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Disturbance does not have a significant impact on waders in an estuary close to conurbations: importance of overlap between birds and people in time and space

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Disturbance of wildlife is a potential cause of conservation concern, not least to overwintering waders Charadrii inhabiting estuaries close to conurbations where human recreational and economic activities are often concentrated. Disturbance from people on and alongside intertidal foraging areas could

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make it more difficult for birds to survive until spring in good condition by reducing the time available for foraging, by increasing energy requirements and by displacing birds to poorer foraging areas. We adopted a two-part approach to testing whether such significant impacts occurred in a Special Protection Area where disturbance risk was high because of its small size and close proximity to conurbations. In part one, we recorded over the whole estuary during stages of the tidal cycle when part or all of the intertidal zone was exposed and so accessible to waders (*i.e.* on receding, low and advancing tides): (i) the numbers and activities of people on the intertidal flats and on the adjacent land in those places where people were visible to waders in the intertidal zone, and (ii) the numbers of waders present and disturbed into flight, the flight distance and flight duration in the 'overlap' areas where people did disturb waders. People occurred on < 25% of the 938 ha of intertidal flats but most waders foraged on mudflats whereas most people were on sandflats. People on land were visible to foraging waders along < 35% of the 16.5 km of shoreline. Waders and people were therefore substantially separated in space. Within overlap areas, people and waders were often frequently separated in time: for example, people on land mostly disturbed waders when only the upper shore levels were exposed. The average overwintering wader spent <0.1% of its foraging time during daylight flying away from people and the additional energy expenditure was equivalent to <0.02% of its daily requirements. The comparison made in part two between our study area and two comparable estuaries showed that the number of visits each day to the overlap areas would need to be 29 or 43 times greater for disturbance to have lowered the birds' body condition and winter survival. Both parts of the study therefore suggested strongly that the amount of disturbance was too trivial to have a significant impact on waders. It is concluded that: (i) to properly assess disturbance risk to waders, both extensive and intensive observations must be made on the behaviour of people and birds to quantify the extent to which they overlap in space and time, and (ii) it should not be assumed that an estuary's close proximity to conurbations, and the presence of large numbers of people in the vicinity of the SPA, necessarily implies a significant disturbance risk to waders.

Keywords: wading birds; disturbance threshold; energy costs; time costs; winter survival; individual-based model; evidence complacency; conservation; estuary management.

Disturbance of birds and other wildlife taxa by people have long been recognised as a potential cause of conservation concern, not least on coasts and estuaries where human recreational and economic activities are often concentrated (Hill *et al.* 1997). The responses of birds to people have been widely researched, partly because they are believed to be analogues of anti-predator behaviour and partly because of their implications for conservation practice. Birds are hypothesised to react to the perceived risk from people as they would to a predator by trading-off the immediate risk to survival against long-term fitness-maximisation (Gill *et al.* 2001, Frid & Dill 2002, Beale & Monaghan 2004a,b, Blumstein *et al.* 2005). In conservation studies, disturbance responses have been used to compare species' sensitivity to different kinds of disturbance and to design mitigation measures. For example, a well-studied response is the distance at which birds fly away from an approaching disturber (Smit & Visser 1993, Bonenfant & Kramer 1996, Blumstein *et al.* 2003, van Dongen *et al.* 2015). Although a larger flight distance does not necessarily imply a greater impact on the birds (Gill *et al.* 2001), it has been used, for example, to determine the dimensions of buffer zones (Glover *et al.* 2011, Weston *et al.* 2012, Chatwin *et al.* 2013, Koch & Paton 2014) and to compare different kinds of disturbance (Lafferty 2001, Glover *et al.* 2011, Schlacher *et al.* 2013, McLeod *et al.* 2013, Guay *et al.* 2014).

The responses of waders Charadrii to disturbance has attracted much research worldwide as they are easy to see on their intertidal foraging grounds and waders are a high conservation priority. Potential correlates of flight distance, for example, include species or body size (Blumstein *et al.* 2003, 2005, Glover *et al.* 2011, Collop *et al.* 2016); flock size (Ikuta & Blumstein 2003, Glover *et al.* 2011, Collop *et al.* 2016); habituation (Ikuta & Blumstein 2003, Lin *et al.* 2012); environmental conditions (Collop *et al.* 2016); hunting pressure (Laursen *et al.* 2005); type of disturbance (Glover *et al.* 2011); starting distance (Ikuta & Blumstein 2003); locations (Collop *et al.* 2016) and individual condition (Beale & Monaghan 2004b). Research on such responses tells us nothing, however, about the population consequences of disturbance, which is the fundamental issue in conservation.

In fact, very few tests of the hypothesis that disturbance affects wader population size have been carried out (Gill *et al.* 1996, 2001, Gill 2007, Stillman *et al.* 2007). The 'disturbance hypothesis' is difficult to test directly from censuses because so many factors, within the site in question and elsewhere in the species range, could affect population size (Goss-Custard & Stillman 2008). An alternative measure of impact would be the effect of disturbance on the birds' survival and/or reproductive rates, the two demographic rates that in combination determine population size. In non-breeding waders, disturbance might affect these demographic rates because: (i) by being disturbed into flight ('flighted'), birds spend extra energy and lose foraging time (Houston *et al.* 2012), and (ii) by being disturbed away from their preferred feeding areas, birds may forage in less suitable places (Gill *et al.* 1996) at higher densities and perhaps intensified competition (Stillman *et al.* 2007) and/or where the risk from predators is higher (Cresswell 1994, Hilton *et al*. 1999, Whitfield 2003a,b). These consequences could make it more difficult for birds to survive the winter, to accumulate sufficient reserves to migrate to the breeding grounds in spring and to reproduce successfully when they arrive. Alone or in combination, these potential consequences of disturbance could lower survival and/or reproductive rates and thus population size.

It is very difficult in practice, however, to test whether these probable consequences of being disturbed actually have a significant impact on the birds. It does seem highly likely, for example, that the energy requirements of birds that are disturbed into flight will be higher than they otherwise would be while, at the same time, the birds will have less time to meet the extra demand because they cannot forage while flying. The question, though, is whether this combination of increased demand but reduced time to meet the demand is sufficiently large to impact the birds - it is a question of quantities. Potential threats are not necessarily realised threats: disturbing 0.001% of the population for 1 second during a non-breeding period of nine months is most unlikely to change a population's demographic rates whereas disturbing 100% continuously would almost certainly do so. The issue is to determine the point between these two extremes at which increasing disturbance begins to affect one or both of the demographic rates: this is termed the 'disturbance threshold' by Goss-Custard & Stillman (in press). If the amount of disturbance exceeds the threshold, disturbance would be having a significant impact so effective mitigation would be appropriate. But if the amount of disturbance is well below the threshold, any proposed 'mitigation' to 'improve things' would be pointless because reducing an impact below zero is impossible.

While describing the disturbance threshold approach is straightforward, testing whether the potential effects of disturbance detailed above, in combination, actually have an impact on the birds is difficult to achieve in practice even – as is usually the case – when only potential impacts within the winter period, and not in the subsequent breeding season, itself are being considered. Currently, the most direct methodology is to build an individual-based model (IBM) of the population in question (Stillman *et al.* 2007). IBMs represent individual birds foraging over a virtual estuary that replicates the spatial and temporal variation in the food supply and, in the cases of estuaries, the tidal regime. Model birds use optimisation decision rules to decide how to obtain most rapidly their daily energy requirements which, in the model as in reality, depend on the ambient temperature. Individuals vary in competitive ability and each bird takes into account the decisions made by competitors in deciding when (*e.g.* night or day), where (*e.g.* which part of the estuary) and on what prey species it should feed. Each model bird attempts first to obtain its requirements by taking the currently most profitable prey species but, should that fail, it expands its diet choice to include other intertidal invertebrates or, in some wader species, terrestrial prey such as earthworms Lumbricidae (Goss-Custard 1969, Heppleston 1971). If a bird is disturbed by people, it can compensate for the resulting time and energy costs by feeding for longer and/or by moving to a less disturbed area if its rate of energy consumption is thereby improved. Once an individual bird has obtained its current daily energy requirements, it stores subsequent consumption as fat up to a daily limit. A bird uses its fat reserves should it ever fail to obtain its daily requirement from current foraging and starves to death if its body reserves ever fall to zero.

