

Cumulative energetic costs of military aircraft, recreational and natural disturbance in roosting shorebirds

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Abstract

Knowing the consequences of disturbance for multiple species and all disturbance sources is crucial to mitigate disturbance impacts in densely populated areas. However, studies that observe the complete disturbance landscape to estimate cumulative costs of disturbance are scarce. Therefore, we quantified responses, frequencies and energetic costs of disturbance of four shorebird species on five high tide roosts in the Wadden Sea. Roosts were located either in a military air force training area or were predominantly affected by recreational disturbance. In the military training area, infrequent transport airplanes and bombing jets elicited the strongest responses, whereas regular, predictable activities of jet fighters and small civil airplanes elicited far smaller responses. Disturbance occurred more frequently at roosts near recreational than near military activities, as recreation was prohibited in the military area during operation days. On average, birds took flight due to military, recreational or natural disturbance (e.g. raptors) 0.20–1.27 times per hour. High tide disturbance increased daily energy expenditure by 0.1%–1.4%, of which 51% was due to anthropogenic disturbance in contrast to natural disturbance. Costs were low for curlews *Numenius arquata*, oystercatchers *Haematopus ostralegus* and gulls *Larus spp.*, but higher – and potentially critical – for bar-tailed godwits *Limosa lapponica* as they were most susceptible to aircraft and raptors. Given that bar-tailed godwits have previously been found to be least susceptible to walker disturbances, our results suggest that interspecific differences in susceptibility depend on disturbance source type. In our study area, aircraft disturbance impacts can be reduced by avoiding jet fighter activities during periods when high water levels force birds closer to military targets and by limiting bombing and transport airplane exercises.

Introduction

A challenge for nature conservation is the increasing level of anthropogenic activities in areas with high natural values, as such activities can affect wildlife and vegetation (Monz *et al.*, 2013). Disturbance of wildlife is one of the most visible adverse effects of anthropogenic activities, and behavioural responses of wildlife to the presence of disturbance sources are well documented for many species (Blumstein *et al.*, 2005; Stankowich, 2008; McLeod *et al.*, 2013; Collop *et al.*, 2016). Yet, our understanding of the negative impact of disturbance at the population level is very limited (Sutherland, 2007). Disturbance sources that cause a large response do not necessarily have a large overall impact if the frequency in which they occur is low. Thus, the extent to which anthropogenic activities negatively affect populations does not only depend on the responses of animals to single

disturbance events but also on the frequency by which disturbance events actually occur. Only if both disturbance responses and disturbance frequency are measured simultaneously for all relevant disturbance sources, modelling tools can be utilized to quantify whether anthropogenic activities have negative effects on the survival and population size of birds (Goss-custard *et al.*, 2006; Houston *et al.*, 2012; Lilleyman *et al.*, 2016; Nolet *et al.*, 2016).

Since most anthropogenic activities happen at a large spatial scale (e.g. recreation), many sites and species are typically affected by disturbance, and to identify vulnerable situations it is thus important to identify how the impact varies among sites and species. The effects of direct disturbance depend on landscape characteristics and the availability of alternative sites (Goss-Custard & Verboven, 1993; Gill *et al.*, 2001), making it difficult to generalize disturbance costs based on results of a single location. Furthermore,

species differ in their responses and susceptibility, which is, for example, linked to body size (Blumstein, 2006). These interspecific differences cause disturbance frequencies to vary among species within the same site (Visser, 1986; Spaans *et al.*, 1996). Additionally, differences in disturbance frequencies might not linearly translate to differences in energetic costs, as the costs of fleeing also vary among species as a function of their flight morphology (Pennycuik, 2008; Collop *et al.*, 2016). Thus, to make proper impact assessments of disturbance on biodiversity, it is crucial to observe the entire disturbance landscape and quantify the cumulative impact of all relevant disturbance sources over a range of species and sites, over longer periods of time, and covering a range of weather conditions, seasons and times of the day (Stillman & Goss-Custard, 2002; Kim & Yoo, 2007).

Shorebirds are well suited for studying disturbance, as they can be easily observed and in many areas frequently encounter disturbance sources. Since shorebirds inhabit areas that humans also heavily use for a variety of activities, they are not only affected by natural disturbances (e.g. raptors) but also by recreational and military disturbances (Smit & Visser, 1993; Spaans *et al.*, 1996). For example, the intertidal areas of the Wadden Sea, a UNESCO World Heritage, are of major importance as stopover and wintering sites for vast numbers of shorebirds (van Roomen *et al.*, 2012). When the tide rises and the intertidal feeding grounds become inaccessible, shorebirds prefer to roost on sites with low predation and disturbance rates to minimize energy expenditure (Mitchell *et al.*, 1988; Rogers *et al.*, 2006a). At the same time, the Wadden Sea lies in some of the most densely populated countries in the world, meaning that the area is also heavily utilized for a range of human activities including recreation, military training and commercial transports (Reneerkens *et al.*, 2005). Anthropogenic activities can increase energy expenditure through disturbance of shorebirds (Meager *et al.*, 2012; Navedo & Herrera, 2012; Martín *et al.*, 2015; Murchison *et al.*, 2016), which could ultimately lower the carrying capacities of intertidal areas for bird populations (Platteeuw & Henkens, 1997).

For many different shorebird species, responses to disturbance sources are well documented for walker disturbance (Collop *et al.*, 2016; Livezey *et al.*, 2016). It is, however, less well known how shorebirds respond to other disturbance sources (Livezey *et al.*, 2016), which is problematic since intertidal areas are not only accessible to walkers but also to motor vehicles, boats and aircraft (Davidson & Rothwell, 1993). In addition, several sites in the Wadden Sea are in use as military training area. Military activities potentially have a high impact on shorebirds as they can cause disturbance by increased sound levels and vehicle movements in the air or on land, affecting large areas (Visser, 1986; Smit & Visser, 1993; Koolhaas *et al.*, 1993). Yet, observations on disturbance of military activities are scarce and have often been published in grey literature and are difficult to access (Visser, 1986; Smit & Visser, 1993; Koolhaas *et al.*, 1993; Smit, 2004; Linssen *et al.*, 2019). Moreover, we especially lack good estimates of how disturbance responses and

disturbance frequencies accumulate and affect daily energy expenditure of multiple bird species in military training areas.

We observed and quantified the anthropogenic as well as non-anthropogenic disturbance landscape for four shorebird species at five high tide roosts in 2017 and 2018. Three of the roosts are located in the military air force training area on the Wadden Island Vlieland. We compare the disturbance impact of six different civil and military aircraft activities and derive energetic costs of disturbance for all disturbance sources. Thus, our main goals were (1) to quantify and compare the direct disturbance responses to different types of aircraft activities as well as other anthropogenic and natural (e.g. raptors) disturbance sources, (2) to quantify actual disturbance frequencies and (3) to derive the cumulative energetic costs of high tide disturbance across species and sites located inside and outside a military air force training area. Based on the results, we identified the conditions where human activity has the highest impact on roosting birds, thus providing means to reduce the effects of disturbance.

