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Spatiotemporal variation in disturbance impacts derived from simultaneous tracking of aircraft and shorebirds

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Abstract

1. Assessing the impacts of disturbance over large areas and long time periods is crucial for nature management, but also challenging since impacts depend on both wildlife responses to disturbance and on the spatiotemporal distribution of disturbance sources. Combined tracking of animals and disturbance sources enables quantification of wildlife responses as a function of the distance to a disturbance source. We provide a framework to derive such distance–response curves and combine those with disturbance source presence data to quantify energetic costs of disturbance at a landscape scale.
2. We tracked 90 Eurasian Oystercatchers *Haematopus ostralegus* and all aircraft in a military training area in the Dutch Wadden Sea. We quantified distance–response curves estimating flight probability and additional displacement for five types of aircraft activities, by comparing bird movement prior to aircraft presence with movement during aircraft presence. We then used the distance–response curves to map mean and variation in additional daily energy expenditure due to cumulative aircraft disturbance across the landscape for a 700-day period.
3. Flight probability and displacement responses differed strongly among aircraft activities and decreased from transport aeroplanes, through bombing jets, helicopters, jets to small civil aeroplanes. Since the most disturbing aircraft activities were also the rarest ones, mean additional daily energy expenditure did not exceed 0.25%. However, days with substantial (>1%) additional expenditure occurred between 0.1% and 3.7% of all days across high-tide roosts in the tidal basin. Notably, expenditure particularly spiked on days with transport aeroplane activity (up to 8.5%).
4. *Synthesis and applications*. We quantified cumulative energetic flight costs due to aircraft disturbance and found that these were low and unlikely to impact survival of oystercatchers in our study area. Our results provide evidence that the legal minimum flight height of 450 m for small civil aeroplanes effectively limits the disturbance of oystercatchers. Mitigation should focus on limiting the number of days when disturbance has a high impact by reducing rare but highly disturbing

activities, especially transport aeroplanes. Our approach can be applied to other species and disturbance sources that are automatically tracked, for example boats and walkers, ultimately to quantify the entire anthropogenic disturbance landscape.

KEYWORDS
biologging, disturbance, energetics, flight, GPS tracking, *Haematopus ostralegus*, recreation ecology, Wadden Sea

1 | INTRODUCTION

Human–nature interactions have increased dramatically in recent decades due to various factors such as the growth in human population and outdoor recreation (Balmford et al., 2009). Human–nature interactions cause wildlife to exhibit anti-predator responses like flight (Frid & Dill, 2002) and altered behavioural rhythms (Gaynor, Hojnowski, Carter, & Brashares, 2018). Consequently, disturbance affects energy expenditure and foraging efficiency (Beale, 2007; Speakman, Webb, & Racey, 1991), which in turn can lower survival and reproduction (Beale & Monaghan, 2004). Since many natural areas are accessible by humans for both recreational and commercial purposes, disturbance is an important consideration for nature management. Ultimately, effective conservation actions require an understanding of which areas and time periods experience disturbance levels above thresholds that lead to reduced survival propensity and reproductive success (Goss-Custard, Triplet, Sueur, & West, 2006; West et al., 2002). However, quantifying disturbance impacts in large areas and over longer time periods is challenging, because impacts depend on both the spatiotemporal distribution of disturbance sources and on the responses of wildlife to disturbance (Sastre, Ponce, Palacín, Martín, & Alonso, 2009; Tablado & Jenni, 2017).

Wildlife responses to disturbance are often quantified in the field by estimating characteristics of the flight response, such as flight initiation distance, flight time and flight distance (Collop et al., 2016; Livezey, Fernández-Juricic, & Blumstein, 2016; Stankowich, 2008). Without simultaneously quantifying disturbance frequencies, however, such response measures provide in itself little information about the potential fitness impacts of disturbance. In addition, measured response characteristics cannot be easily used to derive general disturbance impacts, since they are often measured in specific situations in which focal animals are experimentally approached in a straight line. For example, flight initiation distances and the magnitude of an animal's response depend on the distance at which a disturbance source passes by (Fernández-Juricic, Venier, Renison, & Blumstein, 2005; Frid, 2003). *Distance–response relationships* describe the flight probability and the flight costs of an animal as a function of the minimal distance at which a disturbance source passes by, and would be suitable for assessing such disturbance impacts. However, they have only been quantified for a limited number of species and disturbance sources, including for disturbance of geese and Dall's sheep by aircraft (Frid, 2003; Marcella, Gende, Roby, & Allignol, 2017; Preisler, Ager, & Wisdom, 2006; Ward, Stehn, Erickson, & Derksen, 1999).

Biologging is increasingly applied to study how disturbance influences movement (Preisler et al., 2006), home ranges (Leblond, Dussault, & Ouellet, 2013; Perona, Urios, & López-López, 2019), habitat use (Marchand et al., 2014) and longer term behaviours (Brambilla & Brivio, 2018; Linssen et al., 2019). A novel development in this field is to directly link animal movements with the trajectories of potential disturbance sources (McKenna, Calambokidis, Oleson, Laist, & Goldbogen, 2015). Distance–response relationships can be derived from combined tracking of wildlife and disturbance source movements by identifying whether an animal responds (e.g. a sudden movement) and how strongly it responds (e.g. how far it moves) in relation to the distance to the disturbance source. Combined with data on disturbance source presence this enables predictions of disturbance impacts over large areas, but so far no studies have adopted such an approach.

We aimed to quantify distance–response relationships of Eurasian oystercatcher *Haematopus ostralegus* for aircraft overflights and subsequently to estimate how disturbance impacts varied in space and time. Aircrafts have the potential to cause large ecological impacts given that they traverse large areas, have access to remote natural areas and produce high noise levels (Delaney, Grubb, Beier, Pater, & Reiser, 1999). The oystercatcher population has declined strongly in the last few decades and disturbance is among the many threats listed for the species (van de Pol et al., 2014). Our study was conducted in the Wadden Sea World Heritage nature area, in a part with high levels of aircraft activity due to the presence of both military air force training and frequent overflights of small civil aeroplanes.

The impact of aircraft disturbance on birds varies depending on the type of aircraft (van der Kolk et al., 2019; Smit & Visser, 1993). We therefore related movement tracks of oystercatchers to the activities of both civilian and various military aircraft and quantified flight responses due to disturbance in relation to the minimum distance between an aircraft and bird. We subsequently quantified potential disturbance impacts throughout the study area by calculating additional daily energy expenditure (DEE) of flights caused by aircraft disturbance, a measure relating the costs of disturbance relative to an animal's normal energetic budget (Riddington, Hassall, Lane, Turner, & Walters, 1996). Critical thresholds of disturbance at which winter mortality would increase have previously been estimated at 0.7% and 5.4% additional DEE for oystercatchers in harsh and mild winters respectively (Goss-Custard et al., 2006; see also Section 4). We illustrate how distance–response relationships can be extrapolated across a large (>300 km^2) area to understand how the disturbance impacts of different aircraft activities on DEE vary in space and time, knowledge that is vital for predicting and minimizing the effects of anthropogenic disturbance.

2 | MATERIALS AND METHODS

2.1 | Study system

Oystercatchers are medium-sized (~0.5–0.6 kg) long-lived shorebirds with high site fidelity that spend the winter in coastal areas, feeding on shellfish. Approximately 100,000 oystercatchers winter in the Dutch part of the Wadden Sea. Our study covered a 700-day period (1 May 2017 to 31 March 2019) and focussed on the barrier island Vlieland. Aircraft are common on Vlieland because the western half of the island ('Vliehors') is a military air force training area (4.92°E, 53.24°N) and an airport for small civil aeroplanes is present on the neighbouring island Texel (4.83°E, 53.115°N; Figure 1). The area is remote with few other anthropogenic disturbance sources (van der Kolk et al., 2019).

We distinguished four types of aircraft and two activities of jet fighters, described in Appendix S1 (Supporting Information), resulting in five levels of what we hereon refer to as 'aircraft activity': (a) small civil aeroplanes (Figure 1c), (b) jets, (c) bombing jets, (d) helicopters (Figure 1d) and (e) transport aeroplanes. Small civil aeroplane overflights and exercises with jets were common, whereas bombing jets and transport aeroplanes occurred rarely (Figure 2).