Although procedures have been found to minimise the research effort required to parameterise an IBM for a particular estuary, it can still require resources that are not always available in disturbance studies. Accordingly, less resource-costly, indirect approaches based on the behavioural response of birds to disturbance have been used to gauge the impact of disturbance. One such approach is to measure the foraging space and food supplies that disturbance prevents the birds from exploiting (e.g. Smit & Visser 1993, Gill *et al.* 1996). Another is to measure impact in terms of the foraging time lost ('time-cost') and the extra energy required ('energy cost') each 24 h by the average bird (Collop *et al.* 2016, Collop 2017). If disturbance increases both measures by only a small amount – say by <0.1% - it is most unlikely to have a significant impact but, if they are increased by a large amount, it might. The problem, of course, is defining the values at which demographic rates begin to be affected: is it 5%, for example, or 25%? Another limitation of this 'time- and energy-cost' approach is that it does not consider the 'knock-on' consequences of disturbance following re-distribution or include any compensation that birds might make. At the moment, only IBMs do this. Here, we combined the time- and energy-cost approach with the IBM approach.

The aim was to test the hypothesis that disturbance on the intertidal foraging grounds of a Special Protection Area (SPA) was likely to affect the overwinter survival and body condition of the waders. In part one, we measured the time and energy costs of disturbance to the average overwintering individual of each wader species to determine whether the costs were large enough to be likely to be significant. But as 'significant' could not be quantified in terms of the effect on winter survival and body condition, part two compared the amount of disturbance in our study SPA with disturbance thresholds obtained from individual-based models of two comparable estuaries. Although neither approach on its own would provide a decisive test of the disturbance hypothesis, comparable findings from both were thought likely to be indicative. As our study area, the Exe estuary in SW England, may be among the more disturbed in the UK because of its proximity to major conurbations, location in a popular holiday area, small size and the wide range of recreational and commercial activities that are carried out there (Liley *et al.* 2011, 2014), the study was believed likely to yield results that would be relevant to the evaluation of the threat from disturbance in many other estuary SPAs.

METHODS

Study area and species

The Exe estuary SPA is predominantly a muddy estuary (Supporting Online Material Fig. S1) and is bordered by, or very close to, several villages and larger conurbations (Fig. 1). Most fieldwork was done in winter (mid-October to mid-March) when waders were most numerous and most likely to be pressed for food and vulnerable to disturbance. Data were collected from winter 2009/10 to 2017/18. Only foraging areas were investigated as the birds were well-protected at their high tide roosts in several nature reserves. Observations were made between dawn and dusk as several checks by the lead author showed few people were present at night. The study species were: Pied Avocet *Recurvirostra avosetta* L., Eurasian Curlew *Numenius arquata* L., Eurasian Oystercatcher *Haematopus ostralegus* L., Bar-tailed Godwit *Limosa lapponica* L., Black-tailed Godwit *L. limosa* L., Grey Plover *Pluvialis squatarola* L., Common Redshank *Tringa totanus* L., Common Greenshank *T. nebularia* L., Red Knot *Calidris canutus* L., Dunlin *C. alpina* L. and Common Ringed Plover *Charadrius hiaticula* L.

The individual-based models used for the comparison with the Exe were of Southampton Water and Poole Harbour (Stillman *et al*. 2012, Collop 2017) where the invertebrate fauna is similar to that of the Exe (Warwick *et al.* 1991).

Overall approach

To place the disturbance in the context of the entire estuary, fieldwork was extensive as well as being intensive in those areas – called ‘sectors’ - where most disturbance occurred. The average tidal cycle from one high tide to the next lasted 12.44 h and the tidal range, the difference in the height of the water between high tide and low tide, was up to 5.5m (Admirality Tide Tables). On most tidal cycles, all the intertidal flats were covered at high tide. The first flats to become exposed as the tide receded – and therefore the last to be covered later by the advancing tide - were high-level flats in each of the four corners of the estuary (Fig. 1): the interval between first exposure and last covering of an area by the tide is called the 'exposure period'. Observations over four decades by the senior author showed that few, if any, birds foraged on the high-level intertidal flats at the beginning and end of the exposure period during late summer and autumn. However, increasing numbers did so from November to March when waders generally have the most difficulty in meeting their energy demands and feed throughout the exposure period (e.g. Goss-Custard *et al.* 1977). As the tide receded further, foraging areas lower down the shore became exposed until, at low tide, all the intertidal areas were accessible to waders. In most parts of the estuary, waders followed the tide edge until they reached the low-lying flats where they remained until the advancing tide forced them back up the shore to the higher levels (Goss-Custard *et al.* 1991). These movements resulted in all the intertidal flats of the estuary being utilised by waders at one stage or another of the exposure period. They also resulted in birds being scarce or absent from some areas for long periods during the exposure period, this being particularly the case for high-level flats when the tide was out. These upshore areas were generally – though not exclusively - the ones that were most visited by people using the intertidal zone and, of course, were also closest to people on the adjacent land. Accordingly, whether people in the intertidal zone and on land were close enough to waders to disturb them depended on both location and the stage of the exposure period. As the Exe estuary is partially edged by railway embankments that in some places were built on the intertidal zone, some low-lying flats start to expose as late as 4-4.5 h after high tide whereas the high-level flats bordered by natural marsh exposed about 2 h earlier. Accordingly, the duration of the exposure period varied from *circa* 5 h to 9 h between different areas of the estuary.

We first identified the 'overlap' sectors and stages of the exposure period where waders and people occurred close enough together for birds to be at risk of being disturbed. These comprised six 'land' sectors where waders in the adjacent intertidal zone were disturbed by people on the land and five 'intertidal' sectors where people went onto the flats (Fig. 1, Table 1). Each was then visited to obtain data at the sector-specific stages of the exposure period when birds and people were both present. In some intertidal areas, for example, data were collected only during the hour or so at the beginning and end of the exposure period because no waders were present when the tide was out. In other places, data were collected throughout the exposure period because waders fed there throughout. The species present also varied between sectors.

Data were collected from each sector to obtain an unbiassed and reliable estimate of each of the measurements that were required to estimate the sector-specific values of: (i) the average number of potential disturbance events, or 'visits', in each overlap sector during its sector-specific 'overlap period' in daylight during a typical winter tidal cycle, obtained by multiplying the visit rate (numbers of visits by potential disturbers per hour) by the duration of the overlap period; (ii) the average number of birds that each visit disturbed into flight during its stay in the sector, and (iii) the average duration of the flights of waders that flew away: the time spent pre-flight in being alert and post-flight in recovery prior to resuming feeding were taken from Collop *et al.* (2016).

(i) Number of potential disturbance events: Once identified by recording the distribution of people over the entire intertidal zone of the estuary as described in Goss-Custard et al. (1998), disturbance-free areas could be largely ignored apart from regular spot checks to ensure they remained disturbance-free. The numbers of people and birds were counted regularly throughout the nine years of fieldwork (i) as part of the calculations of the time and energy costs of disturbance and (ii) to compare with the numbers of visits to Southampton Water and Poole Harbour.