Materials and methods

Study system

We observed disturbance of four bird species at five high tide roosts on the islands of Texel and Vlieland in the western Wadden Sea (Fig. 1). Roosts Tankdoel, Nulpunt and Kroon's Polders (henceforth M_1 , M_2 and M_3 , respectively) are located on the Vliehors, a large sandflat on Vlieland in use as a military air force training area (Fig. 1). Jets, helicopters and transport airplanes practice in this area during weekdays. Even though recreation is allowed during the weekends when there are no military activities, it is scarce because the military training area is difficult to access. Roosts M_1 and M_2 are located inside the military training area (Fig. 1). Roost M_3 is located adjacent to the military training area and covers a large area of tidal flats that are largely inaccessible to people over land. Roost M_3 was included to study effects of aircraft activities at a more distant roost in comparison to roosts M_1 and M_2 which are in the military training area. Due to its close proximity to the military training area, M_3 is still considered to be influenced mainly by aircraft disturbance in the analysis. Approximate distances of the roosts to the military aircraft activities are 0–1.5 km, 0.5–2.5 km and 2.5–5 km for M_1 , M_2 and M_3 , respectively (Fig. 1).

Roosts Volharding and Westerse Veld (henceforth R_1 and R_2 , respectively) are located outside the military training area and are mainly influenced by recreational disturbance. Roost R_1 is located on a small peninsula with young dunes in the northeast of Texel (Fig. 1). Walkers sometimes occur in the area, despite access to R_1 being officially prohibited. Roost R_2 is a field protected from the sea by a low dike on the east of Vlieland (Fig. 1). Recreational activities, especially walkers, occurred frequently at this roost since R_2 is located close to the only village on the island. Roost R_1 is located 8 km from M_1 and 10 km from M_2 and R_2 is located 11 km

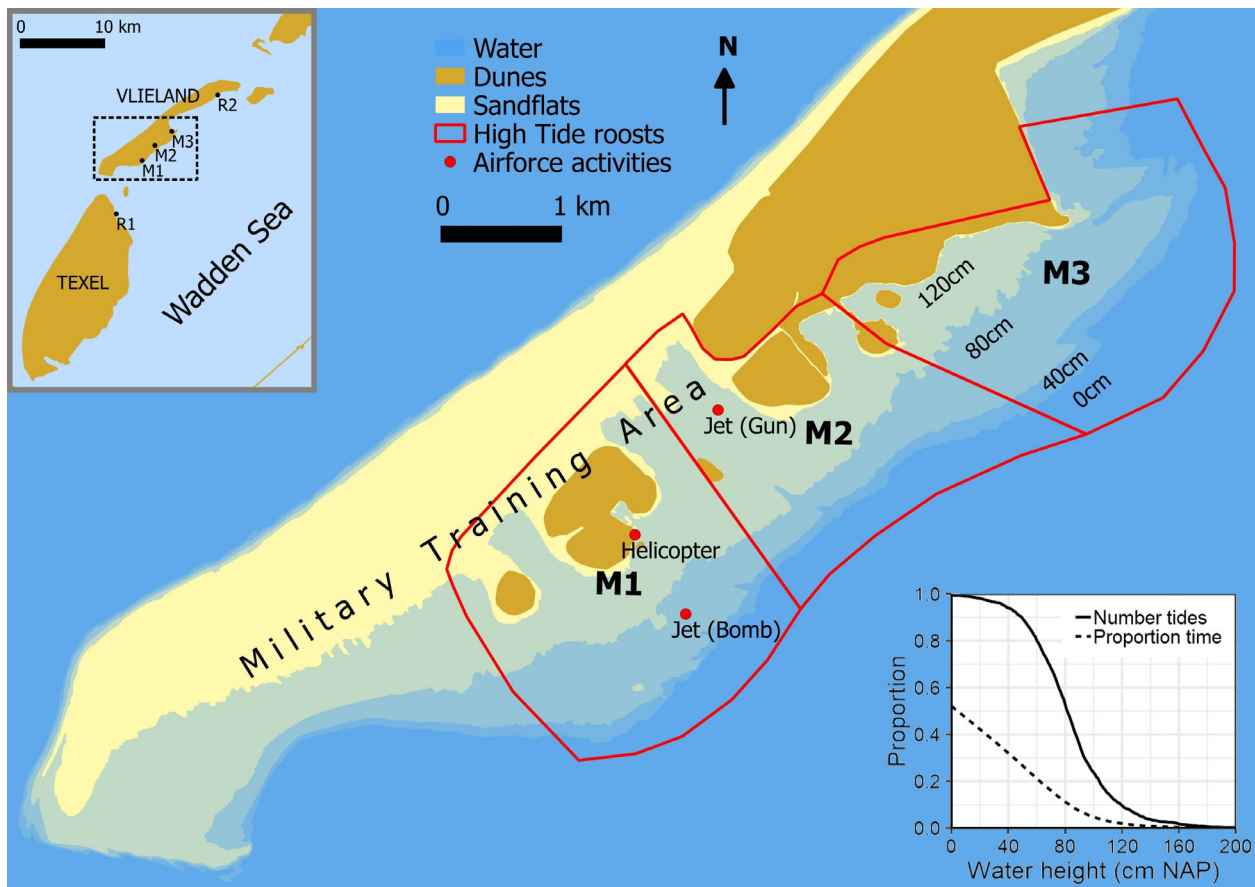


Figure 1 Study area showing locations of high tide roosts observed on the islands of Vlieland and Texel and detailed map of the military training area showing high tide roosts, aircraft activity locations and water levels. The extent to which areas become submerged with increasing water levels is visualized for four water levels (in cm NAP) using a blue-to-yellow gradient. Inset bottom-right shows the distribution of water heights (continuous line: proportion of high tide periods where a specific water level was reached; dashed line: proportion of total time including low tides that water height was above a specific water level). Tidal data for 2017 and 2018 ($n = 1410$ tidal periods), Rijkswaterstaat, 2019. [Colour figure can be viewed at [zslpublications.onlinelibrary.wiley.com](https://onlinelibrary.wiley.com).]

from M_1 and 10 km from M_2 (Fig. 1). Due to the presence of an airfield on Texel, small civil airplanes commonly flew over all roosts along standard routes (following shorelines) at altitudes of generally 450 m.

We observed four bird species that all winter in large numbers in the Wadden Sea (Koffijberg *et al.*, 2003) and that were relatively easy to observe due to their large size and occurrence in well-defined flocks. These species were as follows: Eurasian oystercatcher *Haematopus ostralegus*, bar-tailed godwit *Limosa lapponica*, Eurasian curlew *Numenius arquata* and mixed groups of gulls (mostly black-headed gull *Chroicocephalus ridibundus*, European herring gull *Larus argentatus* and common gull *Larus canus*).

Data collection

We observed high tide roosts from 2.5 h before to 2.5 h after high tide. The observation period was often cut short, for various reasons such as birds abandoning the high tide roost or the high tide being partly outside daylight hours.

Observations were carried out from June 2017 until the end of November 2018, for a total of 1026 h covering 128 high tide periods. The majority of observations were done from August until the end of November (Fig. S1). Not all bird species were always simultaneously present and thereby observed at each high tide roost. At R_1 only, oystercatchers were observed, although gulls and sometimes bar-tailed godwits and curlews were also present. Bar-tailed godwits virtually never used roost R_2 .