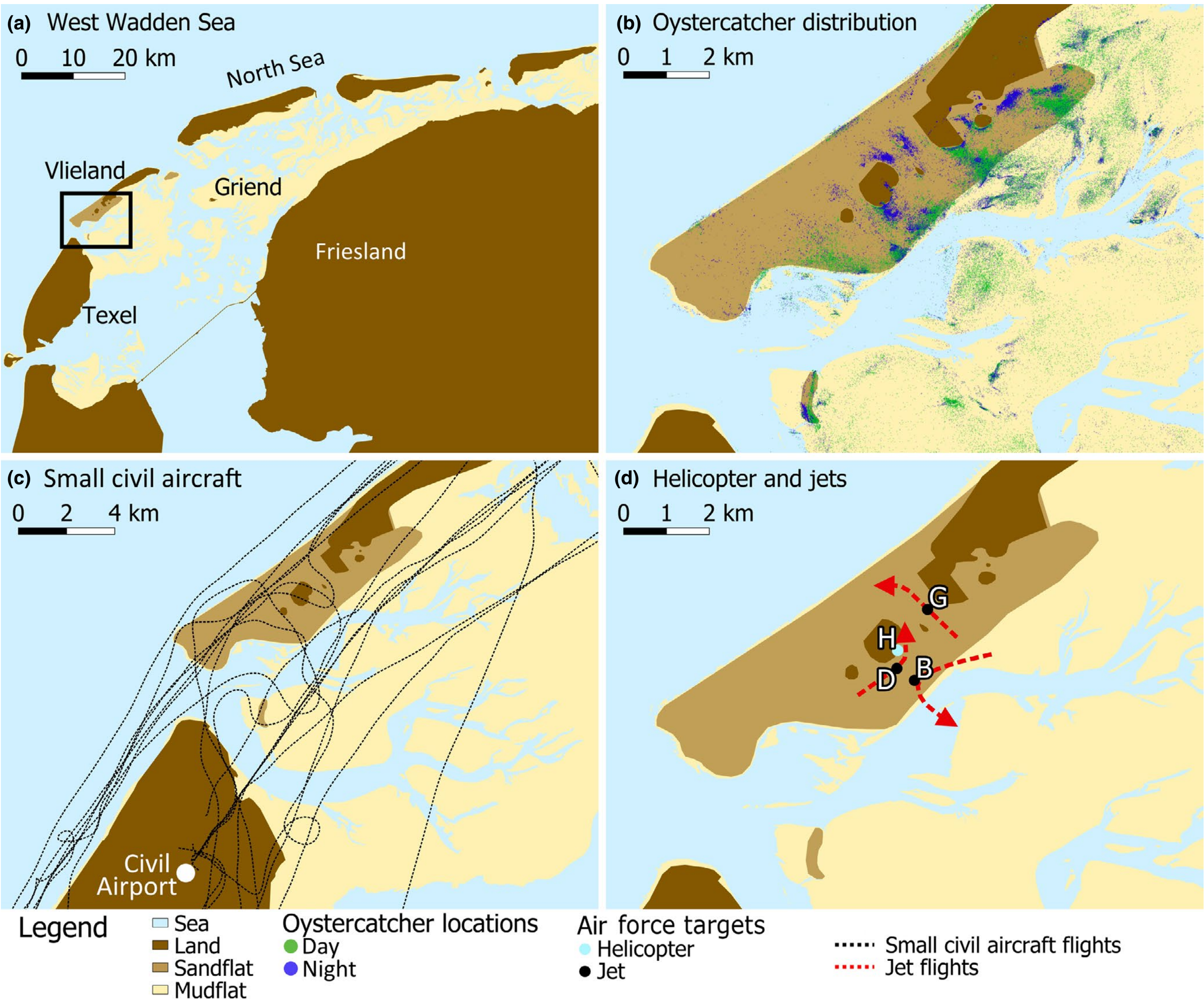

FIGURE 1 (a) Overview of the western Wadden Sea islands of Texel, Vlieland and Griend. Black rectangle is the study area shown in (b)–(d). (b) Locations of GPS-tagged oystercatchers during daytime (green) and night-time (blue). (c) Tracks of small civil aeroplanes over the study area on Saturday 1 September 2018. (d) Targets and flight routes of helicopters and jets. H: helicopter gun shooting target, B: jet target for explosive bombs, D: jet target for dummy bombs, G: jet target for gun shooting. Red flight paths show standard routes of jets when they approach the target and fly at their lowest altitude

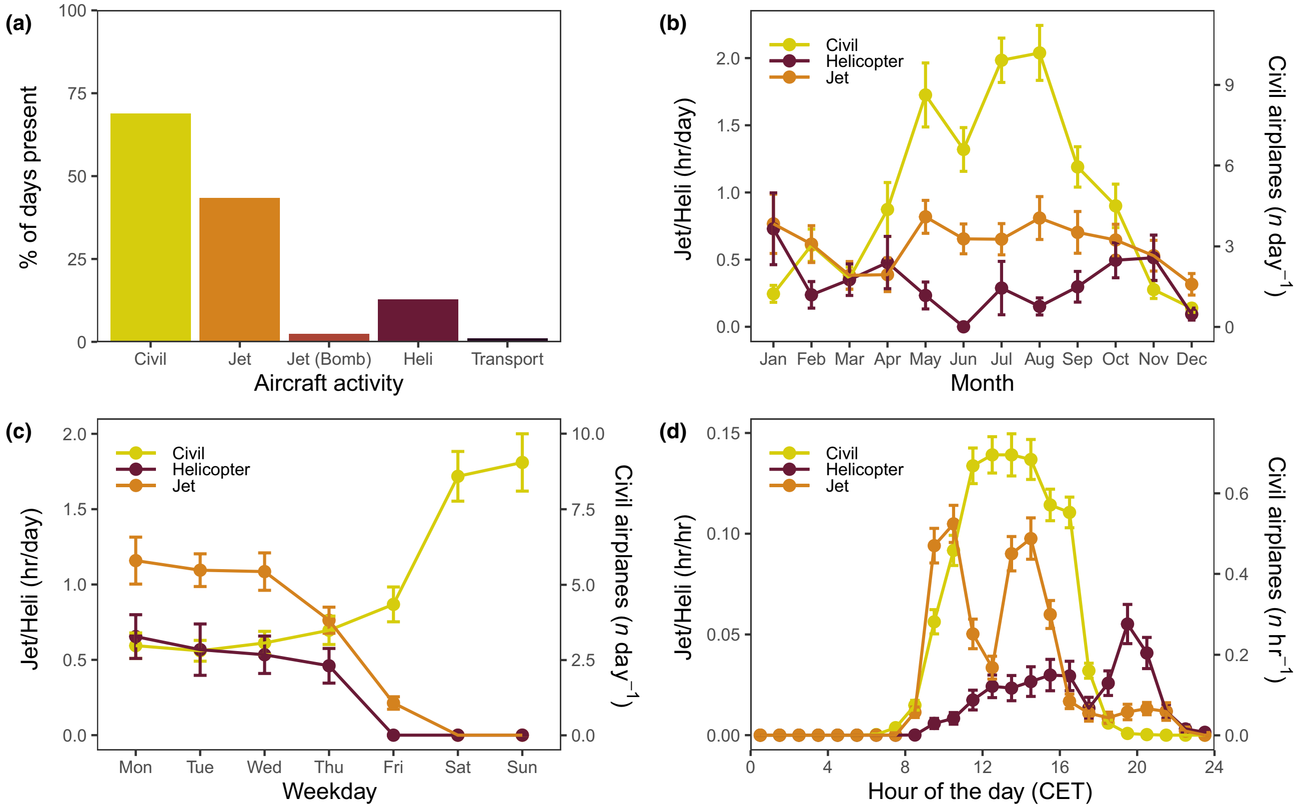

FIGURE 2 Occurrence of each aircraft activity in the study area (a) during the study period, (b) per month, (c) per weekday and (d) per hour of the day, calculated from 1 May 2017 to 31 March 2019. Due to their rare occurrence, bombing jets and transport aeroplanes are not depicted in (b)–(d). Note the different scales on the *y*-axis for military aircraft (left axis, hr/day or hr/hr) and civil aeroplanes (right axis, n/day or n/hr). For small civil aeroplanes, presence is defined as the number of aircraft flights within a 6-km radius of the helicopter target (Figure 1d)

2.2 | Data collection

2.2.1 | Oystercatcher GPS data

Twenty locally breeding (May–July 2017) and 82 wintering oystercatchers (20 in December 2016–January 2017, 42 in December 2017, 20 in December 2018) were caught on Vliehors and equipped with UvA-BiTS 13.5 g GPS trackers (Bouten, Baaij, Shamoun-Baranes, & Camphuysen, 2013). The trackers took GPS fixes with 16-s intervals for maximum 2 hr per day when the battery was fully charged, that is, in summer. Otherwise, the trackers took GPS fixes with 288 s intervals as long as the battery was sufficiently charged (see Appendix S2 and van der Kolk, et al., 2020 for more details). The final GPS dataset comprised 2,820,459 GPS fixes of 90 individuals (14,211 individual-days) inside the study area (Figure 1b).