Counts of bird numbers and the numbers, grouping and activities of people were mostly carried out during overlap periods. Some disturbance events did occur infrequently during the rest of the exposure period so data were also collected, but less intensively, during these 'non-overlap' periods. If the same people walked both ways along a land sector, it was scored as two visits. Since the local time of high and low tide changed from day to day through the 14-day Springs-Neaps tidal cycle, observations had to be made throughout the daylight hours, from dawn to dusk.

An important distinction to note is between the total number of individual people that were present in a sector and the number of potential disturbance events. The number of individual people was always counted and is referred to as 'people numbers'. But often people occurred in groups, and it was the group that disturbed birds, not each individual within it. A group of people that stayed together throughout their presence in a sector was classified as a single disturbance event, or ‘visit’: in that context, a single person would also be classified as a ‘visit’. Accordingly, the analyses focussed either on people numbers or visits, depending on the context.

As several measurements on several species had to be made, it was impossible for one observer simultaneously to record everything that occurred throughout an overlap period in the sector under observation. In land sectors, the number of individuals and groups of people walking through the sector were counted continuously throughout the observation period and later sub-divided into 15 min sampling periods for analysis. In intertidal sectors, counts of both birds and people were made every 15 or 30 minutes through the observation period. In between counts, other data were collected, such as the number of waders disturbed into flight during a visit.

In land sectors, people were usually close enough to disturb birds on the adjacent intertidal flats only at the beginning and end of the exposure period, a combined period of about 3 h. These overlap periods were of a similar length in the intertidal sectors though centred on low tide instead. As the average time between one high tide and the next was 12.44 h, and the time of high tide shifted daily through the 14 days of the Springs-Neaps cycle, not all of the 3 hours of overlap fell every day in the 8-9 h of winter daylight. The amount that did so was calculated as described in Supporting Online Material Fig. S2. Across all sectors, 61% to 77% of the potential overlap period fell in daylight.

(ii) Average number of birds that each visit disturbed into flight and (iii) duration of flights: The numbers and species disturbed into flight (‘flighted’), the duration of the flight (‘flight time’) and, in land sectors only, the distance from the disturber when they flew (‘flight distance’) were measured together. Some flight distances and all flight times were estimated: validation tests of these estimates are given in Supporting Online Material Fig. S3. Most flight distances were measured by Longridge x6 laser range finder. Data were obtained whenever a disturbance event occurred between the regularly-spaced counts of people and birds. On the frequent occasions when no people occurred in the Cockwood and Starcross intertidal sectors, ‘experimental disturbance events’ were conducted to increase sample sizes. In these, the experimenter recorded bird responses as he replicated the route, activity and speed adopted by people who visited the sector.

Flight times could only be recorded on the occasions when the disturbed birds remained within sight so there was an unavoidable bias towards timing flights of below average duration. The proportion of flighted waders whose flight times could be measured was recorded in four land sectors and one intertidal sector, the values being: Powderham 60% (n = 494), Bay and Promontory combined 91% (n = 530), Goatwalk, 96% (n = 69) and Bite, 75% (n = 84). This suggests that, globally, the flight times of only about three-quarters of disturbed birds were measured, and that the true flight times of all birds would have been under-estimated by an unknown amount.

On the other hand, some flighted birds may just have brought forward a flight they would have made anyway so that being disturbed would not have had increased costs. Since birds undoubtedly changed foraging areas for a variety of unobservable reasons associated with foraging, such 'Would Have Anyway (WHA)' flights probably occurred regularly but could not always be identified as such by the observer. They could only be identified objectively (i) when the receding tide was exposing upshore flats in places where our extensive local knowledge showed that birds stopped briefly on their way to a later-emerging foraging site and it was well known that no birds remained after the tide had receded further, even when people were absent, and (ii) when the advancing tide had almost covered the flats and the birds had to move to their next foraging site or roost. WHA flights were probably particularly frequent in the land sectors where most observations were obtained at the beginning and end of the exposure period when birds were particularly likely to change foraging area because of the movement of the tide. The proportion doing so was estimated in two sectors (Bay and Promontory) and 69.5% (n = 443) of the flights whose duration could not be measured were judged likely to have been WHA flights.

The numbers of waders flighted in intertidal sectors were recorded in two ways, depending on the person's activity and therefore the duration of the visit. In 'short' visits, people walked some distance out onto the flats and then returned to the shore without stopping. Counts of the waders flighted were made on people walking out and on people walking back, though not necessarily both on a given visit. The sum of the average of these two measurements gave the number of waders flighted per short visit. For 'long' visits during which a prolonged activity such as bait-digging was carried out, frequent measurements were made of the number of waders disturbed during 15 min sampling intervals (the 'disturbance rate') between the disturber's recorded arrival and departure times. The product of the duration of a disturber's presence and the disturbance rate estimated the number of waders disturbed/visit. For land sectors, the numbers of each species flighted from the adjacent intertidal zone when people passed by were recorded. Flight distance was measured whenever the opportunity arose. To do this, the observer moved to where the disturber had been when the birds flew away and measured the distance to an object near to where the flighted birds had been, such as a boulder or pool.

Because it is frequently ignored in studies of wader disturbance, it is worth noting that birds gradually left, or were disturbed from, a sector as the tide receded so that the numbers flighted/visit declined as the exposure period proceeded. An example is from Cockle Sand where almost all the waders were Oystercatchers. On average, the first five visits to arrive on Cockle Sand during an exposure period disturbed 7.72 (se = ±1.80, n = 90) Oystercatchers, the next five visits disturbed fewer birds (2.87 (se = ±1.13, n = 23, t = 2.29, P = 0.024). After ten visits, no more Oystercatchers were flighted at all (n = 17).

The overall aim of the calculations was to determine the average time per day (*i.e.* during the hours of daylight) that the average individual of each species in the wintering population spent in being disturbed by people. The calculations were rather complex as they involved combining several measurements; a worked example for one species in one sector is given in Supporting Online Material Table S2. This required estimates to be obtained for the species-specific and sector-specific average values for each of the component measurements.

The procedure for calculating the average time spent per day by the average bird in flying away from people was to divide the total aggregate time spent in disturbance flights by the whole population during daylight on a typical day by the number of individuals in the wintering population. For a given sector, the average time spent reacting by all flighted birds of species *s* (T_s) during the overlap period in daylight is:

$$T_s = (Nv)(Nf_s)(Tf_s + Tar_s) \text{ ……………………………………………Equation 1}$$

where Nv = number of potential disturbance events, or 'visits', to the sector during the daylight overlap period, Nf_s = average number of birds of species s that each visit disturbed into flight throughout its stay in the sector, Tf_s = the average duration of flights of flighted individuals of species *s* and Tar_s = time spent by the average flighted individual of species *s* being alert prior to flying away plus the time taken to resume foraging after landing; Tar_s was taken from Collop *et al.* (2016).. Summing the values of T_s for all sectors where species *s* occurred gives, Tt_s, the aggregate time spent in flight by all the flighted individuals of that species over the entire estuary during a typical winter exposure period. Dividing Tt_s by Tn_s, the average number of individuals of species *s* on the estuary during winter, gives Ti_s, the average time spent by the average bird in reacting to disturbance during a typical exposure period in winter. Although few disturbance events occurred during the non-overlap periods, the same calculations were made and the resulting average values added to those obtained for the overlap periods.

These calculations were made for only those occasions where the disturbed birds flew away and so excluded those where birds just walked away from a disturber, sometimes while continuing to forage. The percentage of waders walking and flying away was measured at Powderham, where 22% walked and 78% flew (n = 173). Although not quantified in other sectors, walking away was very noticeably a much less frequent response than flying in all sectors, and these percentages from Powderham did not seem untypical.