Observation protocols consisted of at least hourly counts of bird numbers of all focal bird groups on the high tide roosts. We additionally recorded the type and time of all potential disturbance sources that entered the high tide roost area (outlined in Fig. 1), and documented whether or not they evoked a disturbance response in birds (Fig. 2). We defined a disturbance as an occasion where birds took flight when approached by a disturbance source. We also documented flight responses resembling disturbance (i.e. tortuous flights) where no disturbance source could be identified and grouped them under natural disturbances. We assumed that

those flights were mainly caused by raptors that were not detected by the observers. Some of these reactions, however, may have been false responses to alarm calls or to a few birds flying up to relocate (Hilton *et al.*, 1999; Proctor *et al.*, 2001). We did not record flights that were caused by rising water levels due to upcoming tide and that resulted in birds relocating to higher grounds or flying away.

We classified disturbance sources into eight categories: natural sources, anthropogenic sources on land and six different aircraft activities. Natural sources included raptors and disturbances with an unknown cause (see above). Disturbance from anthropogenic sources on land was mainly caused by walkers and land vehicles, including military land vehicles. Aircraft activities were categorized in (1) small civil airplanes, (2) jet fighters, (3) shooting jet fighters, (4) jet fighters dropping explosive bombs, (5) helicopters and (6) transport airplanes. On the roost sites on the military training area, we consistently noted all military aircraft activities. Jets and helicopters always trained at specific locations, circling widely around fixed targets along a series of more or less standard flight patterns (Fig. 1). Every aircraft passage was treated as a potential moment at which birds could be disturbed. When disturbed, we estimated flight duration. Estimating flight duration was not always possible when birds flew to roost sites outside observation range or intermixed

with other groups of birds. Consequently, flight duration estimates were missing for 8% of the disturbances (123 out of 1561 total disturbances) and occurred especially during large disturbances. For the energetic costs analysis, missing flight durations were imputed from the mean flight durations of the given disturbance source and bird species.

We used water height as explanatory variable in our model for disturbance probability, as this affected the location of exposed mudflats that are available to roost and therewith how far flocks roost from the military training activities (Fig. 1). Water height measurements expressed in Amsterdam Ordnance Datum (cm NAP) were obtained with 10-minute intervals from Vlieland harbour for the entire study period (Rijkswaterstaat, 2019). Based on field calibrations, high tides at roosts M_1 , M_2 and M_3 occurred with a 20-minute delay from Vlieland harbour, for which we corrected in the analysis.

Data analysis

Overview and definitions

From our data, we derived and analysed (1) disturbance probability, (2) flight duration, (3) disturbance frequency and (4) additional energy expenditure caused by disturbance.

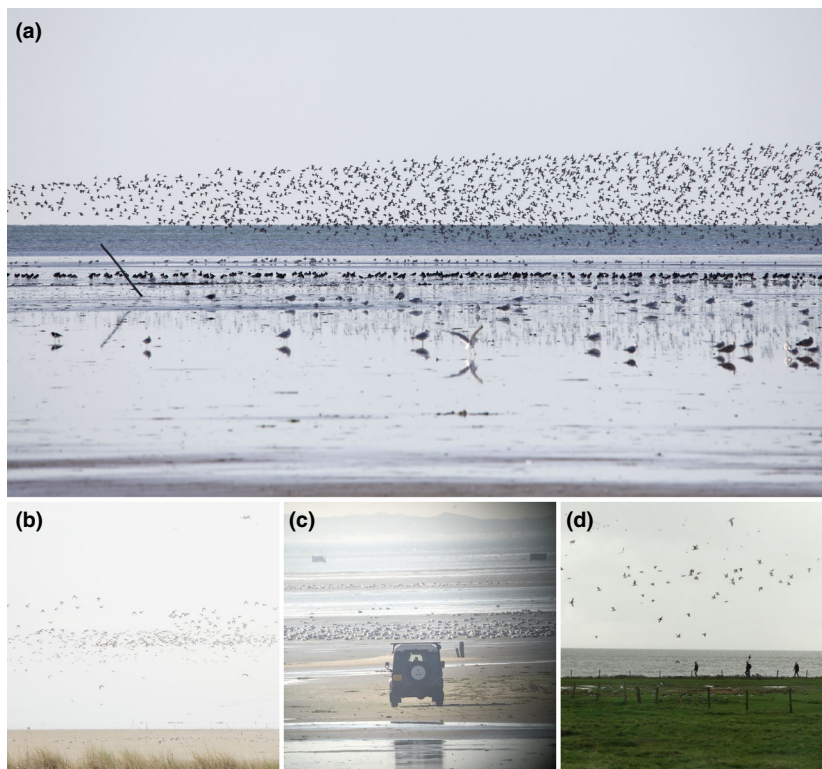


Figure 2 Examples of disturbance sources and disturbances at high tide roosts. (a) Flock of bar-tailed godwits disturbed by military airplane activities at M_2 , whereas oystercatchers and gulls are not responding. (b) Transport Airplane (Douglas DC-10, top right corner in picture) in an airshow at Texel Airport disturbing oystercatchers but not gulls at M_2 . (c) Car approaching gulls at M_2 . (d) Walkers disturbing oystercatchers and gulls at R_2 . Pictures by Ingrid D. van der Spoel (a), Donny Dolman (c) and Henk-Jan van der Kolk (b,d). [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

Disturbance probability was defined as the probability that a disturbance source evoked a flight response to at least 1% of the observed flock. Flight duration was defined as the flight time of the flock after a disturbance occurred. Disturbance frequency was defined as the number of times an average individual was put to flight by disturbance sources. Lastly, by combining disturbance frequency and flight duration, we calculated how much the daily energy expenditure of an individual bird increased due to disturbance over a 6-hour high tide period. All analyses were performed in R (R Core Team, 2017).

Disturbance probability and flight duration

We first analysed whether disturbance probability and flight duration upon disturbance differed among disturbance source types and bird species. We focussed the analysis of disturbance probability on aircraft activities on the military range. Flocks at R₁ and R₂ were 8 km or more away from the military range and they almost never responded to military training activities, and were therefore not included in this analysis. We did not include disturbances from anthropogenic land sources and natural sources in the analysis of disturbance probability, as our data did not allow accurate probability estimates for these sources. Anthropogenic disturbance sources on land were too variable (cars, cyclists, walkers and quads) and covered too many different circumstances (no consistency in following paths or routes) to obtain an objective, well-balanced and sufficiently large sample size. Natural sources, for example, low-flying falcons, were easily missed by the observer, making it impossible to accurately estimate disturbance probability. Note that our inability to measure disturbance probability for above sources did not prevent us to calculate their energetic costs, as these were derived using only flight duration and disturbance frequency. For analyses of flight duration, data from all disturbance sources and from all roosts including R₁ and R₂ were used.

To analyse disturbance probability, we selected all occurrences of aircraft activity on roosts M₁, M₂ and M₃ and determined whether or not they evoked a flight response in the focal bird groups. We used logistic mixed regression models to detect differences in disturbance probability among aircraft types and bird species. We added water height as explanatory variable as this is an important determinant of how close birds were resting to the military air force activities (Fig. 1). We added high tide roost as random factor to correct for differences among roosts. We determined statistical significance of explanatory variables by log likelihood ratio test.