2.2.2 | Aircraft data

The Royal Netherlands Air Force provided start and end times for all military aircraft exercises on Vliehors. Exact timings of when jets approached targets and whether they were dropping explosive bombs were also recorded, but for helicopters these data were unavailable. In contrast to the highly standardized flight paths of jets, helicopter movements were less standardized. Consequently, our results are less accurate for helicopters than for the other aircraft activities. High-accuracy GPS locations and altitudes with 4-s intervals of small civil aeroplanes and military transport aeroplanes were provided for the vicinity of the Vliehors for the whole study period, and for small civil aeroplanes in the entire Dutch Wadden Sea area for July–September 2018 [source Flight Track and Aircraft Noise Monitoring System (FANAMOS) from the Netherlands Aerospace Centre (NLR)].

2.2.3 | Environmental data

Tidal water height data with 10-min intervals were obtained for Vlieland harbour (Rijkswaterstaat, 2019). These data were used to determine whether small civil aeroplanes flew over during low or high tide using a threshold water level of −10 cm Amsterdam Ordnance Datum (NAP), below which intertidal flats become exposed.

2.2.4 | Oystercatcher–aircraft interactions

We combined oystercatcher GPS data with aircraft data to obtain timings of interactions and minimum horizontal distances between aircraft and birds. Given the differences in aircraft behaviour and available data, methods differed slightly among the five aircraft activities.

1. *Small civil aeroplanes*. We determined the exact time when the aeroplane was closest to the bird, and used this aeroplane position to calculate the distance to the bird, aeroplane height and path tortuosity over the previous minute (mean 4-s turning angle).
2. *Jets*. A bird–jet interaction could occur at three moments during military training: (a) when jets entered the study area (flying at low altitude in northward direction at 53.2276°N, 4.932°E), (b) when jets first approached the dummy bombs target (Figure 1d) or (c) when jets first approached the gun shooting target (Figure 1d). In the field, we observed that disturbance of oystercatchers mostly occurred upon first approach of the targets (van der Kolk et al., 2019).
3. *Bombing jets*. We selected all timings of explosive bombs dropped from jets and used the explosive bombing target as the disturbance location for this event (Figure 1d).
4. *Helicopters*. We selected all start times of helicopter exercises and used the most frequently used helicopter target as location for this event (Figure 1d). Since the actual flight paths of helicopters were not available and actual disturbance may occur 1–2 km away from this point, the estimated distance–response curves may underestimate responses when helicopters fly near oystercatchers, but overestimate the distance at which disturbance is initiated by a single helicopter overflight.
5. *Transport aeroplanes*. Most transport aeroplanes caused disturbance from large distances. Therefore, for every transport aeroplane we selected the timestamp at which a disturbance was initiated. This occurred when mass responses (i.e. flight initiation, see Video S1) were detected in the study area. Based on the aircraft track, we calculated the minimum distance between transport aeroplanes and each bird using the bird's last control position before disturbance was initiated.

2.2.5 | Control and disturbed displacement

To quantify the effects of aircraft disturbance, oystercatcher displacement during aircraft presence ('disturbed displacement') was compared with pre-disturbance displacement ('control displacement') directly preceding the disturbance bout (Figure 3b). This paired sampling design ensured that other factors that can influence movement, such as season, weather, tide and time of the day, were similar between control and disturbed displacement and thus did not need to be accounted for in statistical models.

The control and disturbed displacements were compared using three different measurement durations: 96 s (six 16-s GPS intervals), 10 min (one 10-min GPS interval) and 1 hr (six 10-min GPS intervals; Figure 3b). The 96-s and 10-min measurements were chosen because they were expected to be long enough to capture typical flight responses, that normally last for less than a minute (van der Kolk et al., 2019), but also to be as short as possible to minimize the chance that movements were caused by factors other than disturbance. Specifically, we expected that the 96-s measurements would detect small disturbances when birds were briefly in flight, and at times may return to the same location (Figure 3c). We furthermore expected the 10-min and 1-hr measurements to detect disturbances in which birds did not return to the same location (Figure 3c). The 1-hr measurements were included to accurately measure displacement responses to rare large disturbances (i.e. transport aeroplanes), that were not fully captured by the 10-min measurements. In all measurements, a time buffer between the end of the control measurement and aircraft presence was included to ensure that birds did not respond to aircraft presence during the control measurements (Figure 3b; Appendix S3).

The aircraft data did not allow response measurements for all aircraft activities on all temporal scales. Ninety-six-second measurements were only possible for small civil aeroplanes, as other aircraft activities were too infrequent and high-frequency bird GPS data were limited. All aircraft activities were included for the 10-min measurements except for helicopter exercises because only start time and end time of helicopter exercises were available, while disturbance often occurred when helicopters approached and fired on targets (field observations). As these moments were not exactly known, only 1-hr measurements were calculated for helicopters. We did not calculate 1-hr displacement of oystercatchers in response to civil aeroplanes, as the effects of civil aeroplanes were small (see Results) and overflights were frequent, such that control measurements without civil aeroplane presence could not be acquired for 73% of the 1-hr measurements (see Table S1 for sample sizes of final datasets).

In the analysis, data from all seasons were pooled for two reasons. First, most (~70%) oystercatcher–aircraft interactions were obtained between July and October (Figure S1). Most oystercatchers returned from their breeding grounds in July, and the solar-powered GPS trackers generally remained fully charged until autumn. The GPS trackers collected little data in November–February when there was insufficient sunlight to charge the battery. After February most birds were at their breeding grounds and not in the study area. Second, the most disturbing activities (transport aeroplanes and bombing activities) were rare and these limited datasets could not be further divided into different categories. Consequently, the results generally apply to oystercatchers in the non-breeding season in autumn. Although shorebird responses to disturbance can vary throughout the year (Stillman & Goss-Custard, 2002), such variation may be relatively small in comparison to variation in responses to different aircraft activities.

2.3 | Analysis

2.3.1 | Definitions for flight probability and additional displacement

Two response variables were derived from the paired control and disturbed displacement measurements. First, a binary variable described whether the control or the disturbed displacement was

