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Variability in the area, energy and time costs of wintering waders responding to disturbance

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Birds' responses to human disturbance are interesting due to their similarities to anti-predator behaviour, and understanding this behaviour has practical applications for conservation management by informing measures like buffer zones to protect priority species. To understand better the costs of disturbance and whether it will impact on population size, studies should quantify time-related responses as well as the more commonly reported flight

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initiation distance (FID). Using waders wintering on an estuarine area, we experimentally disturbed foraging birds on the Wash Embayment, UK, by walking towards them and recording their responses (FID, alert time, time spent in flight, time taken to resume feeding, and total feeding time lost). We present data for 10 species of conservation concern: Curlew *Numenius arquata*, Oystercatcher *Haematopus ostralegus*, Bar-tailed Godwit *Limosa lapponica*, Grey Plover *Pluvialis squatarola*, Redshank *Tringa totanus*, Knot *Calidris canutus*, Turnstone *Arenaria interpres*, Ringed Plover *Charadrius hiaticula*, Sanderling *Calidris alba* and Dunlin *Calidris alpina*. Larger species responded more strongly, response magnitude was greater under milder environmental conditions, and responses varied over both small and large spatial scales. The energetic costs of individual disturbance events, however, were low relative to daily requirements and unlikely to be frequent enough to seriously limit foraging time. We suggest, therefore, that wintering wader populations on the Wash are not currently significantly negatively impacted by human disturbance during the intertidal foraging period. This is also likely to be the case at other estuarine sites with comparable access levels, visitor patterns, invertebrate food availability and environmental conditions.

Keywords

Anti-predator behaviour; flight initiation distance; non-breeding season; shorebirds.

Disturbance can mean, in its broadest sense, any event that leads to a change in behaviour or physiology. This might be for example due to natural events, such as attack by a predator, or anthropogenic disturbance whereby recreation or industry brings humans and birds into close proximity, or indirect disturbance through pollution events or noise impacts. For the purposes of this paper in relation to wintering waders, we use the definition adopted by signatories to the African-Eurasian Waterbirds Agreement (AEWA 2015), as given by Fox and Madsen (1997):‘Any human-induced activity that constitutes a stimulus (equivalent to a predation threat) sufficient to disrupt normal activities and/or distribution of waterbirds relative to the situation in the absence of that activity.’

As recognised in this definition and according to the widely accepted risk-disturbance hypothesis (Frid & Dill 2002, Beale & Monaghan 2004, Blumstein *et al.* 2005), animals respond to the perceived risk from human disturbances in the same way that they respond to predation risk, i.e. by making trade-offs between avoidance of the risk and prioritizing other fitness-maximizing activities such as feeding, mating or parental care (Frid & Dill 2002). Birds' responses to disturbance can therefore be expected to vary between individuals according to a variety of factors related to the perceived risk, the individual's current state and the costs of responding (Gill *et al.* 2001a, Beale & Monaghan 2004).

For day-to-day survival, particularly in winter, birds must optimize their daily energy intake to avoid starvation, whilst minimizing the risk of predation and disease. Consequently, human activities can impact a bird's energy budget since responding to disturbance events results in both reduced time and area available for feeding (Gill *et al.* 1996) as well as increased energy expenditure through locomotion (Houston *et al.* 2012) or physiological responses (Ackerman *et al.* 2004). Survival will be reduced as a result if the birds are unable to compensate, for example by moving to other sites and/or increasing feeding time or efficiency (Urfi *et al.* 1996, Gill *et al.* 2001a, 2001b, Stillman *et al.* 2001, West *et al.* 2002, Navedo & Masero 2007).