To determine whether flight duration depended on bird species or disturbance source type (including anthropogenic land and natural sources), we used linear mixed-effects modelling. We used flight duration as response variable and bird species and disturbance source type as explanatory variables. Flight duration was log-transformed prior to analysis to approximate a normal distribution. We accounted for differences among high tide periods, roosts and observers by including them as random factors.

Disturbance frequencies and energy expenditure

We calculated the average disturbance frequency (number of disturbances per hour) for every roost site and species and disturbance source. We corrected for the proportion of birds in the group that were actually disturbed, by dividing the number of disturbed birds by the number of birds present at each hour of observation. The disturbance frequency thus shows the number of flights per hour of high tide that an average bird made due to disturbance.

Based on the observed disturbance frequencies and flight durations, we derived the energetic costs of disturbance for every disturbance source and high tide roost and bird species. We expressed the additional energy costs as the percentage of daily energy expenditure caused by disturbance during a 6-h high tide period. To estimate flight costs, we used the *findMinimumPowerSpeed* function in the *afpt* R package, which estimates the optimal flight speed and flight costs of birds based on bird mass, wing span and wing area (Pennycuick, 2008; Klein Heerenbrink *et al.*, 2015). We estimated daily energy requirements in kJ based on the mass (*M*) of the bird species (Nagy *et al.*, 1999):

$$\text{Daily energy requirement} = 10.5 \times (M \times 1000)^{0.681} \quad ((1))$$

We used the following parameters for our study species to estimate flight costs and daily energy requirements (*M* = mass, *b* = wingspan, *s* = wing area): Bar-tailed godwit (*M* = 0.305 kg, *b* = 0.6855 m, *s* = 0.051 m²), curlew (*M* = 0.850 kg, *b* = 1.044 m, *s* = 0.1175 m²), oystercatcher (*M* = 0.550 kg, *b* = 0.805 m, *s* = 0.0622 m²) and gulls (data for *Larus canus*, *M* = 0.390 kg, *b* = 1.08 m, *s* = 0.1149 m²) (Greenewalt, 1962; Johnson, 1985; Piersma & Jukema, 1990). Our study species show body size and mass variation among sexes and over the season. Therefore, we used different combinations of body mass and wing dimensions to determine whether this affected our calculations for energy expenditure due to disturbance (Table S1). The combinations included male and female bar-tailed godwits, three of the common observed gull species (black-headed gull, common gull and European herring gull) and seasonal minimum and maximum weights for all sexes and species (Table S1). These results lead to changes in the estimated additional energy expenditure which were small (−15% to +15%) in waders, but larger (−31% to +61%) in gulls. However, since calculated energy expenditure due to disturbance was very small for gulls (see Results), the use of different wing areas or body masses does not strongly affect the interpretations of our results and conclusions (Table S1). Consequently, we henceforth only reported results for the average parameter combinations in the main text.

To test whether energetic consequences differed among high tide roosts and bird species, we used a generalized linear mixed model with a gamma response distribution and a log link function. We used energy expenditure due to disturbance (expressed as additional daily energy expenditure per 6-hour high tide period) as response variable and high tide roost and bird species as explanatory variables. The high tide

period was added as random factor to the model. We used post-hoc Tukey tests to detect significant differences among high tide roosts and bird species.

Jet disturbance effects in relation to water level

Water height was an important determinant of the distance between roosting birds and fighter jet activities, and thereby moderates the impact of disturbance (see Results). We therefore performed additional calculations to determine the mitigating effect of having fewer jet activities when birds were roosting close to military activities. To this end, we quantified how much the additional energy expenditure due to disturbance would be reduced if jet exercises that took place at water levels above 80 cm NAP were performed at levels of 50 cm NAP instead, thus simulating fewer activities when birds were roosting close to military targets and more activities when they roosted further away. For this purpose, we used a subset of our data (jets and shooting jets at M₁, M₂ and M₃ only) to accurately model disturbance probability by fighter jets with bird species, roost site, water height and fighter jet activity as explanatory variables in a logistic regression model (Table S2). Interactions between water height and bird species, high tide roost or aircraft activity were non-significant. Using linear regression analysis, we also determined that there was no effect of water level on the proportion of the flock that was disturbed. Consequently, for each disturbance at water heights above 80 cm NAP, we reduced the number of disturbed birds proportionally to the difference in predicted disturbance probability at 50 cm NAP. With these proportional numbers, we calculated energy expenditure for this mitigation scenario and its difference with the original dataset (control scenario).

Results

On average, we observed 6400 bar-tailed godwits, 1900 curlews, 1400 oystercatchers and 2600 gulls per roost per high tide observation period. In the whole military training area (roosts M₁, M₂ and M₃), bird numbers were highest for bar-tailed godwits and gulls and lower for curlews and oystercatchers (Fig. 3a). Disturbances from natural sources were common at all roosts. In the military training area, jets and small civil airplanes were the most common disturbance sources, while transport airplanes (Airbus A400m and Douglas DC-10) were only observed during two high tides (Fig. 3b). In total, for all species and roosts, we observed 1561 disturbances of bird flocks, most of them (66%) caused by natural sources such as raptors. The remaining 34% of disturbances were of anthropogenic origin, of which 71% was caused by aircraft (358 disturbances inside and 16 outside the military training area, respectively) and 29% was caused by anthropogenic land sources.

Responses to disturbance

In the military training area, we observed 5818 instances where a focal group was confronted with aircraft activity, of

which only a small number (358) resulted in an actual disturbance. Disturbance probabilities varied among bird species ($\chi^2_{df=3} = 70.1$, $P < 0.0001$; Table S3) and among aircraft types ($\chi^2_{df=5} = 152.7$, $P < 0.0001$; Table S3). Disturbance probabilities were highest in bar-tailed godwits and lowest in oystercatchers and gulls (Fig. 3c). Furthermore, transport airplanes and explosive bombs fired from jets had a high probability of causing disturbance, whereas small civil airplanes, jets, firing jets and helicopters gave low disturbance probability (Fig. 3d). In general, relative differences in disturbance probabilities by different aircraft were similar across species, with the exception that oystercatchers responded remarkably strong to transport aircraft (Table 1). The disturbance probability was positively related to water height ($\chi^2_{df=1} = 90.7$, $P < 0.0001$; Table S3).