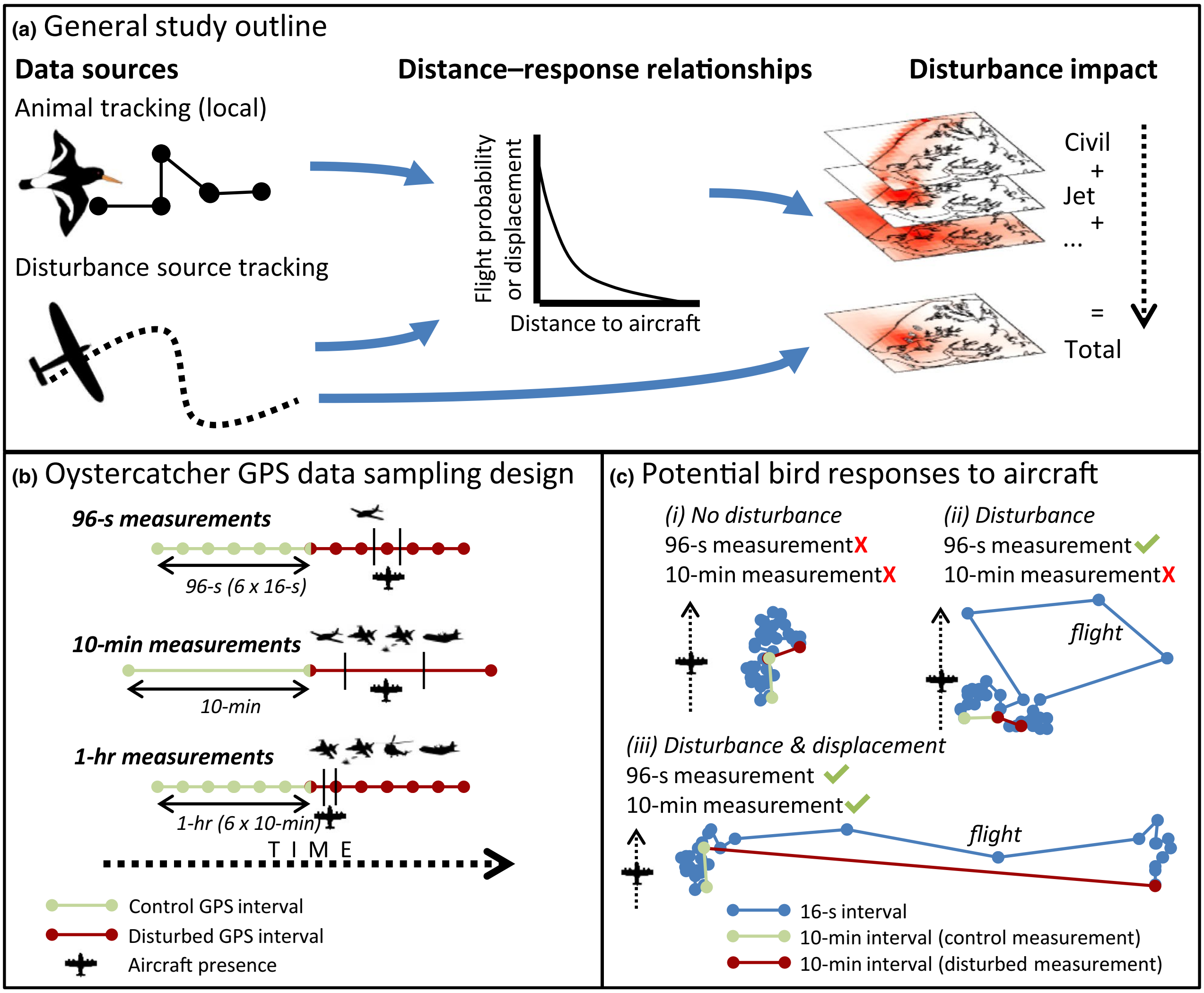

FIGURE 3 (a) General outline of study design: From raw tracking data of animal and disturbance sources to disturbance landscape maps. (b) Data sampling schemes comparing displacement during aircraft presence with control displacement before aircraft presence. Aircraft icons indicate for which aircraft types each measurement was used (see main text for details). Black lines in the disturbed measurements indicate when an aircraft was closest to the bird. (c) Potential responses of birds to aircraft depicted with hypothetical GPS data with 16-s and 10-m intervals: (a) no response to aircraft overflight, (b) flight response to aircraft overflight where bird returns to same location, (c) flight response to aircraft overflight where bird displaces to another location

highest. From this variable, we modelled *flight probability*, that is, the probability that aircraft presence caused birds to displace further during disturbed bouts. Under a scenario of no disturbance responses, we expected a probability of 0.5 by chance that disturbed displacement was higher than control displacement and we used this as a null model before calculating the actual *flight probability* (see Section 2.3.2). Second, we calculated the displacement difference in metres (m) between control and disturbed measurements. We used the displacement difference to quantify the effects of aircraft presence on *additional displacement*.

2.3.2 | Distance–response relationships

We modelled both *flight probability* and *additional displacement* using logistic regression to generate distance–response curves in a biologically relevant way, that is the response curves would approach (but not drop below) zero when birds were at large distances from aircraft. Equation 1 shows the general form of the logistic function in which the minimum y-axis asymptote (y_{min}) and maximum y-axis asymptote (y_{max}) are specified. To derive flight probability, the probability that disturbed displacement was larger than the control displacement ($P_{disturbed > control}$) was modelled using Equation 2, which is derived from Equation 1 by setting the minimum asymptote (y_{min}) at 0.5 and the maximum asymptote (y_{max}) at 1. The minimum asymptote was set at 0.5 as this was the expected probability that displacement was larger in the disturbed measurement if no response to disturbance occurred (null model). It is important to note that this function is now very similar to a conventional binomial regression model, where y_{min}, however, would be set at 0. After estimating $P_{disturbed > control}$ from our data, the actual flight probability (P_{flight}) due to disturbance was derived from $P_{disturbed > control}$ (Equation 3).

Consequently, the lower asymptote of 0.5 in Equation 2 translated into a flight probability of 0 in Equation 3.

$$y = \frac{y_{\max} - y_{\min}}{1 + e^{-(\beta_0 + \beta_1 \times x_1 + \beta_2 \times x_2 \ldots)}} + y_{\min} \quad (1)$$

$$P_{\text{disturbed > control}} = \frac{1 - 0.5}{1 + e^{-(\beta_0 + \beta_1 \times x_1 + \beta_2 \times x_2 \ldots)}} + 0.5 \quad (2)$$

$$P_{\text{flight}} = 2 \times (P_{\text{disturbed > control}} - 0.5) \quad (3)$$

The logistic function was also used to estimate the distance–response curves for *additional displacement*. For this purpose, the minimum asymptote ($y_{\min}$) was set to 0 and the maximum asymptote ($y_{\max}$) was estimated for each model separately (Equation 4). β_0 Varied per aircraft activity, as the shape of the response curve differed among aircraft activities. For each aircraft activity, we fitted models ranging β_0 between −5 and 5 and selected the model with the minimum residual sum of squares. Using this approach, β_0 was set on −5 for small civil aeroplanes, bombing jet fighters and transport aeroplanes and on 5 for jet fighters and helicopters. For the 10-min measurement of bombing jet fighters we manually changed β_0 to 1.5: In contrast to oystercatchers at 2 to 4 km distance, oystercatchers at 1 to 2 km distance surprisingly responded less strong to disturbance. This would have forced an unrealistic steep slope in the distance–response curve of bombing jets (see Figure 4c). See Figure S2 how β_0 affects the shape of the distance–response curves. It is important to note that the additional displacement reflects the average of events with (additional displacement > 0) and without (additional displacement ≈ 0) actual disturbance and consequently is determined by both how often a bird is actually disturbed (flight probability) and the displacement responses upon actual disturbances.

$$\text{Additional displacement}\,(m) = \frac{y_{\max}}{1 + e^{-(\beta_0 + \beta_1 \times x_1 + \beta_2 \times x_2 \ldots)}} \quad (4)$$

Separate models were constructed for combinations of response variable, aircraft activity and temporal scale at which data were available (total of 18 models). In all models, the main predictor of a disturbance effect was the distance to the aircraft. For small civil aeroplanes 10-min measurements, the large sample size (n = 18,193) allowed inclusion of aircraft height, tortuosity (tortuous or non-tortuous flight; threshold at 20° per 4 s, see Figure S3) and tide (high or low tide) as additional predictor variables. Small civil aeroplanes' height was scaled prior to analysis by subtracting the minimum flight height detected in our dataset (69 m) from all values. In the final models used to quantify spatiotemporal disturbance impacts (see Section 2.3.3), distance and height were always retained even though they were sometimes

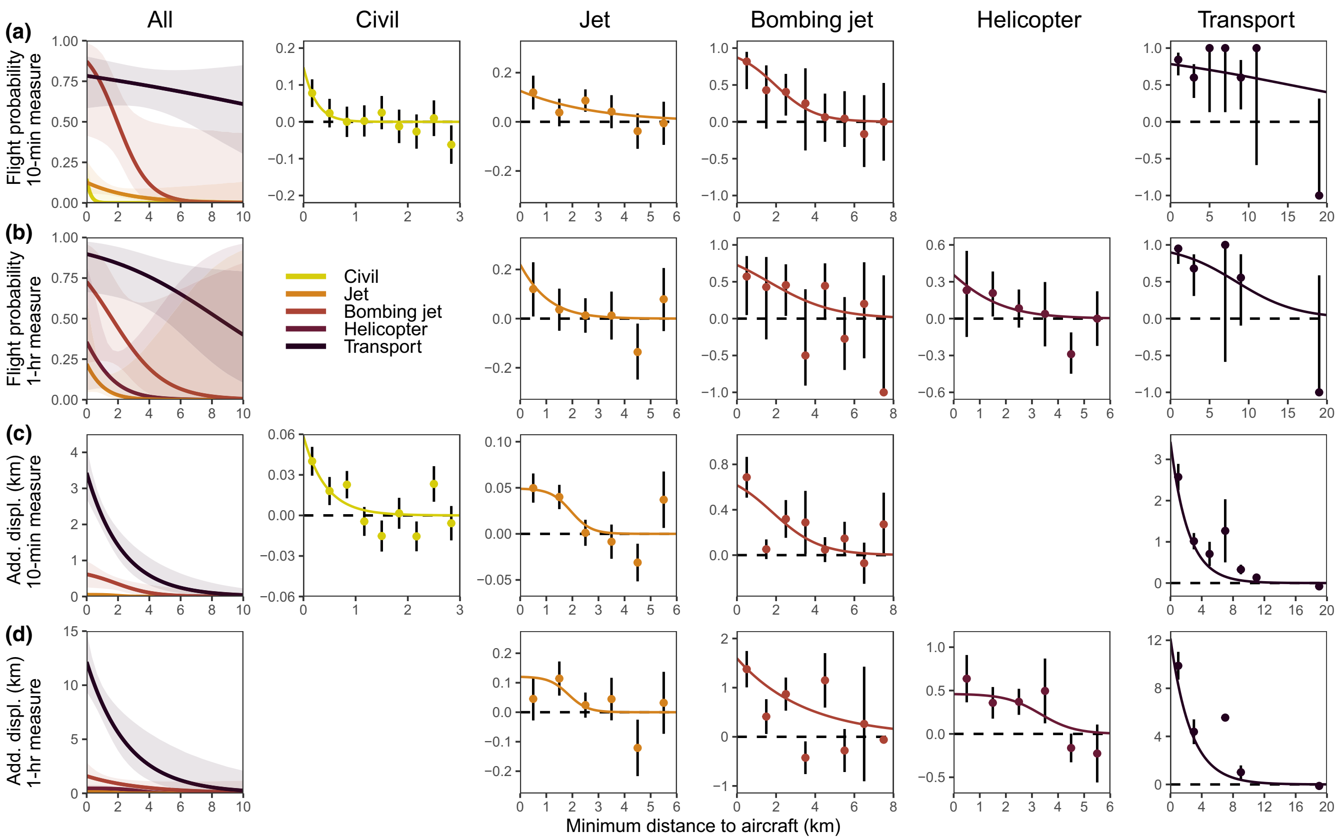

FIGURE 4 Distance–response relationships of aircraft disturbance: Oystercatcher flight probability (a: 10-min measurements, b: 1-hr measurements) and additional displacement (c: 10-min measurements, d: 1-hr measurements) in response to different aircraft types. Note that the effect of civil aeroplanes in (c) is small, and that the line is therefore not visible in the plot showing all aircraft types. Data are binned for graphical purposes only

not significant because effects were small or sample sizes low. Leaving out distance or height, however, would result in unrealistic models that would predict a similar disturbance effect over an infinite range of distances at which aircraft pass by oystercatchers. For small civil aeroplanes, we did not retain tortuosity and tide in the final model.