Wader population sizes on the Exe estuary in winter (Tn_s) were from BTO (2018). Tar_s was obtained by subtracting the species flight time measured on the Exe estuary from the total time lost per disturbance by waders on the Wash, as detailed in Table 1 of Collop *et al.* (2016): the untested assumption was that Wash and Exe values would be similar. In the Wash study, observers approached a bird at a steady pace and recorded the length of time between when the bird first became visibly alert and when it flew away. The 'flight time' was measured on the Wash in the same way as it was on the Exe (the period from taking off to landing) but, in addition, the 'latency time' (length of time between landing and the first attempt at feeding) was recorded. Total time lost per disturbance event on the Wash was calculated by summing alert time, flas c time and latency time. The energy expended per second of flight and the daily energy requirements on the Exe were taken from standard equations in Collop *et al.* (2016) and were used to estimate the energy costs of disturbance flights.

Statistical analysis

The effect of several factors on people and bird numbers in a sector and on the number of birds flighted was explored to determine the best conditions to calculate representative values. The software used was Minitab, release 13 (www.minitab.com). We used manual, step-down regression until all remaining variables had a *P*-value <0.05 to identify the conditions for each sector that would be most representative of the typical winter daylight period. The explanatory variables included for both land and intertidal sectors were: (i) day of the week, with weekend or public holiday = 1, working weekday = 0; (ii) stage of the winter, measured as the days elapsed since 1 November – as birds were present in the intertidal sectors during autumn, data were sometimes obtained in September and October whereupon this variable took a negative value; (iii) hours before or after low tide for intertidal sectors and high tide for land sectors. Additional variables used for land sectors were (iv) hours before or after midday and (v) bad weather = 1, defined subjectively as an unpleasant combination of rain, low temperature and strong wind considered likely to deter recreational walkers alongside the estuary, with otherwise = 0. Additional variables used for intertidal sectors were: (iv) the winter, with 2009/10 = 1, 2010/11 = 2, 2011/12 = 3 etc: this variable was not used for land sectors because most data were collected over the last 2-3 years only, (v) predicted tide height at dead low tide at Exmouth, and (vi) dawn, with counts made within 30 min of dawn = 1 and at other times = 0. For example, the analysis for a particular sector might show that people numbers/15 min were low at the very beginning and end of the day and differed between weekdays and weekends. Our estimate of the typical visit rate in this case would then be the separate means of all the visits made during the middle portion of the day on weekdays and at weekends. The mean visit rate for the typical week would be the average of these two values, weighted in the ratio of 5:2. If the visit rate had also depended on the stage of the exposure period or winter, only counts made during those parts of the exposure period and winter when the greatest number of visits were present were used to calculate the mean values for the sector: that is, we adopted a precautionary approach that would tend to overestimate the actual visit rate.

After the most important correlates of people numbers had been identified for each of the intensively studied sectors, we used General Linear Modelling (GLM) to test for differences between sectors. Data from all sectors were used, including the less well-investigated ones. 'Sector' was included as a categorical variable and the main correlates on people numbers as previously identified for individual sectors by manual step-down regression (Supporting Online Material Table S3) were included as covariates. Interactions between 'Sector' and each covariate were also included in a manual step-down selection procedure in which the criterion for rejection was $P > 0.05$. The same procedure was adopted for the numbers of waders flighted/visit but only one covariate, 'Time', was used. 'Time' was measured in land sectors as the minutes before or after high tide and in intertidal sectors as minutes before or after low tide. In land sectors, this variable captured the distance of waders from people onshore as well as the numbers of waders present and so available to be disturbed. In intertidal sectors, it captured the number of waders available to be disturbed because wader numbers were either at their highest (Cockwood) or at their lowest (Bite, Cockle Sand) at that stage of the exposure period.

RESULTS

Overlap between birds and people

***Spatial* -** People on the land were visible to foraging waders along about 35% of the 16.5 km frontage where they were in direct line of sight to waders on the flats and were not hidden behind features such as a railway embankment, hedges, clump of trees and buildings or, indeed, were just too far away. People were present throughout the daylight hours, irrespective of tidal state, and people numbers varied widely within and between sectors (Supporting Online Material Fig. S4). Multiple regression analysis of the correlates of people numbers showed that, as would be expected, rates were higher at weekends/public holidays than on weekdays, lower in bad weather and lowest at the beginning and end of the day (Table 2 & Supporting Online Material Table S3A).

People numbers also varied greatly within and between intertidal sectors (Supplementary Online Material Fig. S5). Multiple regression analysis showed that people numbers were highest around low tide and were higher on Spring tides than on Neaps and at weekends (Table 2 & Supporting Online Material Table S3B). People numbers also decreased through the winter and over the nine years of the study.

To compare people numbers in each part of the estuary under comparable conditions, we selected counts made when people numbers were at their greatest; *i.e.* within 1 hour of low tide on Spring tides, defined as low-tide height <0.8 m which occurred around midday on the Exe (Admiralty Tide Tables). An average total of 18.6 people was present in the intertidal zone at low tide on winter Spring tides across all winters combined. While all the intertidal flats were exploited by waders as they moved around with the ebb and flow of the tide (Goss-Custard *et al.* 1991; Hughes 1992), people mainly visited the easily-accessible sandflats and mussel beds in the lower reaches of the estuary (Fig.

1). Accordingly, there was overlap between people and waders in, at most, 25% of the maximal 938 ha of intertidal area exposed at low tide.

Temporal - In land sectors, waders were most at risk of being disturbed by people on the land when the upshore flats were exposed at the beginning and end of the tidal exposure period. This was because waders followed the tide out and back and were, for much of the exposure period, some hundreds of metres away from people on the land and so too distant to be disturbed (Supplementary Online Material Fig. S6). Accordingly, the overlap periods in the land sectors all occurred during the first and last parts of the tidal exposure period (Table 4).

This was not the case for the intertidal sectors, however. The potential for overlap between birds and people depended whether birds foraged there throughout the exposure period, as at Cockwood (Supplementary Online Material Fig. S7, Goss-Custard 2016b, 2017) or mainly at the beginning and end of the exposure period, as at the Bite and Cockle Sand (Supplementary Online Material Fig. S8, Fig. S9, respectively). Therefore, according to the behaviour of both the people and birds that occurred there, the precise timing of the overlap periods within the exposure period also varied between intertidal sectors (Table 4).

Costs of disturbance

As the numbers of people and of waders flighted per disturbance event differed significantly between sectors in both land and intertidal sectors, sector-specific estimates of both measurements were used in calculating disturbance costs.

Visit rate and bird responses: The number of visits by a single person or group and the number of waders of all species combined that were disturbed into flight during the daytime overlap period in each sector are summarised in Table 4. Estuary-wide, most waders flighted by people were Curlew, Oystercatchers, Redshank, Turnstone and Dunlin (Table 5). The number of each species flighted was the product of the total number of waders flighted and the species composition of flighted birds. Only flight time in Redshank and Oystercatcher varied between sectors (Table 6). The flight times of waders that left a sector after being disturbed could not be measured, so the data refer only to the *circa* >75% of birds that remained in sector whose flight times could be measured.

Time and energy costs: Estuary-wide, time costs from disturbance flights were equivalent to <0.1% of the available daylight foraging time of 9 h per tidal cycle and, because waders feed at night, <0.05% of the foraging time per 24 h (Table 7). Energy costs were equally small, being equivalent to only 0.02% of the daily energy requirements of an individual bird (Table 8). Estuary-wide, 99.5% of flighted birds were disturbed during overlap periods (Table 9).

These calculations are for the average bird across the whole estuary whereas some individuals may have been at a disproportionate risk because of where they fed. The likely magnitude of any such bias was explored in Oystercatchers, the most frequently disturbed species. Even if (improbably) all the disturbance costs only fell on the one-third of the total estuary Oystercatcher population that foraged in the lower reaches of the estuary within which there was much bird movement, the time and energy costs would have been only 0.21% and 0.05%, respectively, in daylight and less than half these amounts over 24 h.