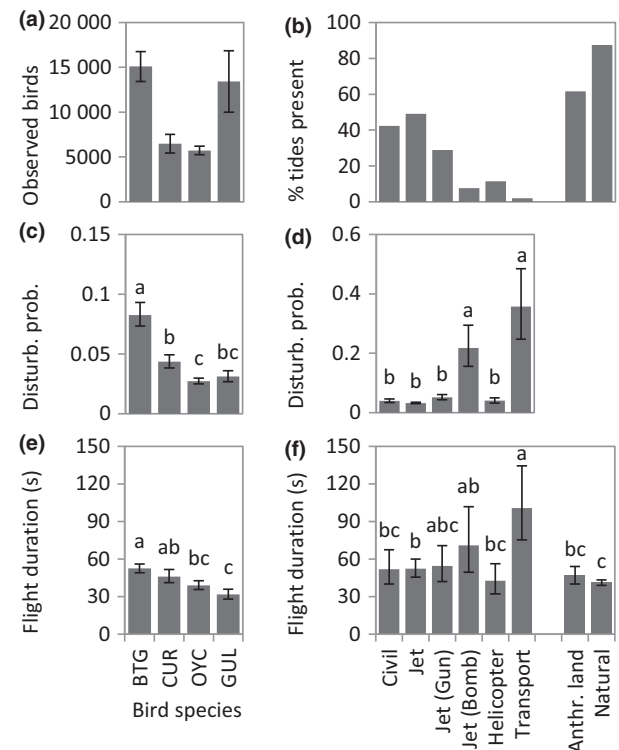


Figure 3 Immediate responses of birds to disturbance sources. (a) Average number of birds observed on the military range (roosts M₁, M₂ and M₃). (b) Percentage of high tides ($n = 110$) that aircraft activities were observed on the military range. (c) Disturbance probability of bird species per event. (d) Disturbance probability of disturbance source types per event. (e) Flight duration (s) of bird species after disturbance. (f) Flight duration (s) of birds after disturbance by different sources. Error bars represent standard errors. Dependent variables are corrected for additional explanatory variables in the models. Letters indicate significant differences between groups determined by post-hoc Tukey test. Bird species: BTG = Bar-tailed godwit, CUR = Curlew, OYC = Oystercatcher, GUL = Gulls. In (d) disturbance probability of anthropogenic land and natural sources is not estimated, see main text for details

For birds that were disturbed, the flight duration was typically less than a minute, but nonetheless varied significantly among bird species ($\chi^2_{df=3} = 43.5$, $P < 0.0001$; Table S4) and disturbance source types ($\chi^2_{df=7} = 45.6$, $P < 0.0001$; Table S4). The patterns were highly similar to those observed for the disturbance probability. Flight duration after a disturbance was longest in bar-tailed godwits, followed by curlews, oystercatchers and gulls, respectively (Fig. 3e). Transport airplanes and explosive bombs tended to cause longer flight durations than the other disturbance source types and especially when compared to natural disturbances (Fig. 3f).

Disturbance frequencies

Disturbance frequencies varied among bird species and roost sites, ranging from 0.20 to 1.27 disturbances per hour (Table 1, Fig. 4a). Disturbance frequencies were distinctly higher in bar-tailed godwits than in the other three species. Bar-tailed godwits were especially sensitive to natural disturbance, but were also more frequently disturbed by anthropogenic sources in comparison to the other species (Table 1, Fig. 4a). Aircraft disturbance frequencies were, in general, higher at roosts located closest to the military training area (M_1 and M_2 vs. M_3). At R_1 , 8 km away from the training area, disturbance from jets and bombing jets exercising at the military training area was rarely observed. Anthropogenic disturbance from sources on land was common and showed highest frequencies at R_2 (up to 0.30 disturbances per hour). Although anthropogenic land disturbance sources were observed during many high tides (Fig. 3b), their occurrence on the military training area was low compared to the roosts outside the training area, and their actual disturbance frequency at the military training area was therefore small (Table 1). Consequently, total anthropogenic disturbance frequencies were slightly higher in R_1 and R_2 than M_1 , M_2 and M_3 (Table 1, Fig. 4a).

Energy expenditure

Using an average body mass value, we calculated that the observed levels of disturbance increased daily energy expenditure on average by 0.1% to 1.4% per high tide period of 6 h, of which on average 51% was due to anthropogenic disturbance (Fig. 4b). Energetic costs of disturbance differed significantly among bird species ($\chi^2_{df=3} = 202.7$, $P < 0.0001$), being highest for bar-tailed godwits and lowest for oystercatchers and gulls (estimated for common gull) (Fig. 4b). Energetic costs of disturbance did not significantly vary among roosts ($\chi^2_{df=4} = 3.9$, $P = 0.43$). Specifically, energy expenditure was not significantly different outside the military training area, as the absence of additional energetic costs (or disturbance) due to military aircraft was replaced by additional energetic costs due to recreation (roosts R_1 and R_2 vs. M_1 , M_2 and M_3 ; Fig. 4b). Given that most disturbance sources are exclusively present or active during daylight and that there is on average one full high tide during daylight, the estimated costs per high tide period may well reflect the daily flight costs of high tide disturbance.

Jet disturbance effects in relation to water level

Disturbance probabilities by jets strongly increased with water levels (Fig. 5; Table S2). We estimated that a rescheduling of jet exercises from periods of water heights above 80 cm NAP to periods of water heights of 50 cm NAP would result in a reduction of energy expenditure due to disturbance by 13.5% of anthropogenic and by 6.8% of the total disturbance at the military training area (Fig. 4b). On a daily basis, the mitigating effect on overall additional energy expenditure would, however, be very low for most species–roost combinations. Only for bar-tailed godwits at M_1 and M_2 , and curlews at M_2 , the reduction in terms of daily energy expenditure exceeded 0.1% of their daily energy expenditure (Fig. 4b).

Discussion

Shorebird species differ in their susceptibility to disturbance sources, causing species that roost together to differ in their disturbance frequency and flight duration upon disturbance. By combining disturbance frequencies with data on flight duration and flight costs, we estimated that flight costs of high tide disturbance increased daily energy expenditure by 0.1%–1.4% per high tide period, depending on bird species and roost site.

Different susceptibilities to aircraft activities

Transport airplanes and explosive bombs were consistently the most disturbing aircraft activities, across roosts and species. Transport airplanes were the most disturbing source, although the distance to the birds was on average larger than any of the other aircraft activities. Low-flying transport airplanes initiated flights in oystercatchers at distances of up to 11 km (estimated using aircraft GPS tracks provided by the Royal Netherlands Air Force). All transport aircraft were large and slow planes that showed abnormal flight behaviour, flying at highly unusual routes (e.g. a flight demonstration at Texel air show) and at low altitudes, which may well have led to the large disturbing effects. These findings are in line with previous studies that reported strong disturbance responses elicited by low-flying transport airplanes in the Wadden Sea area (Smit & Visser, 1993; Smit, 2004).

Based on our observations, we interpret our results that birds barely responded to common and predictable aircraft activities. Predictability is suggested to be an important factor determining disturbance responses in birds (Platteeuw & Henkens, 1997). Birds perceive a certain level of danger from an object (Blumstein, 2006), and when the object is very different from usual objects or shows abnormal behaviour, it will perceive a higher risk of danger and respond accordingly. We observed that small civil airplanes standardly flew along fixed routes and at a standard altitude of 450 m. Their impact was normally small and disturbance occurred almost exclusively when planes flew at lower

Table 1. Disturbance probabilities and disturbance frequencies for different species and disturbance sources (between brackets: number of observation hours) at high tide roosts in 2017–2018, mainly August–November

Roost M ₁	Distance to aircraft	Bar-tailed godwit (14 h)		Curlew (23 h)		Oystercatcher (165 h)		Gulls (31 h)	
		Prob. (n)	Freq. h ⁻¹	Prob. (n)	Freq. h ⁻¹	Prob. (n)	Freq. h ⁻¹	Prob. (n)	Freq. h ⁻¹
Civil	<1.5 km	0% (11)	0.000	0% (16)	0.000	4% (53)	0.012	4% (25)	0.001
Jet	~1.5 km	24% (33)	0.399	4% (51)	0.021	2% (341)	0.028	1% (83)	0.032
Jet (Gun)	~1.5 km	33% (6)	0.041	0% (10)	0.000	0% (67)	0.000	0% (13)	0.000
Jet (Bomb)	~0.75 km	(0)	0.000	0% (3)	0.000	19% (16)	0.002	0% (1)	0.000
Helicopter	~0.75 km	0% (4)	0.000	56% (9)	0.147	10% (70)	0.046	0% (8)	0.000
Transport	1–11 km	(0)	0.000	(0)	0.000	(0)	0.000	0% (7)	0.000
Anthr. Land			0.000		0.074		0.012		0.000
Natural			0.351		0.130		0.091		0.164
Total			0.791		0.372		0.191		0.197