All parameters, standard errors and p values were estimated using nonlinear least squares analysis with the *nls* function in R (R Core Team, 2019). Confidence intervals were computed using the *predictNLS* function from the PROPAGATE R package.

2.3.3 | Spatiotemporal disturbance impacts

We used distance–response curves for additional displacement and aircraft presence data to predict how disturbance costs varied spatiotemporally and to construct cumulative aircraft disturbance maps for our study area. For every grid cell (500 × 500 m), additional displacement (m) due to disturbance was calculated per day (1 May 2017–31 March 2019; $n = 700$ days) for every aircraft activity. We used the 10-min distance–response curve for civil, jet and bombing disturbance and the 1-hr distance–response curve for helicopter and transport aeroplane disturbance, since disturbance responses to transport aeroplanes extended beyond 10 min. We converted additional displacement to % DEE using the following parameters: Displacement speed during disturbance 8.3 m/s (Figure S4), flight costs 36 J/s (Pennycuick, 2008) and DEE 700 kJ (Zwarts, Ens, Goss-Custard, Hulscher, & Kersten, 1996). A DEE of 700 kJ is representative for a bird with a weight of 550 g, which is the mean body weight of oystercatchers in autumn. Energy expenditure is often higher in winter (~860 kJ), when it is colder and when oystercatchers store more fat. Consequently, 700 kJ per day is a precautionary estimate, since higher DEE values result in lower estimates of additional energy expenditure caused by disturbance. Maps were constructed for mean daily disturbance levels for each aircraft activity separately and all aircraft activities combined. To quantify how disturbance impacts varied over time, predicted additional DEE for all days during the study period was compared among the seven main high-tide roosts in the study area.

Finally, to illustrate how distance–response curves can be extrapolated to predict disturbance impacts over a larger area, small civil aeroplane data for July–September 2018 were used to construct a disturbance impact map for the entire Dutch Wadden Sea. We identified which high-tide roosts experienced the highest mean disturbance impacts by small civil aeroplanes. Oystercatcher high-tide roost counts for July–September 2014–2018 were provided by the Dutch Centre for Field Ornithology and were per roost expressed as the percentage of the total population (~100,000 individuals).

3 | RESULTS

3.1 | Distance–response relationships

The flight probability of oystercatchers was lowest for small civil aeroplanes and increased via jets, helicopters and bombing jets to being highest for transport aeroplanes (Figure 4a,b; Table S2; Video S1). For example, the distance from the aircraft at which flight probability was 5% was 0.26, 2.5, 2.9, 5.0 and >10 km for small civil aeroplanes, jets, helicopters, bombing jets and transport aeroplanes respectively (Figure 4a, for helicopters Figure 4b). The results were very similar between the 10-min and 1-hr measurements (Figure 4a,b).

The effects of aircraft on additional displacement were similar to the flight probability curves, but differences between aircraft activities were even more pronounced (Figure 4c,d). Based on the 10-min measurements, a directly overhead flight of an aircraft would result in 0.058, 0.049, 0.616 and 3.4 km additional displacement for small civil aeroplanes, jets, bombing jets and transport aeroplanes respectively (Figure 4c). Following disturbance by transport aeroplanes, oystercatchers often flew to other islands. Consequently, additional displacement was large in the hour following disturbance and up to 12.1 km when transport aeroplanes flew directly overhead focal birds (Figure 4d).

Small civil aeroplanes were the most frequent disturbance source, but evoked generally little response (Figures 4 and 5). The distance–response curves for small civil aeroplanes were slightly higher using the 96-s measurements in comparison to the 10-min measurements, but due to a smaller dataset the 96-s curves were also less precise (Figure S5; Table S2). Using the 10-min measurements, we quantified that the height of small civil aeroplanes affected flight probability and additional displacement similarly as the horizontal distance of the

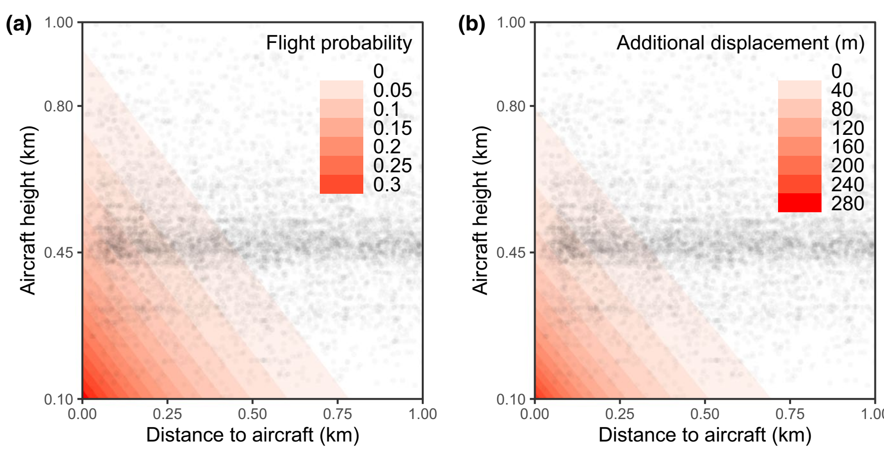

FIGURE 5 Combined effects of height and distance of small civil aeroplanes on oystercatcher flight probability (a) and additional displacement (b). Data points are plotted as grey dots

aircraft to the bird (Figure 5). Tide (low or high tide) and aircraft tortuosity (tortuous or non-tortuous flight) did not significantly affect the flight probability or additional displacement of birds following small civil aeroplane overflights (Table S2). When small civil aeroplanes flew directly overhead an oystercatcher (distance = 0), at a height of 450 m (by law the minimum flight height in the Wadden Sea area) the estimated flight probability was 14% and resulted in 73 m additional displacement.

3.2 | Spatiotemporal disturbance impacts

We constructed disturbance maps for our study area to estimate spatiotemporal variation in disturbance impact over a 700-day period expressed in % additional DEE (Figure 6). The mean additional DEE due to cumulative aircraft disturbance was higher towards the centre of the military air force training area and maximally 0.25%

