Hockley, K., Jarvis, D., & Witt, M. J. (2018). Pinnipeds, people and photo identification: The implications of grey seal movements for effective management of the species. *Journal of the Marine Biological Association of the United Kingdom*, *99*(5), 1221-1230. https://doi.org/10.1017/S0025315418001170

Shuert, C. R., Pomeroy, P. P., & Twiss, S. D. (2020). Coping styles in capital breeders modulate behavioural trade-offs in time allocation: Assessing fine-scale activity budgets in lactating grey seals (*Halichoerus grypus*) using accelerometry and heart rate variability. *Behavioral Ecology and Sociobiology*, *74*(1), 1-17. https://doi.org/10.1007/s00265-019-2783-8

Twiss, S. D., Shuert, C. R., Brannan, N., Bishop, A. M., & Pomeroy, P. P. (2020). Reactive stress-coping styles show more variable reproductive expenditure and fitness outcomes. *Scientific Reports*, *10*(1), 1-12. https://doi.org/10.1038/s41598-020-66597-3

van Polanen Petel, T., Giese, M., & Hindell, M. (2008). A preliminary investigation of the effect of repeated pedestrian approaches to Weddell seals (*Leptonychotes weddellii*). *Applied Animal Behaviour Science*, *112*(1-2), 205-211. https://doi.org/10.1016/j.applanim.2007.07.005

Young, C., Gende, S. M., & Harvey, J. T. (2014). Effects of vessels on harbor seals in Glacier Bay National Park. *Tourism in Marine Environments*, *10*(1-2), 5-20. https://doi.org/10.3727/154427314X14056884441626

Zuur, A. F., & Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution*, *7*(6), 636-645. https://doi.org/10.1111/2041-210X.12577

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3-14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). GLM and GAM for absence–Presence and proportional data. In A. F. Zuur, E. N. Ieno, N. J. Walker, A. A. Saveliev, & G. M. Smith (Eds.), *Mixed effects models and extensions in ecology with R* (pp. 245-259). Springer.