Roost M ₂	Distance to aircraft	Bar-tailed godwit (146 h)		Curlew (116 h)		Oystercatcher (349 h)		Gulls (134 h)	
		Prob. (n)	Freq. h ⁻¹	Prob. (n)	Freq. h ⁻¹	Prob. (n)	Freq. h ⁻¹	Prob. (n)	Freq. h ⁻¹
Civil	<1.5 km	16% (55)	0.030	2% (43)	0.005	5% (164)	0.013	4% (89)	0.016
Jet	~1.1 km	12% (346)	0.149	8% (286)	0.092	3% (803)	0.027	2% (352)	0.046
Jet (Gun)	~1.1 km	24% (55)	0.023	22% (50)	0.035	6% (139)	0.008	14% (73)	0.038
Jet (Bomb)	~2.4 km	29% (17)	0.023	33% (18)	0.026	40% (20)	0.007	67% (3)	0.004
Helicopter	~2.4 km	32% (57)	0.085	0% (27)	0.000	4% (90)	0.003	9% (43)	0.030
Transport	1–11 km	18% (11)	0.026	0% (2)	0.000	75% (12)	0.030	33% (12)	0.012
Anthr. Land			0.034		0.041		0.010		0.016
Natural			0.900		0.215		0.144		0.152
Total			1.270		0.414		0.242		0.314

Roost M ₃	Distance to aircraft	Bar-tailed godwit (216 h)		Curlew (241 h)		Oystercatcher (219 h)		Gulls (49 h)	
		Prob. (n)	Freq. h ⁻¹	Prob. (n)	Freq. h ⁻¹	Prob. (n)	Freq. h ⁻¹	Prob. (n)	Freq. h ⁻¹
Civil	<1.5 km	6% (110)	0.031	3% (122)	0.008	4% (114)	0.008	7% (29)	0.009
Jet	~3.5 km	6% (377)	0.064	4% (405)	0.043	1% (469)	0.018	2% (116)	0.006
Jet (Gun)	~3.5 km	3% (71)	0.007	2% (82)	0.006	0% (80)	0.000	3% (32)	0.012
Jet (Bomb)	~4.7 km	31% (13)	0.014	17% (18)	0.007	7% (14)	0.020	(0)	0.000
Helicopter	~4.7 km	9% (45)	0.011	0% (48)	0.000	0% (48)	0.000	(0)	0.000
Transport	1–11 km	25% (4)	0.011	50% (6)	0.018	92% (13)	0.085	38% (8)	0.019
Anthr. Land			0.014		0.006		0.000		0.012
Natural			1.055		0.233		0.146		0.140
Total			1.207		0.321		0.277		0.198

Roost R ₁	Oystercatcher (80 h)	
	Prob. (n)	Freq. h ⁻¹
Civil		0.043
Jet		0.004
Jet (Gun)		0.000
Jet (Bomb)		0.002
Helicopter		0.000
Transport		0.048
Anthr. Land		0.083
Natural		0.166
Total		0.346

Roost R ₂	Curlew (24 h)		Oystercatcher (59 h)		Gulls (52 h)	
	Prob. (n)	Freq. h ⁻¹	Prob. (n)	Freq. h ⁻¹	Prob. (n)	Freq. h ⁻¹
Civil		0.000		0.000		0.004
Jet		0.000		0.000		0.000
Jet (Gun)		0.000		0.000		0.000
Jet (Bomb)		0.000		0.000		0.000
Helicopter		0.000		0.000		0.000

Table 1 Continued.

Roost R ₂	Curlew (24 h)	Oystercatcher (59 h)	Gulls (52 h)
	Freq. h ⁻¹	Freq. h ⁻¹	Freq. h ⁻¹
Transport	0.000	0.000	0.000
Anthr. Land	0.259	0.249	0.299
Natural	0.090	0.220	0.293
Total	0.349	0.469	0.596

Approximate distances to aircraft activities and disturbance probabilities are indicated for roosts in the military training area (roosts M₁, M₂ and M₃). Probability is the probability that a disturbance source causes at least part of the flock to take flight. The disturbance frequency is the frequency at which an average bird has to take flight due to disturbance.

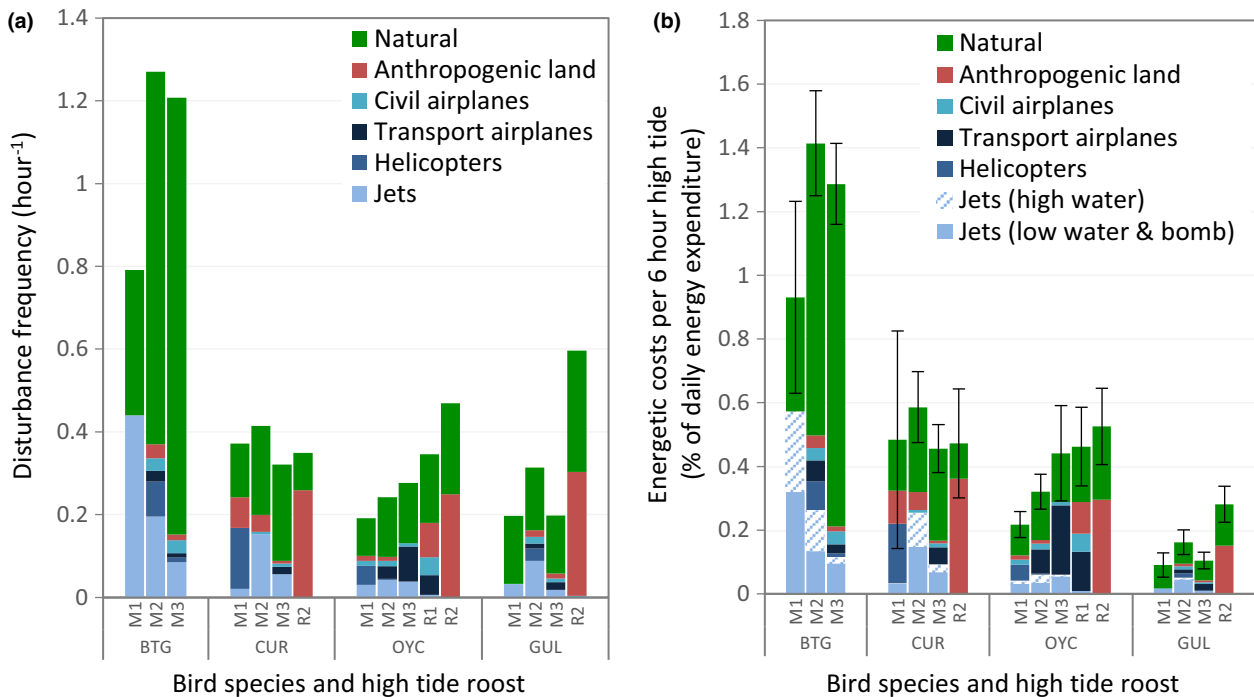


Figure 4 (a) Disturbance frequencies and (b) additional energy expenditure (in percentage of daily energy expenditure per roosting period of 6 h) ± standard error due to disturbance by different sources for different species on high tide roosts. Jets include shooting and bombing jets. The category ‘Jets (high water)’ indicates the energy expenditure that was caused due to increased disturbance probability during jet exercises with water levels higher than 80 cm NAP (see methods). Bird species: BTG = Bar-tailed godwit, CUR = Curlew, OYC = Oystercatcher, GUL = Gulls. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