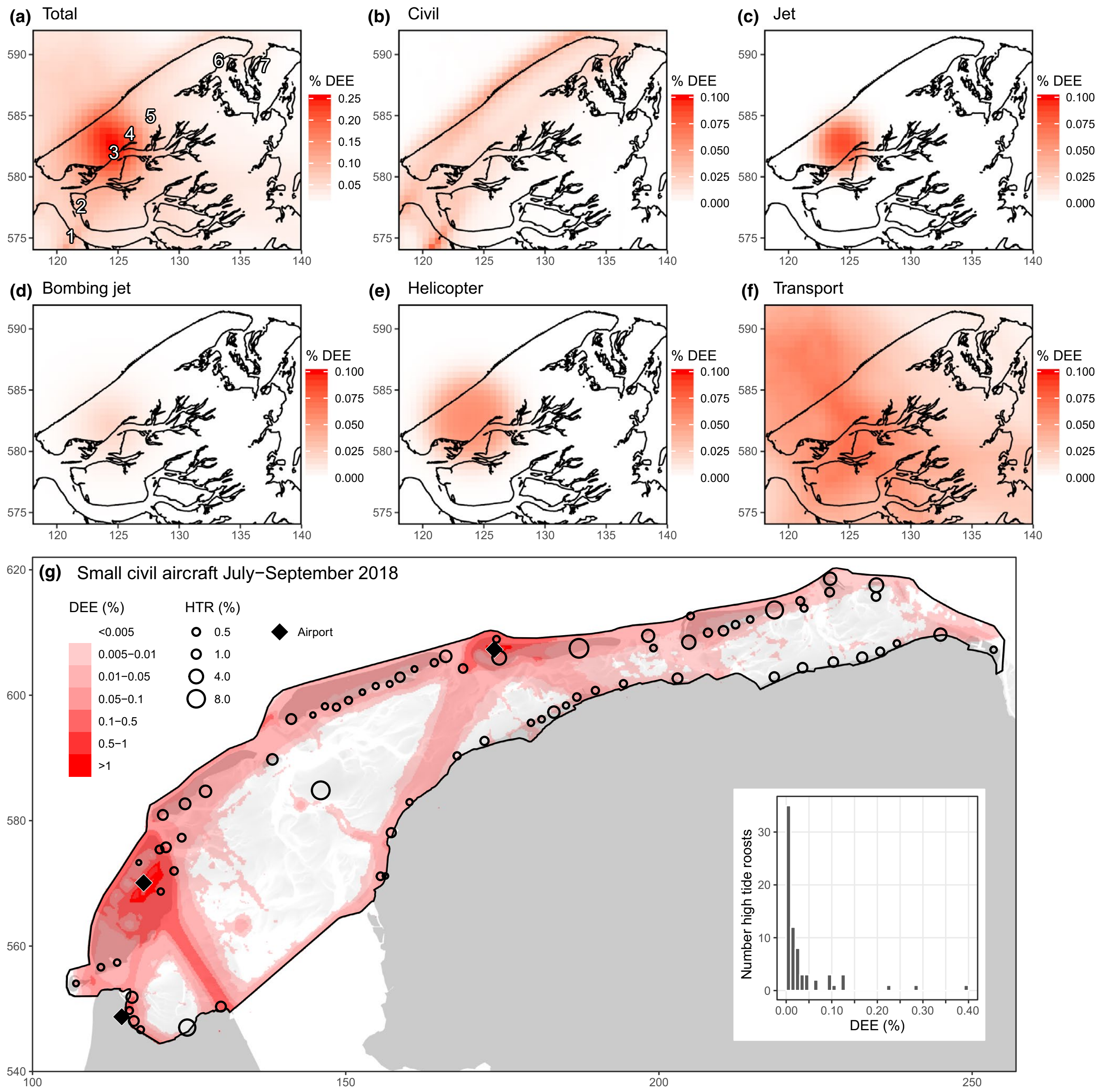

FIGURE 6 Spatial differences in aircraft disturbance costs for oystercatchers, expressed as the average percentage of additional daily energy expenditure (% DEE). (a–f) Disturbance landscape maps for total aircraft activity and all aircraft activities separately in the study area from 1 May 2017 to 31 March 2019. (g) Disturbance landscape map of the entire Dutch Wadden Sea for July–September 2018 for small civil aeroplanes showing predicted disturbance costs and high-tide roost locations of oystercatchers as percentage of the total population size of approximately 100,000 (inset: Frequency distribution of high-tide roosts with respect to average disturbance cost). Coordinates are in the Dutch RD coordinates system (one unit is 1 km). Note that (a) and (g) have different colour scales than (b)–(f). (a) Numbers 1–7 show the locations of high-tide roosts displayed in Figure 7

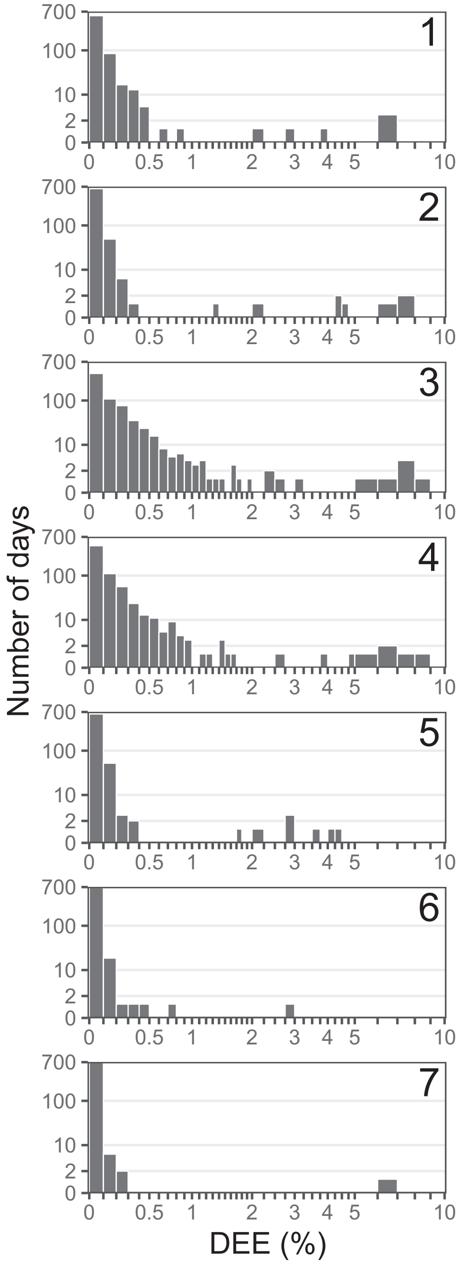

FIGURE 7 Daily variation in disturbance impacts within seven high-tide roosts in the main study area (numbers refer to locations in Figure 6a). Shown is the distribution of additional daily energy expenditure (DEE) for all days for the whole study period (1 May 2017 to 31 March 2019; $n = 700$ days). Note the transformed *x*-axis (0.1% intervals between 0% and 2%, 0.25% intervals between 2% and 5%, 1% intervals between 5% and 10%) and log-transformed *y*-axis

(Figure 6a). For small civil aeroplanes throughout the entire Dutch Wadden Sea, highest disturbance frequencies were predicted to occur at flight routes to and from the airports on the islands of Texel and Ameland (Figure 6g). Impacts of small civil aeroplane disturbance were below 0.01% DEE for 48% (35 of 73) of high-tide roosts and above 0.1% for 10% (7 of 73) of the roosts (Figure 6g), during the months of the year when small civil aeroplanes were most abundant (July–September 2018).

Although average disturbance impacts were low, they varied strongly over time. Additional DEE due to total aircraft disturbance was estimated to be very low (below 0.1%) on 56%–99% of the days (390–691 out of 700) across the seven high-tide roosts in the study area (Figure 7). On days with multiple helicopters or bombing jets and, especially, on days with transport aeroplanes, DEE spiked and maximally reached 8.5% (Figure S6). Across the seven high-tide roosts, on 0.1%–3.7% of the days (1–26 out of 700), DEE increased by at least 1% due to aircraft disturbance (Figure 7).

4 | DISCUSSION

We simultaneously tracked oystercatchers and collected five types of aircraft activity data to estimate distance–response curves of flight probability and additional displacement. The distance–response curves differed largely among aircraft activities: Flight probability upon directly overhead flights ranged from 15% for small civil aeroplanes to about 80% for bombing jets and transport aeroplanes. Transport aeroplanes could disturb oystercatchers at distances of 10 km. We combined the distance–response curves with the spatiotemporal distribution of disturbance sources, and estimated that additional energetic costs of aircraft disturbance were on average quite low: not exceeding 0.25% DEE at the most disturbed locations. However, additional energetic costs could occasionally be high on single days (maximally 8.5%) when transport aeroplanes were present.

4.1 | Spatiotemporal disturbance impacts

Additional energetic costs of oystercatcher flight responses to aircraft disturbance were generally quite low in our study area. In comparison, existing model studies for wintering oystercatchers, although applied on the Baie de Somme in France, suggest that these costs are far below disturbance thresholds at which mortality increases (Goss-Custard et al., 2006). Oystercatcher winter mortality was predicted to increase when disturbance costs exceeded 0.29%–1.14% DEE in winters with bad weather and low food availability or 2.1%–8.6% in winters with good conditions (0.2 and 1.5 disturbances of 1–4 kJ per hour daylight, respectively, and assuming 10 hr daylight per day; Goss-Custard et al., 2006). Aircraft disturbance costs were on average low because birds rarely reacted to common aircraft activities: small civil aeroplanes and jets. However, daily costs spiked at 8.5% (59.7 kJ) on days when low-flying transport aeroplanes were present or on days where impacts of different sources (e.g. bombings and helicopters) accumulated. Model studies have mainly included disturbance costs as a constant daily factor over longer time periods (Goss-Custard et al., 2006; West et al., 2002), and the effect of rare, but higher-impact, disturbance events needs better assessment in future scenario analyses.