Visit rates and disturbance thresholds

The visit rates in the individual-based models for Southampton Water and Poole Harbour were measured as the number of visits/day/ha, thus combining people numbers along the linear shoreline with those in the intertidal area (Stillman *et al.* 2007; Collop 2017). The disturbance thresholds were, respectively, 30 and 20 visits/ha/day for Southampton Water and Poole Harbour. The visit rate on the Exe estuary was (638+15)/938, or 0.696 visits/ha/day, or 1/43 and 1/29, respectively, of the disturbance thresholds predicted for Southampton Water and Poole Harbour.

DISCUSSION

Amount of disturbance

The average time cost incurred by the average wader being disturbed into flight by people on land and in the intertidal zone was less than 0.1% of the time available each day for foraging in daylight and the average additional energy expenditure was equivalent to <0.02% of daily requirements. Such small amounts are most unlikely to have affected winter mortality or spring migration. This argument is strongly supported by the disturbance thresholds for Southampton Water and Poole Harbour: according to individual-based modelling, the number of people overlapping with foraging waders on the Exe would need to have been 43 and 29 times higher, respectively, for mortality to have been increased.

Only two estimates of the disturbance threshold are currently available so by how much its value varies between winters and sites is not yet established. Their average value of 36 can therefore only be taken as an 'orders of magnitude' estimate of the gap between how much disturbance is required to harm the waders and the amount that actually occurred in our study SPA. Sampling errors are most unlikely to close the gap by a significant amount, even though their magnitude cannot be precisely estimated. Although our calculations included most of the observable responses to a disturbance event (alert, flight and recovery before resuming foraging), they omitted the probably small extra costs incurred by the minority of disturbed birds that walked away, often while continuing to forage. It was also necessary to assume that the time cost of being alert and recovery were similar on the Exe to that on the Wash. The bias incurred by measuring the flight times of only those birds that remained in sight also means that the time and energy costs of flying away from disturbance events would have been underestimated by an unknown amount – although the very fact that they did leave the sector may have been because they were shortly to move to another part of the estuary anyway. On the other hand, precautionary choices were made in the cost calculations. An important one was not deducting from the costs of disturbance the unknown number of unidentified as well as the many identified WHA flights. Another was assuming the exposure period lasted 9 hours when it was often longer, depending on wind strength and direction and tide height. Furthermore, three of the five most affected species - Oystercatcher, Curlew, Redshank - regularly fed in fields over high tide, thus extending their foraging time even more (pers. obs.). The very small time- and energy-costs and the very large gap between the visit rates on the Exe and the disturbance thresholds does argue strongly that, whatever omissions and sampling errors were present, it is very unlikely they would reverse the conclusion that disturbance was of trivial significance in this system. The results are consistent with the observation made by other researchers that simply showing that disturbance occurs is not sufficient grounds for concluding that the birds are necessarily harmed (Gill *et al.* 2001, Goss-Custard & Stillman in press).

Overlap between people and birds

The study has demonstrated the critical importance of taking into account the extent of the spatio-temporal overlap between birds and people. The number of visits by groups of one or more people during the average winter day was distributed almost equally between overlap and non-overlap periods yet, estuary-wide, 99.5% of flighted birds were disturbed during overlap periods. The main periods of overlap were (i) either side of low tide in the intertidal sectors – from where most birds were flighted (Table 9) - and (ii) at the beginning and end of the exposure period in land and shoreline sectors when only the upper part of the shore was accessible to the birds.

As occurs in many estuaries, overlap in space was limited by substrate: people avoided the muddy, upper and middle reaches where most waders foraged (Hughes 1992). It could be argued, of course, that waders avoided some frequently disturbed areas altogether and that this partly explains the spatial separation between birds and people. This is very unlikely except for short periods when disturbance was continuous and intense. Most birds that were disturbed just moved along or down the shore or moved to an area they would have gone to shortly afterwards anyway. Such redistributions were temporary and we identified no frequently-disturbed places where birds did not ever occur when people were absent.

Overlap in time was limited in several ways. First, people were mostly present in daylight whereas waders fed day and night. Second, on the high-level flats used by waders on the receding tide people generally went onto the flats after many birds had moved to later-emerging feeding areas. Many people delayed walking their dogs on Cockle Sand, for example, until the substrate had partially drained (pers. obs.). In the Bite, professional crab collectors waited until the crab tiles downshore became exposed by which time most birds had left (Goss-Custard 2016b). Additionally, having been driven away by the people that arrived first, there were often few or no birds left to be disturbed by subsequent arrivals. Finally, many wader species in many estuaries follow the receding tide to reach more profitable (e.g. Smith 1975) and probably safer (Cresswell 1994) foraging areas downshore which automatically takes them away from disturbance on land. Unless factors that limit overlap in space and time between people and birds are taken into account, an exaggerated impression of the importance of disturbance can easily be obtained (Goss-Custard 2016a).

Impact on the birds

In addition to the low costs in time and energy that disturbance imparted on waders, the visit rates were far below the disturbance thresholds predicted by modelling for both Southampton Water and Poole Harbour (Stillman *et al.* 2012; Collop 2017). This was the case despite both models being very precautionary in some or all of the following respects: (i) Waders could not escape to undisturbed foraging areas upriver; (ii) waders could not forage at the beginning and end of the exposure period which is of great importance for their survival (Goss-Custard *et al.* 2006b); (iii) waders did not follow the receding tide beyond the disturbance distance of people on land; (iv) some species could not forage in fields over high tide and (v) birds could not habituate to people (Goss-Custard & Stillman in press) or reduce their response to disturbance when hungry. Despite having all five omissions, the Southampton Water model predicted it would take 43 times more people than occurred on the Exe for the disturbance threshold to be reached. Even this may be a large under-estimate of the difference because, in our study, the many return visits along a land sector were scored as two visits whereas, in the Southampton model, they would have been regarded as one. For the Poole Harbour model, which contained omissions (ii), (iii) and (v), the value was 29. This is powerful support for the notion that, on the Exe estuary, disturbance of waders on their foraging grounds was of no significance. Clearly, the amount birds and people overlap in time and space should be made an important component in the conceptual framework required when assessing the impact of disturbance on waders. This conceptual scheme may apply equally to other birds for which the Exe is an important wintering site, notably the Brant Goose *Branta bernicola bernicola* L. and Eurasian Wigeon *Mareca penelope* L.

As the present study has illustrated, it is not a simple matter to test the hypothesis that shorebirds are affected significantly by disturbance from people. Despite the many millions of people that have been estimated to visit the vicinity of the Exe estuary annually (Liley *et al.* 2014), it took an intensive field study to show just how few of them actually disturb the birds because of their infrequent overlap in time and space. It really is a case of the devil being in the detail, and the detail is often overlooked. This needs to be taken into account wherever the impact of disturbance on the waders of an estuary SPA is being assessed, especially as the risk from disturbance on the Exe is thought to be high compared with that on many other estuary SPAs. If the trivial impact of disturbance on waders in the Exe estuary SPA is also found to be the case for wildfowl, local conservation authorities should perhaps re-evaluate their current policy of automatically imposing levies on new buildings to mitigate the presumed increase in disturbance arising from the assumed resulting increase in visitor numbers. Especially so as the number of people on the three, most populated intertidal areas on the Exe – where

83% of disturbed birds had been foraging and whose management was essentially unchanged during the study - decreased over the last decade, despite the house-building that had taken place throughout. As one reviewer of this paper commented: '*The emotional response most people feel when they observe wildlife retreating from human activity, and the difficulty of measuring the true cost of disturbance on wild animals, makes understanding the optimum approach for managing disturbance difficult. In my experience, it may also obscure the importance of more pressing constraints, such as habitat and nest loss, or direct mortality.* Our concern is that, by wasting valuable resources and risking the loss of the support of sceptical commercial and recreational estuary-users, the mitigation of unsubstantiated disturbance of wintering shorebirds risks becoming a classic and very expensive example of 'evidence complacency hampering conservation' (Sutherland & Wordley 2017).