altitudes or with tortuous patterns. We observed that jet fighters mostly only disturbed upon first arrival in the training area or when initiating gun firing. This sometimes caused birds to relocate at somewhat larger distances, after which disturbance responses were even rarer to occur. Similarly, Smit & Visser (1993) showed that frequent jet trainings on military air force training areas tended to cause little disturbance. Helicopters mostly caused disturbance during gun firing exercises while they were circling near the roosts. Given the different behaviours of helicopters and jets (frequency, flight pattern, location and altitude), it is difficult to compare disturbance effects between the two. In the literature, there is no clear consensus whether jets or helicopters cause disturbance more often (Dunnet, 1977; Smit & Visser, 1993;

Goudie, 2006). Most likely, this also depends on the animal species, frequency of occurrence, behaviour of the aircraft as well as landscape characteristics.

Interspecific variation in disturbance susceptibility

Assuming that birds receive airplanes as birds of prey, susceptibility to raptor predation can explain interspecific differences in susceptibility to aircraft presence. The peregrine falcon *Falco peregrinus*, a common bird of prey in our study area, prefers to target mid-sized waders such as knots *Calidris canutus* and bar-tailed godwits rather than larger waders such as oystercatchers and curlews (van den Hout

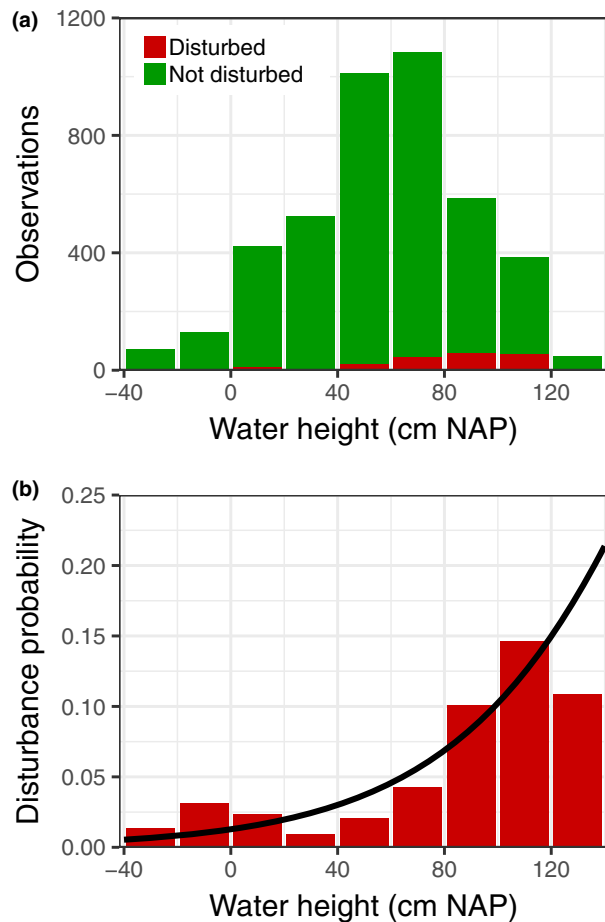


Figure 5 Disturbance probability in relation to water height, where (a) is number of observations of jets (including shooting jets) and (b) is disturbance probability (proportion of jets resulting in a disturbance) on the military training area (roosts M_1 , M_2 and M_3) in relation to actual water height at the time of the activity. Disturbance proportions in (b) are a reflection of the proportion disturbed–not disturbed shown in (a). Bars are constructed from binned raw data of all species. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

et al., 2008; van den Hout, 2009). Consistent with this idea, bar-tailed godwits responded more strongly to raptors and aircraft than the other species considered in our study, which has also been observed in other studies (Visser, 1986; Spaans *et al.*, 1996). If bar-tailed godwits are more often at risk of predation from aerial raptors, this may explain why they are more responsive to perceived dangers in the sky in comparison to larger wader species, and thus are also more susceptible to aerial objects such as aircraft. Another possible explanation is that bar-tailed godwits perceive more danger from aircraft since they breed in the Arctic in remote areas where aircraft are infrequent. A large part of the populations of curlews, oystercatchers and gulls breed in Western Europe where aircraft are more common.

Oystercatchers showed a persistent lack of response to many potential disturbances in our study. In other studies in

the Wadden Sea area, oystercatchers and gulls were found to be comparatively tolerant to aircraft disturbance as well (Visser, 1986; Smit & Visser, 1989). In that light, it is remarkable that in comparison to the other shorebirds, oystercatchers responded very strongly to transport planes, even at very large distances. It may be that this species adapts more quickly than others to activities in its surroundings, while it is more sensitive to unknown, rare objects that are large and slow-flying and thus may be perceived as potentially dangerous.

Which species responds most strongly to anthropogenic activities might well depend on the type of disturbance they are confronted with. We found that bar-tailed godwits were most susceptible to aircraft presence. By contrast, Collop *et al.* (2016) found that bar-tailed godwits were less susceptible to walker disturbance than oystercatchers and curlews, both in their flight initiation distance and in their flight time after disturbance. It has been hypothesized that smaller species react less to disturbance as the costs of fleeing expressed in daily energy expenditure are higher (Blumstein *et al.*, 2005; Blumstein, 2006; Collop *et al.*, 2016). Our results suggest that this relationship depends on how bird species assess the risk of predation by disturbance sources, and that not necessarily the largest species responds most strongly to disturbance, but the species that perceives the highest danger from the disturbance source. This hypothesis could be further investigated by including smaller-sized waders in observational studies in areas where airplane activities and raptors frequently occur.

Disturbance frequencies and energetic costs

Several previous studies quantified frequencies with which disturbances occur in the field (Visser, 1986; Spaans *et al.*, 1996; Madsen, 1998; Goss-Custard *et al.*, 2006; Kim & Yoo, 2007; Dwyer, 2010; Lilleyman *et al.*, 2016). Quantifying disturbance frequencies are crucial to determine cumulative costs of disturbance that wildlife experiences. Our estimates of aircraft disturbance frequencies for bar-tailed godwits, curlews and oystercatchers are in the same order of magnitude as observed by Visser (1986) in 1980–1984 in a military air force training area on the neighbouring island of Terschelling. A remarkable difference with our study is that Visser (1986) found low disturbance frequencies by raptors. During our observations, one or two peregrine falcons were always present in the military training area. Of the raptor species present in the area, peregrine falcons were most frequently seen hunting and disturbing roosting shorebirds. Wintering peregrine falcons have increased over the last decades in the Dutch Wadden Sea (Sovon, 2018).