Under normal conditions, it is unlikely that aircraft disturbance affects oystercatcher survival by increased energetic costs due to flight responses. However, disturbance can also negatively impact wildlife in other ways, for example through increasing stress levels (Blickley et al., 2012), limiting foraging time (Klett-Mingo, Pavón, & Gil, 2016) and reducing foraging efficiency (Coleman, Salmon, & Hawkins, 2003). It is important that all these effects are assessed when inferring population consequences. Whether disturbance ultimately affects survival will also depend on the available food sources and weather conditions, since these determine the ability of animals to compensate for disturbance (Burton, 2007; Goss-Custard et al., 2006). Animals can also avoid disturbed areas which may limit available breeding or foraging areas (Dwinnell et al., 2019; Leblond et al., 2013; Mallord, Dolman, Brown, & Sutherland, 2007). Disturbance impact maps, as presented here, could be combined with data on food availability and animal presence to determine whether some areas are underutilized by animals because of disturbance.

4.2 | Effects of different aircraft activities

All aircraft can cause disturbance, but the disturbance potential varies strongly among aircraft activities, indicating that birds perceive different threat levels from different aircraft (Derose-Wilson, Fraser, Karpanty, & Hillman, 2015; Frid & Dill, 2002; van der Kolk et al., 2019). Transport aeroplanes elicited disturbances from 10-km distance and caused large responses probably because they were rare, large and slow flying. Although aircraft sound can cause disturbance (Brown, 1990), sound levels may not be the primary cause of transport aeroplane disturbance: despite transport aeroplanes being clearly visible, they could not be heard by humans at the distances at which they caused disturbance (field observations). Oystercatchers rarely responded to small civil aeroplanes and jets, which were frequent and predictable in the study area, meaning that oystercatchers may have become habituated to these disturbance sources. Alternatively, birds could have redistributed such that individuals that are susceptible to aircraft disturbance have moved to other areas, while individuals that are less susceptible have remained in the area (Bejder, Samuels, Whitehead, Finn, & Allen, 2009).

Our results regarding the disturbance potential of different aircraft activities and energetic costs of disturbance are consistent with field observations in the same study area (van der Kolk et al., 2019; Figure S7). However, here we were able to estimate distance–response relationships which we could use to estimate disturbance impacts over larger areas and time spans. Distance–response curves can only be estimated when accurate positions of both animals and disturbance sources are known. In the field, a range finder can be used to measure distances between disturbance sources and animals (e.g. Marcella et al., 2017), but studies have rarely obtained sufficient sample sizes to reliably estimate flight probability curves. In addition, by using biologging techniques, it is possible to follow animals over longer time periods and study longer term impacts of disturbance, such as additional displacement (Brambilla & Brivio, 2018; Linssen et al., 2019). In our study, we showed how the impact of transport aeroplanes on displacement was much higher when measured over a 1-hr period in comparison to a 10-min period. Such prolonged disturbance responses are difficult to quantify in the field when birds fly out of sight (van der Kolk et al., 2019). We also observed that even after the most heavy disturbances, all GPS-tracked birds returned to the study area, often within a few hours. There was no indication that individuals permanently moved away from the study area.

4.3 | Management implications and future perspectives

In nature areas where there is high intensity of human activities, disturbance source presence needs to be regulated and coordinated to minimize impacts on individual animals and on populations. Our results show that the energetic flight costs due to aircraft disturbance are probably low for oystercatchers in an area where aircraft are frequent. Especially the impact of small civil aeroplanes was low, and our distance–response curves provide further scientific underpinning that the minimum flight height of 450 m for aircraft in the Wadden Sea is an effective policy tool for oystercatchers. However, birds cannot anticipate (e.g. by avoiding specific areas) rare disturbance sources like transport aeroplanes, which are unpredictable and initiate disturbance responses from large distances. Consequently, restricting flights of low-flying transport aeroplanes is currently the most effective measure to reduce the number of days on which the flight costs of disturbance are high, thereby also significantly reducing overall aircraft disturbance impacts. The number of days with high impact can be further reduced by avoiding multiple disturbing aircraft activities on the same day, for example, bombing and helicopter exercises. The timing of disturbing aircraft activities is also an important consideration, since large additional energetic costs are expected to impact the condition and survival of oystercatchers more under harsh conditions, such as cold weather or prolonged periods with high water levels when feeding grounds are inaccessible.

Levels of aircraft activities are high in our study area, since the airspace is heavily utilized by both military and civil aircraft. In many other intertidal areas aircraft occur less frequently, and consequently our results suggest that energetic costs of flight due to aircraft disturbance may be low for oystercatchers throughout most of their wintering range. However, given the long presence of both civil and military aircraft in our study area, it is difficult to determine to what extent habituation has occurred or if the most susceptible individuals have permanently moved away. Such potential effects of disturbance source presence could be evaluated at locations where aircraft activities begin or increase. Nonetheless, our study provides insights on distance–response curves for frequent generally straight-flying aircraft and thus how birds near civil airports may respond. Furthermore, our distance–response curves of infrequent disturbances may be especially relevant for assessing how novel aircraft may disturb wildlife. Consequently, our results emphasise the value of quantifying distance–response curves across a gradient of disturbance frequencies but our results should also be inferred to other areas with caution, and there remains a need to quantify flight responses to aircraft presence in areas where small civil aeroplanes and jet fighters are less frequent.

Our approach enables quantification of energetic flight costs of disturbance over large areas and long time periods and can be applied to other species and disturbance sources. Besides aircraft, automated tracking of boats (AIS; McKenna et al., 2015) and humans via GPS and smartphone apps can provide data that can be linked with animal tracking data to quantify disturbance distance–response relationships. Studies that combine human-tracking data and animal movement data could yield new insights about the magnitude of, and varying distance–response relationships of human disturbance on wildlife and improve the accuracy and quality of mapping disturbance landscapes. Ultimately, this results in disturbance impact maps of the complete cumulative disturbance landscape, including all disturbance sources, which can then be used to quantify disturbance impacts on animal survival and distributions.

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AUTHORS' CONTRIBUTIONS

H.-J.v.d.K., B.J.E. and M.v.d.P. with the support of A.M.A. and E.J. designed the study; H.-J.v.d.K. and K.O. collected the data; H.-J.v.d.K. with the support of A.M.A. and M.v.d.P. analysed the study; H.-J.v.d.K. with the support of A.M.A. and M.v.d.P. and critical comments from all the authors wrote the manuscript. All the authors read and approved the final version.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.wh70rxwkd (van der Kolk et al., 2020).

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REFERENCES

Balmford, A., Beresford, J., Green, J., Naidoo, R., Walpole, M., & Manica, A. (2009). A global perspective on trends in nature-based tourism. *PLoS Biology*, *7*(6), e1000144. https://doi.org/10.1371/journal.pbio.1000144

Beale, C. M. (2007). The behavioral ecology of disturbance responses. *International Journal of Comparative Psychology*, *20*(2), 111–120.

Beale, C. M., & Monaghan, P. (2004). Human disturbance: People as predation-free predators? *Journal of Applied Ecology*, *41*(2), 335–343. https://doi.org/10.1111/j.0021-8901.2004.00900.x

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

Blickley, J. L., Word, K. R., Krakauer, A. H., Phillips, J. L., Sells, S. N., Taff, C. C., … Patricelli, G. L. (2012). Experimental chronic noise is related to elevated fecal corticosteroid metabolites in lekking male greater sage-grouse (*Centrocercus urophasianus*). *PLoS ONE*, *7*(11), e50462. https://doi.org/10.1371/journal.pone.0050462

Bouten, W., Baaij, E. W., Shamoun-Baranes, J., & Camphuysen, K. C. (2013). A flexible GPS tracking system for studying bird behaviour at multiple scales. *Journal of Ornithology*, *154*(2), 571–580. https://doi.org/10.1007/s10336-012-0908-1

Brambilla, A., & Brivio, F. (2018). Assessing the effects of helicopter disturbance in a mountain ungulate on different time scales. *Mammalian Biology*, *90*, 30–37. https://doi.org/10.1016/j.mambio.2018.02.001

Brown, A. L. (1990). Measuring the effect of aircraft noise on sea birds. *Environment International*, *16*(4–6), 587–592. https://doi.org/10.1016/0160-4120(90)90029-6

Burton, N. H. (2007). Landscape approaches to studying the effects of disturbance on waterbirds. *Ibis*, *149*, 95–101. https://doi.org/10.1111/j.1474-919X.2007.00658.x

Coleman, R. A., Salmon, N. A., & Hawkins, S. J. (2003). Sub-dispersive human disturbance of foraging oystercatchers *Haematopus ostralegus*. *Ardea*, *91*(2), 263–268.