Generalising the findings to other cases

The two approaches to testing the significance of disturbance for wintering waders have been used previously but no published study has combined them in the way employed here. IBMs have been applied to a range of species and sites and have addressed several issues relating to disturbance (Stillman *et al.* 2007). West *et al.* (2002) showed that Oystercatchers on the Exe estuary were more badly affected by multiple small disturbance events than by a smaller number of major ones. Goss-Custard *et al.* (2006) showed that both food abundance and severity of the winter weather had a large influence on the magnitude of the disturbance threshold in Oystercatchers of the baie de Somme and that, despite large numbers of people regularly being present on the feeding grounds, the amount of disturbance was usually insufficient to harm the birds. Stillman *et al.* (2012) and Collop (2017) showed that this was also the case for several species of waders in Southampton Water and Poole Harbour, respectively, and identified the visit rate above which the overwinter survival rate of the birds would be reduced, and the species to which this was most likely to happen. The time-cost and energy-cost approach to testing the significance of disturbance was applied to several species of wading birds on the Wash by Collop *et al.* (2016). As most species seldom foraged for >95% of the exposure period, this was taken to be a suitable indicator of whether disturbance was likely to be increasing the time- and energy-costs of the birds to harmful levels. In fact, the frequency of disturbance required to increase the birds' time-costs by >5% were considered extremely unlikely to be found on the Wash in most circumstances.

These studies, along with the present one, demonstrate that being disturbed by people does not necessarily lower the overwinter survival rate of waders, but that the disturbance threshold can sometimes be surpassed in particular circumstances. In contrast, the many studies carried out on the behavioural responses of waders to disturbance – such as flight distance and distribution – are unable on their own to test whether the disturbance threshold is likely to have been surpassed in a particular species in a particular place at a particular time (Gill *et al.* 2001). Yet the only methodology currently available – an IBM – can be very time consuming and costly to apply yet simpler and less costly approaches, such as measuring the time-cost of disturbance, does not provide a critical test of the disturbance hypothesis.

While more easily applied alternative approaches to IBMs may well be developed in the future, the present project suggests one possible solution to resolving the dilemma. The time- and energy-costs in all wader species on the Exe were very small indeed, and most unlikely to represent costs to which the birds could not readily adapt. The comparison with the visit rates at the disturbance thresholds measured in Southampton Water and Poole Harbour also supported the conclusion that the waders foraging on the intertidal flats of the Exe estuary were well short of being subjected to a harmful amount of disturbance. The suggestion arising from these mutually supporting results is that time-costs and visit rates, either alone or in combination, could be used to measure the disturbance risk in other estuaries if the value of the disturbance threshold of each measurement was known for a sufficient sample of estuaries. Our proposal is that, whenever the resources can be made available, IBMs could be used to measure the visit rates and the daytime time-costs of disturbance to waders at which the disturbance threshold is exceeded. After a general rule had been established from a sufficient sample of estuaries, it would then be possible to test whether the visit rates of people during overlap periods and the time-costs they inflict on the birds are equally reliable predictors of whether the disturbance threshold is being exceeded. Subsequent Environmental Impact Assessments could then choose the method that could most easily be applied in their particular case. The key assumption is that, by concentrating fieldwork in the overlap periods at the most critical part of the non-breeding season, fewer resources would be required than would be needed to build and test an IBM. If successful, the approach could perhaps open the way for the measurement of time-costs and/or visit rates to be used on their own, or in combination, as convenient and reliable tests as to whether waders are actually being harmed by disturbance.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of the article:

Table S1. Mean numbers of people recorded on Spring tides in different parts of the estuary at low tide

Table S2. Calculating the total time spent by one species in one sector in flying away from disturbers during an average winter day

Table S3. Regression analysis of people numbers in the most populated land and intertidal sectors.

Table S4. Visit rates to each land and intertidal sector

Table S5. Numbers of waders flighted by people arriving and leaving Cockle Sand

Table S6. The number of waders flighted in the other intertidal sectors

Fig. S1. Sediments of the Exe estuary

Fig. S2. Allowing for the daily shift in the tidal cycle

Fig. S3. Validating measures of flight distance and flight time

Fig. S4. Numbers of people walking in the Powderham and Goatwalk land sectors

Fig. S5. People counts through the exposure period in the Bite (left) and Cockle Sand (right) intertidal sectors.

Fig. S6. Temporal overlap between people on land and waders in the intertidal zone

Fig. S7. Temporal overlap between people and waders on the Cockwood mussel bed

Fig. S8. Temporal overlap between people and waders on the Bite

Fig. S9. Temporal overlap between people and waders at Cockle Sand

Fig. S10. Estimating visit rate in the less intensively investigated intertidal sectors

Fig. S11. The number of waders disturbed into flight by people on land sectors

Fig. S12. The number of waders disturbed into flight by people in intertidal sectors

TABLES

Table 1. The intensively-studied six 'land' and five 'intertidal' overlap sectors. The average time for people to traverse the land sectors ('transit time') was calculated from the time taken by randomly-chosen people to traverse four of the sectors (Powderham, Goatwalk, Bay and Promontory) of GPS-measured length. The mean speed across the four sectors of 1.58s/m (n = 65, se = ±0.089) was used to convert transit time to the approximate length of each of the six sectors.

Type	Sector name	Description	Length (m)	Time (min)
Land	South-east corner	Sand/gravel upper shore or grass verge	400	10.35
	Promontory	Grass footpath or gravel upper shore	270	7.08
	Bay	Top of seawall or gravel upper shore	940	24.52
	Lympstone		825	21.49
	Goatwalk		250	6.37
	Powderham		650	17.12
Intertidal	Bull Hill	Mussel bed		
	Cockle Sand	Sand flat		
	Starcross	Stony mudflat		
	Cockwood	Mussel bed		
	Bite	Mudflat		

Table 2. General Linear Modelling comparing the number of people recorded across all sectors taking into account covariates identified in Supplementary Online Material Table S3. The two right-

hand columns show sample sizes (*n*). In land sectors, people number was defined as the number of individual people passing through the sector per 15 min. In intertidal sectors, the data were counts of people present at any one time.

LAND SECTORS						
Source	*df*	*F*	*p*		Sector	*n*
Sector	5	92.44	<0.001		Powderham	203
Time of day (hours before or after 12.00 h)	1	16.42	<0.001		Goatwalk	72
Day (weekday = 0 weekend/holiday = 1)	1	27.10	<0.001		Bay	167
Weather (good weather = 0 bad weather = 1)	1	12.66	<0.001		Promontory	168
Sector x Weather	1	5.62	0.018		South-east corner	242
Sector x Time of day	1	7.45	0.006		Lympstone	11
Error	813					
Total	823					

INTERTIDAL SECTORS						
Source	*DF*	*F*	*P*		Sector	*N*
Sector	4	53.59	<0.001		Bite	425
Day (weekday = 0 weekend/holiday = 1)	1	40.12	<0.001		Cockwood	306
Year (winter 2009/10 = 1, 2010/11 = 2 *etc*)	1	21.82	<0.001		Cockle Sand	384
Time (mins before or after low tide)	1	116.58	<0.001		Bull Hill	289
Sector x Year	1	6.23	0.013		Starcross	62
Sector x Time	1	27.95	<0.001			
Error	1438					
Total	1447					

Table 3. General Linear Modelling comparing the number of waders flying away from a disturbance event across all sectors taking into account the state of the tide which largely

determined the numbers of waders available to be disturbed. The two right-hand columns show sample sizes (*n*).