Energetic costs of disturbance in our study area were low for curlews, oystercatchers and gulls, but higher and potentially critical for bar-tailed godwits. When disturbance levels exceed a threshold level beyond which birds cannot compensate for the increased energetic costs anymore, they will suffer increased mortality (Goss-Custard *et al.*, 2006). Goss-Custard *et al.* (2006) identified that mortality of wintering

oystercatchers in the Baie de Somme in France would increase when disturbance exceeded 1.5 disturbances per hour daylight under mild weather and abundant food conditions and 0.5 disturbances per daylight hour under harsh conditions. Our estimated energetic cost of an average disturbance for oystercatchers (1.46 kJ) is in the range of energetic costs modelled by Goss-Custard *et al.* (2006) (1–4 kJ). As disturbance frequencies are below 0.5 disturbances per hour at all roosts in our study, we expect that disturbance has a minimal effect on winter survival of oystercatchers. Given that disturbance in curlews and gulls results in similar or lower energetic costs, we expect that current disturbance in our study area has no adverse survival effects for these species either.

For bar-tailed godwits, current disturbance levels potentially impact survival, especially under harsh conditions with severe weather or low food availability. Bar-tailed godwits experienced disturbance frequencies of up to 1.27 disturbances per hour (from both natural and anthropogenic causes). Additionally, the flight duration upon being disturbed was longer in comparison to the other study species. In this light, the increased number of peregrine falcons wintering in the Wadden Sea area (van den Hout, 2009; Sovon, 2018) can be of concern for bar-tailed godwits. Bar-tailed godwits, and potentially other smaller waders, may experience elevated energetic costs due to natural disturbance on many roosts, even in remote areas. If we want to maintain or improve the condition for bar-tailed godwits, focus should be on minimizing disturbance by anthropogenic activity. Natural disturbance cannot be avoided, since most of the natural disturbances were caused by raptors that are protected by national legislation.

Even though energetic costs of disturbance are generally low, birds might still suffer from condition loss if there is insufficient time available to compensate for energetic losses. Current literature suggests that shorebirds can extend their foraging time at least to some extent. For example, knots could in theory extend their foraging time by moving further along with the tidal wave (van Gils *et al.*, 2005). Moreover, oystercatchers that were disturbed early in the low tide period were able to extend their foraging time at the end of that low tide period (Urfi *et al.*, 1996). Also model studies suggest that oystercatchers have the ability to compensate for energetic losses due to disturbance (Goss-Custard *et al.*, 2006). A model study on our study system may improve our understanding on the impacts of the current energetic costs of disturbance on survival, which is especially relevant for bar-tailed godwits.

It is important to note that our study does not reflect the total costs of disturbance, as we do not include aspects other than direct flight responses. For instance, disturbance during low tide may have other effects than during high tide. Disturbance during low tide may not only cause energetic (flight) costs but also reduce food intake by shortening available foraging time or decreasing foraging efficiency (Rutten *et al.*, 2010; Navedo *et al.*, 2019). Furthermore, we did not measure to what extent birds avoided our roost sites, which is an important aspect of disturbance when considering

population consequences (Mitchell *et al.*, 1988; Gill *et al.*, 2001; Bejder *et al.*, 2009). If anthropogenic disturbance is too high, birds eventually abandon roost sites and relocate to sites where anthropogenic disturbance is less (Spaans *et al.*, 1996; Rogers *et al.*, 2006b; Martín *et al.*, 2015). We likely observed this in our study area for oystercatchers roosting in areas with high recreational activity such as R₂, where birds often temporarily disappeared if recreation started in the morning. The similarity in bird numbers roosting in the military training area in periods with and without military activities suggests that large relocations of birds normally do not taken place here.

Through observations in the field, it is difficult to follow birds flying to remote places after disturbance, especially when large flocks simultaneously respond to a single disturbance source. In our study, this was especially the case for disturbances by transport airplanes. The effects of disturbance sources that evoked strong responses in birds may therefore be underestimated in our study. Such disturbances were infrequent and the bias effect will therefore be limited, but it requires further studies to determine whether incidental severe disturbances have larger population consequences than multiple small disturbances. For this purpose, GPS trackers can be used to more accurately study disturbance effects on displacement and foraging behaviour (e.g. Linssen *et al.*, 2019). The use of GPS trackers can also reveal whether there are significant differences in responses among individuals. Even though average disturbance frequencies are low, additional energetic expenditure can be high for susceptible individuals if there is large among-individual variation in susceptibility.

Implications for conservation

In our study area, energetic costs of high tide disturbance are low for larger shorebird species, with the exception of bar-tailed godwits for which costs are assessed as potentially critical. Our results indicate that the relative interspecific differences in disturbance susceptibility depend on the disturbance source type. Impact assessments should therefore take into account that responses of birds to aircraft may not follow the previously suggested rule that larger species respond most; instead, smaller species may potentially be more vulnerable. If this is the case, smaller shorebird species as knots, grey plovers *Pluvialis squatarola* and dunlins *Calidris alpina*, that all roost in high numbers in the study area, might experience similar or perhaps even more costs from aircraft disturbance as bar-tailed godwits.

Disturbance costs in the military training area are likely limited since military aircraft exercises are generally highly predictable and recreational disturbance is rare. Also, upon disturbance the vast 10 km long sandflat area normally allows birds to roost and relocate outside the area in which disturbance occurs. With increasing water height, however, the available roosting area is restricted, resulting in birds being forced to sit closer to the air force targets. Consequently, disturbance probabilities increase with water height. For roosts in other military aircraft training areas, we

consequently expect higher costs of disturbance in situations where there is little available area for birds to relocate upon disturbance or where recreational disturbance is more frequent. Ultimately, recreational and military disturbance can facilitate each other resulting in increased flight responses, as has been observed in other areas (Visser, 1986). It is noteworthy that the total cumulative costs of disturbance highly depend on the amount of natural disturbance, which is currently probably high in our study area. Natural disturbance can be less in areas where raptors are absent, or more in areas where more different raptor species cause disturbance.

In our study area, under harsh conditions (e.g. prolonged periods of cold weather or low food availability in midwinter) energetic costs of high tide disturbance might approach critical levels for bar-tailed godwits. Under these conditions, any measures to reduce impact should focus on reducing the most disturbing aircraft activities, that is, jet exercises at high water levels, bombing jets and transport aircraft. Moving shooting and bombing targets further away from roosting birds may be a solution in some areas, but in our study area virtually impossible without affecting other bird species (e.g. breeding little terns *Sternula albifrons* and kentish plovers *Charadrius alexandrinus* on sandflats or wintering common eiders *Somateria mollissima* on the North Sea) or causing more disturbance for local human residents.

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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. Overview of the hours that high tide roost sites in the study area were observed for every month during the study period.

Table S1. Effect of variation in body mass and wing size on flight costs, daily energy expenditure (Daily EE) and estimates of additional energy expenditure due to disturbance. Change gives the difference to the value used in the main article.

Table S2. Results of binomial model estimating the effect of waterheight on disturbance probability of jets (including shooting jets).

Table S3. Results of binomial mixed model for the effects of aircraft type and bird species on the disturbance probability.

Table S4. Results of linear mixed model for the effects of aircraft type and bird species on flight duration (s).