Collop, C., Stillman, R. A., Garbutt, A., Yates, M. G., Rispin, E., & Yates, T. (2016). Variability in the area, energy and time costs of wintering waders responding to disturbance. *Ibis*, *158*(4), 711–725. https://doi.org/10.1111/ibi.12399

Delaney, D. K., Grubb, T. G., Beier, P., Pater, L. L., & Reiser, M. H. (1999). Effects of helicopter noise on Mexican spotted owls. *Journal of Wildlife Management*, *63*, 60–76. https://doi.org/10.2307/3802487

Derose-Wilson, A., Fraser, J. D., Karpanty, S. M., & Hillman, M. D. (2015). Effects of overflights on incubating Wilson's plover behavior and heart rate. *Journal of Wildlife Management*, *79*, 1246–1254. https://doi.org/10.1002/jwmg.959

Dwinnell, S. P., Sawyer, H., Randall, J. E., Beck, J. L., Forbey, J. S., Fralick, G. L., & Monteith, K. L. (2019). Where to forage when afraid: Does perceived risk impair use of the foodscape? *Ecological Applications*, *29*(7), e01972. https://doi.org/10.1002/eap.1972

Fernández-Juricic, E., Venier, M. P., Renison, D., & Blumstein, D. T. (2005). Sensitivity of wildlife to spatial patterns of recreationist behavior: A critical assessment of minimum approaching distances and buffer areas for grassland birds. *Biological Conservation*, *125*(2), 225–235. https://doi.org/10.1016/j.biocon.2005.03.020

Frid, A. (2003). Dall's sheep responses to overflights by helicopter and fixed-wing aircraft. *Biological Conservation*, *110*(3), 387–399. https://doi.org/10.1016/S0006-3207(02)00236-7

Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, *6*(1), 11. https://doi.org/10.5751/ES-00404-060111

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, *360*(6394), 1232–1235. https://doi.org/10.1126/science.aar7121

Goss-Custard, J. D., Triplet, P., Sueur, F., & West, A. D. (2006). Critical thresholds of disturbance by people and raptors in foraging wading birds. *Biological Conservation*, *127*(1), 88–97. https://doi.org/10.1016/j.biocon.2005.07.015

Klett-Mingo, J. I., Pavón, I., & Gil, D. (2016). Great tits, *Parus major*, increase vigilance time and reduce feeding effort during peaks of aircraft noise. *Animal Behaviour*, *115*, 29–34. https://doi.org/10.1016/j.anbehav.2016.02.021

Leblond, M., Dussault, C., & Ouellet, J. P. (2013). Avoidance of roads by large herbivores and its relation to disturbance intensity. *Journal of Zoology*, *289*(1), 32–40. https://doi.org/10.1111/j.1469-7998.2012.00959.x

Linssen, H., van de Pol, M., Allen, A. M., Jans, M., Ens, B. J., Krijgsveld, K. L., … van der Kolk, H. J. (2019). Disturbance increases high tide travel distance of a roosting shorebird but only marginally affects daily energy expenditure. *Avian Research*, *10*(1), 1–11. https://doi.org/10.1186/s40657-019-0171-8

Livezey, K. B., Fernández-Juricic, E., & Blumstein, D. T. (2016). Database of bird flight initiation distances to assist in estimating effects from human disturbance and delineating buffer areas. *Journal of Fish and Wildlife Management*, *7*(1), 181–191. https://doi.org/10.3996/082015-JFWM-078

Mallord, J. W., Dolman, P. M., Brown, A. F., & Sutherland, W. J. (2007). Linking recreational disturbance to population size in a ground-nesting passerine. *Journal of Applied Ecology*, *44*(1), 185–195. https://doi.org/10.1111/j.1365-2664.2006.01242.x

Marcella, T. K., Gende, S. M., Roby, D. D., & Allignol, A. (2017). Disturbance of a rare seabird by ship-based tourism in a marine protected area. *PLoS ONE*, *12*(5), e0176176. https://doi.org/10.1371/journal.pone.0176176

Marchand, P., Garel, M., Bourgoin, G., Dubray, D., Maillard, D., & Loison, A. (2014). Impacts of tourism and hunting on a large herbivore's spatio-temporal behavior in and around a French protected area. *Biological Conservation*, *177*, 1–11. https://doi.org/10.1016/j.biocon.2014.05.022

McKenna, M. F., Calambokidis, J., Oleson, E. M., Laist, D. W., & Goldbogen, J. A. (2015). Simultaneous tracking of blue whales and large ships demonstrates limited behavioral responses for avoiding collision. *Endangered Species Research*, *27*(3), 219–232. https://doi.org/10.3354/esr00666

Pennycuick, C. J. (2008). *Modelling the flying bird*. Oxford, UK: Academic Press, Elsevier.

Perona, A. M., Urios, V., & López-López, P. (2019). Holidays? Not for all. Eagles have larger home ranges on holidays as a consequence of human disturbance. *Biological Conservation*, *231*, 59–66. https://doi.org/10.1016/j.biocon.2019.01.010

Preisler, H. K., Ager, A. A., & Wisdom, M. J. (2006). Statistical methods for analysing responses of wildlife to human disturbance. *Journal of Applied Ecology*, *43*(1), 164–172. https://doi.org/10.1111/j.1365-2664.2005.01123.x

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

Riddington, R., Hassall, M., Lane, S. J., Turner, P. A., & Walters, R. (1996). The impact of disturbance on the behaviour and energy budgets of Brent Geese *Branta b. bernicla*. *Bird Study*, *43*(3), 269–279. https://doi.org/10.1080/00063659609461019

Rijkswaterstaat. (2019). *Waterinfo*. Retrieved from https://waterinfo.rws.nl/

Sastre, P., Ponce, C., Palacín, C., Martín, C. A., & Alonso, J. C. (2009). Disturbances to great bustards (*Otis tarda*) in central Spain: Human activities, bird responses and management implications. *European Journal of Wildlife Research*, *55*(4), 425–432. https://doi.org/10.1007/s10344-009-0254-7

Smit, C. J., & Visser, G. J. M. (1993). Effects of disturbance on shorebirds: A summary of existing knowledge from the Dutch Wadden Sea and Delta area. *Wader Study Group Bulletin*, *68*, 6–19.

Speakman, J. R., Webb, P. I., & Racey, P. A. (1991). Effects of disturbance on the energy expenditure of hibernating bats. *Journal of Applied Ecology*, *28*, 1087–1104. https://doi.org/10.2307/2404227

Stankowich, T. (2008). Ungulate flight responses to human disturbance: A review and meta-analysis. *Biological Conservation*, *141*(9), 2159–2173. https://doi.org/10.1016/j.biocon.2008.06.026

Stillman, R. A., & Goss-Custard, J. D. (2002). Seasonal changes in the response of oystercatchers *Haematopus ostralegus* to human disturbance. *Journal of Avian Biology*, *33*(4), 358–365. https://doi.org/10.1034/j.1600-048X.2002.02925.x

Tablado, Z., & Jenni, L. (2017). Determinants of uncertainty in wildlife responses to human disturbance. *Biological Reviews*, *92*(1), 216–233. https://doi.org/10.1111/brv.12224

van de Pol, M., Atkinson, P. W., Blew, J., Duriez, O. P. M., Ens, B. J., Hälterlein, B., … Thorup, O. (2014). A global assessment of the conservation status of the nominate subspecies of Eurasian oystercatcher (*Haematopus ostralegus ostralegus*). *International Wader Studies*, *20*, 47–61.

van der Kolk, H.-J., Allen, A. M., Ens, B. J., Oosterbeek, K., Jongejans, E., & van de Pol, M. (2020). Data from: Spatiotemporal variation in disturbance impacts derived from simultaneous tracking of aircraft and shorebirds. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.wh70rxwkd

van der Kolk, H.-J., Ens, B. J., Oosterbeek, K., Bouten, W., Allen, A. M., Frauendorf, M., … van de Pol, M. (2020). Shorebird feeding specialists differ in how environmental conditions alter their foraging time. *Behavioral Ecology*, *31*, 371–382. https://doi.org/10.1093/beheco/arz189

van der Kolk, H.-J., Krijgsveld, K. L., Linssen, H., Diertens, R., Dolman, D., Jans, M., … van de Pol, M. (2019). Cumulative energetic costs of high tide disturbance by aircrafts are mostly low in large shorebird species. *Animal Conservation*. https://doi.org/10.1111/acv.12546

Ward, D. H., Stehn, R. A., Erickson, W. P., & Derksen, D. V. (1999). Response of fall-staging brant and Canada geese to aircraft overflights in southwestern Alaska. *Journal of Wildlife Management*, *63*, 373–381. https://doi.org/10.2307/3802522

West, A. D., Goss-Custard, J. D., Stillman, R. A., Caldow, R. W., Durell, S. E. A. le V. dit, & McGrorty, S. (2002). Predicting the impacts of disturbance on shorebird mortality using a behaviour-based model. *Biological Conservation*, *106*(3), 319–328. https://doi.org/10.1016/S0006-3207(01)00257-9

Zwarts, L., Ens, B. J., Goss-Custard, J. D., Hulscher, J. B., & Kersten, M. (1996). Why oystercatchers *Haematopus ostralegus* cannot meet their daily energy requirements in a single low water period. *Ardea*, *84*, 269–290.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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