LAND SECTORS						
Source	*df*	*F*	*p*		Sector	*n*
Sector	5	6.41	<0.001		Powderham	822
Time (mins before or after high tide)	1	4.42	0.036		Goatwalk	361
Error	992				Bay	300
Total	998				Promontory	260
					South-east corner	93
					Lympstone	11

INTERTIDAL SECTORS						
Source	*DF*	*F*	*p*		Sector	*n*
Sector	4	29.56	<0.001		Bite	84
Time (mins before or after low tide)	1	25.64	<0.001		Cockwood	130
Sector x Time	1	25.63	<0.001		Cockle Sand	1034
Error	806				Bull Hill	17
Total	812				Starcross	51

Table 4. The duration of overlap periods over the whole exposure period and over that part falling in daylight and the number of visits and of waders flighted by them during daylight overlap periods in the main places where overlap occurred. Data from which visit rates were calculated, along with the mean, *se* and *n* are in Supplementary Online Materials Figure S10 and Table S4. Data from which the numbers of all species of wader that were flighted by a single visit were calculated are in Supplementary Online Material Figs. S11 & S12 and Tables S5 & S6.

Sector	Overlap period	Duration (h)	Duration in daylight (h)	Visits/daytime overlap	Total waders flighted
Intertidal	(mins from low tide)				
Bite	-180 to 0	3.0	2.16	2.56	18.7
Cockwood	-180 to 0	3.0	2.16	2.08	69.6
Starcross	-120 to -60	1.0	0.71	1.19	11.3
Bull Hill	-120 to 0	2.0	1.44	1.04	106.3
Cockle Sand	-240 to -60 & +60 to +300	7.0	5.41	59.39	12.0
Land	**(mins from high tide)**				
Powderham	+120 to +240 & -180 to -60	4.0	1.85	14.76	7.84

Bay & Promontory	+160 to +220 & -220 to -100	3.0	1.82	5.99	26.40
Promontory alone	+160 to +220 & -220 to -100	3.0	1.82	0.81	5.80
Upper shore	**(mins from low tide)**				
Lympstone	-180 to +180	6.0	4.13	15.6	3.16
South-east corner	-300 to -180 & +180 to +330	4.5	3.13	23.95	1.60

Table 5. Species composition (%), by sector, of waders flighted by people in the intertidal zone or on land. Not shown are the data from Cockle Sand where almost all flighted birds were Oystercatchers (Supporting Online Material Fig. S9). '*N*' is the numbers of waders of each species flighted in each sector.

Species	Bite	Cockwood	Starcross	Powderham	Goatwalk	Bay	Promontory
Curlew	2.8	3.0	17.9	1.6	0	1.3	2.0
Oystercatcher	18.8	79.2	18.5	9.4	0	6.1	3.5
Black-tailed Godwit	0	0	0	0.1	0	0	0
Bar-tailed Godwit	11.1	0.7	0	4.2	0	0	0
Grey Plover	0.3	0	0	2.7	0	0.1	0
Redshank	8.4	13.5	28.5	11.7	19.4	27.2	25.3
Turnstone	0	2.6	4.6	0.6	14.5	11.6	8.0
Dunlin	58.4	0.8	27.8	70.0	64.5	53.7	61.1
Ringed Plover	0	0	0	0	0	0	0
Greenshank	0.2	0.1	2.6	0	0	0	0
Avocet	0	0	0	0	1.6	0	0
n	1302	2606	151	1268	62	3981	880

Table 6. Flight duration, or flight time, of waders disturbed by people. GLM showed that significant differences between sectors only occurred in Redshank (6 sectors, n = 207, P = 0.02) and Oystercatcher (7 sectors, n = 141, P = 0.003). Pair-wise comparison between sector means identified two groups of sectors between which flight times differed significantly ($P < 0.05$) in these species: the values for t and P between the groups are given in the right-hand two columns. In Redshank, A refers to the Bay, Starcross and Cockwood sectors and B refers to the Promontory, Bite and Powderham sectors. In Oystercatchers, A refers to Cockwood and B to all the other sectors. In the remaining five species, GLM revealed no between-sector differences, the sample sizes being: Curlew, 6 sectors, n = 49; Bar-tailed Godwit, 3 sectors, n = 11; Grey Plover, 3 sectors, n = 21; Turnstone, 5 sectors, n = 43; Dunlin, 5 sectors, n = 52.

Species	Sectors	Mean flight time (s)	N	se		
Curlew	all	13.1	49	1.42		
Bar-tailed Godwit	all	16.8	11	3.66		
Grey Plover	all	18.0	21	4.67		
Turnstone	all	9.5	43	1.03		
Dunlin	all	10.9	52	1.96		
					t	*P*
Redshank	A	9.7	129	0.69	3.20	0.002
	B	15.5	77	1.65		
Oystercatcher	A	22.6	27	2.56	3.49	0.001
	B	13.1	113	0.98		

Table 7. Average estuary-wide time-costs/day for the most disturbed waders during winter daylight hours. Flight time is the duration of the flight of a single bird that has been disturbed by people. The alert plus recovery time is the time spent alert (and therefore not foraging) before flying away combined with the time taken after landing to resume feeding. Column 5 is the total time cost for each disturbed bird of each flight, and is obtained by summing columns 3 and 4. Column 6 is the average winter population on the Exe in recent years (BTO 2018). Column 7 is time lost by the whole estuary population, the product of columns 2 and 5. The final column is based on an average exposure period of 9hrs.

Species	Number flighted per daytime overlap period	Flight time (s)	Alert plus recovery time (s)	Time cost per flight (s)	Population size	Time lost by total population (s)	Foraging time lost by average bird: (s)	(%)
Oystercatcher	970	14.2	38.7	52.9	2228	51329	23.04	0.0711
Redshank	190	12.0	27.7	39.7	613	7537	12.30	0.0379
Dunlin	285	10.9	18.4	29.3	4065	8349	2.05	0.0063
Curlew	14	13.1	54.1	67.2	749	934	1.25	0.0038
Turnstone	45	9.5	20.0	29.5	194	1328	6.85	0.0211

Table 8. Per bird average estuary-wide energy-costs of disturbance during daylight in the five most disturbed wader species. The time spent in flight (column 2) is the time spent in post-disturbance flight by the average bird during daylight and was calculated by dividing the total aggregate time spent in flight by all the birds that had been disturbed by the number of birds in the wintering population. Energy costs of flying (column 3) and daily energy requirements (column 5) are from Collop (2017). Energy spent in flight after disturbance (Column 4) is the product of columns 2 and 3. Column 2 comes from the data in three columns of Table 3 and is: (column 2 x column 3)/column 6.

Species	Time spent in flight (s)	Energy spent/s of flying (kJ)	kJ spent flying per daylight overlap period	Thermoneutral energy requirement (kJ/24h)	Energy spent flighting as a percentage of 24h requirements
Oystercatcher	6.19	0.0206	0.1278	723	0.0177
Redshank	3.71	0.0130	0.0483	308	0.0157
Dunlin	0.76	0.0086	0.0066	147	0.0045
Curlew	0.24	0.0240	0.0056	954	0.0006
Turnstone	2.22	0.0115	0.0256	250	0.0102

Table 9. Where and when waders were disturbed into flight by people. (A) Visits per day by a single person or group and the total waders of all species they disturbed into flight during winter daylight overlap and non-overlap periods. (B) Waders of all species disturbed into flight by people just during overlap periods according to sector type. The shoreline was the usually stony interface at the top of the intertidal zone, immediately adjacent to the land.

Period	Sectors	Visits/day	Waders flighted
(A)			
Overlap	All	287.6	262.8
Non-overlap	All	350.3	1.6
Total	All	637.9	264.4
(B)			
Overlap	Intertidal		217.9
Overlap	Shoreline		4.8
Overlap	Land		40.0
Total			262.8

FIGURES

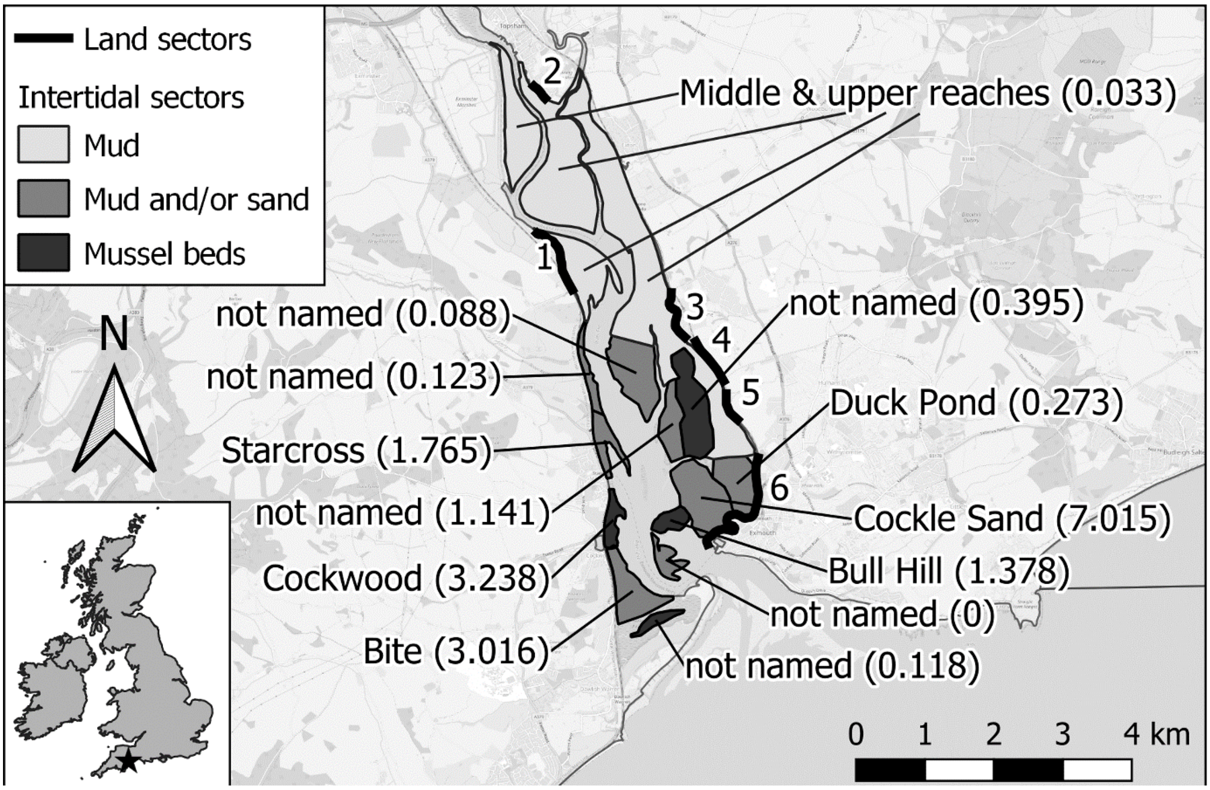

Figure 1. Mean numbers of individual people during low tide on Spring tides in all the intertidal regions of the Exe estuary. A group of three people would be scored as three. Sample sizes and standard errors of each mean value are in the Supplementary Online Material, Table S1. The black lines show the approximate position of the six land sectors, named: 1 Powderham; 2 Goatwalk; 3 Lympstone; 4 Bay; 5 Promontory; 6 South-east corner. The grey shading shows built-up areas around the estuary while the inset shows its location within the UK (Latitude, 50° 38' 50'' N. Longitude, 03° 26' 32'' W).

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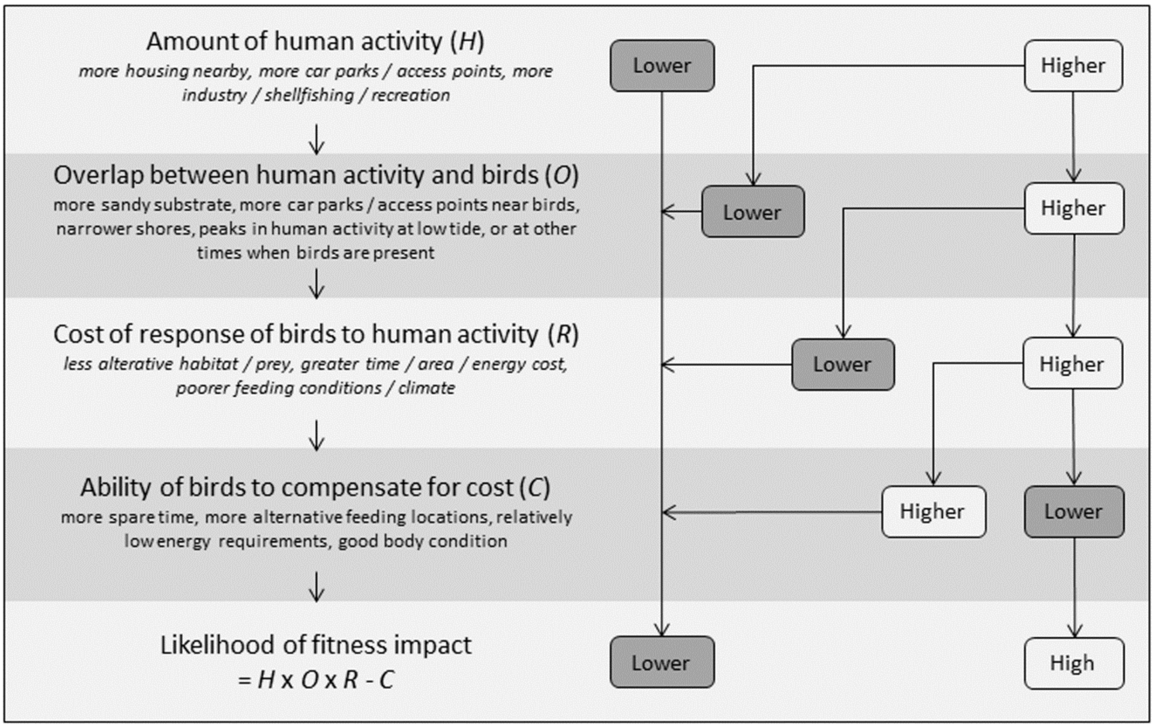

Pathway for disturbance to have an impact on the fitness of wading birds. Whether or not disturbance affects fitness depends on four variables: the amount of human activity (*H*); the amount of overlap between human activity and birds in space and time (*O*); the cost of the response of birds to human activity (R); and the ability of birds to compensate for the time, area and energy lost to disturbance (*C*). The left of the figure show these variables and factors that are likely to increase their magnitude. The right of the figure shows how the relative size of fitness impact depends on the relative values of these variable. A higher fitness impact will occur when the amount of human activity is higher, there is higher overlap in space and time, there is a greater cost of the response, and the birds have a lower ability to compensate.

Figure 2. Pathway for disturbance to have an impact on the fitness of wading birds. Whether or not disturbance affects fitness depends on four variables: the amount of human activity (H); the amount of overlap between human activity and birds in space and time (O); the cost of the response of birds to human activity (R); and the ability of birds to compensate for the time, area and energy lost to disturbance (C). The left of the figure shows these variables and factors that are likely to increase their magnitude. The right of the figure shows how the relative size of fitness impact depends on the relative values of these variable. A higher fitness impact will occur when the amount of human activity is higher, there is higher overlap in space and time, there is a greater cost of the response, and the birds have a lower ability to compensate.