We can investigate birds' responses to disturbance and test the relative importance of potential explanatory factors using experimentally collected field data. Walking towards animals and recording characteristics of their response is a frequently used and effective method for studying disturbance avoidance behaviour, and the most commonly reported measure of response to disturbance is FID – flight initiation distance. Also known as 'escape distance' or 'flush distance', FID measures the distance between the disturbance source and animal when it begins to flee (Bonenfant & Kramer 1996, Blumstein *et al.* 2003). The method has been used for a range of taxa including mammals (Li *et al.* 2011), birds (Van Dongen *et al.* 2015), reptiles (Cooper 2009), fish (Gotanda *et al.* 2009) and amphibians (Rodriguez-Prieto & Fernandez-Juricic 2005). However, FID does not quantify the full time and potential energy costs incurred between the point that an animal detects a disturber and when it returns to its original behaviour and physiological state. Very few researchers have studied or reported these time- or energy-related measures, which is a clear knowledge gap that we seek to address here.

Other studies have identified a variety of potential explanatory factors, including species or body size (Blumstein *et al.* 2003, 2005, Glover *et al.* 2011), flock size (Ikuta & Blumstein

2003, Glover *et al.* 2011), habituation (Urfi *et al.* 1996, Ikuta & Blumstein 2003, Lin *et al.* 2012), whether or not birds are quarry species (Laursen *et al.* 2005), environmental conditions (Stillman & Goss-Custard 2002), type of disturbance (Glover *et al.* 2011), starting distance (Ikuta & Blumstein 2003) and individual condition (Beale & Monaghan 2004). Whilst this shows that FID has been relatively well studied in waders, much of the research has been carried out in Australia and North America (Blumstein *et al.* 2003, 2005, Ikuta & Blumstein 2003, Glover *et al.* 2011, Koch & Paton 2014), with multi-species studies of the birds of the East Atlantic Flyway being limited to the Dutch and Danish Wadden Sea (Smit & Visser 1993, Laursen *et al.* 2005). By focussing our research on the Wash Embayment in eastern England, we are therefore adding new understanding to the suite of information available on birds’ responses to disturbance around the world. Estuarine sites, given their importance for both wildlife and human activities (Ramsar Convention 1971, Millennium Ecosystem Assessment 2005), offer useful study systems for such research. We focus on waders (Charadriiformes) as they comprise a relatively long-lived group of species and many are migratory, so survival during the non-breeding period is an important part of the annual cycle with regards to the long-term persistence and viability of populations (Recher 1966, Saether *et al.* 1996, Piersma & Baker 2000, Piersma *et al.* 2016).

Measuring physiological responses to disturbance was beyond the scope of this study and flushing behaviour is a good indicator of acute physiological changes associated with experimental disturbance (Ackerman *et al.* 2004), so we chose to focus on visible behavioural responses. We use our field data to explore the differences in those responses between species, identify key explanatory variables and test four expectations: (1) all aspects of the visible response to disturbance are positively correlated with each other; (2) FID, time spent in flight and total time lost to disturbance differ between species and increase with body size; (3) the magnitude of response (FID, time spent in flight and total time lost) decreases under harsher weather conditions; and (4) responses (FID, time spent in flight and total time lost) vary from site to site and over time (number of days through the winter season).

METHODS

Study site

The study took place on the Wash (52˚ 56' 16" N, 00˚ 17' 16" E), a large embayment in eastern England on the North Sea coast with extensive intertidal sand and mudflats. Its conservation importance is recognized through several national and international designations including Site of Special Scientific Interest, Special Area for Conservation, Special Protection Area and Ramsar site status (Doody & Barnet 1987, JNCC 2014). 'In terms of total numbers, the Wash is the key site for wintering waterbirds in the UK' (Austin *et al.* 2014) and supports internationally important wintering populations of all the species that we included in this study: Curlew *Numenius arquata*, Oystercatcher *Haematopus ostralegus*, Bar-tailed Godwit *Limosa lapponica*, Grey Plover *Pluvialis squatarola*, Redshank *Tringa totanus*, Knot *Calidris canutus*, Turnstone *Arenaria interpres*, Ringed Plover *Charadrius hiaticula*, Sanderling *Calidris alba* and Dunlin *Calidris alpina*.

The intertidal flats used for the disturbance experiments (Fig. 1) were selected because of the wide range of wader species that were known to feed at low tide (Goss-Custard *et al.* 1988, Goss-Custard & Yates 1992, Yates *et al.* 2004) and the relatively even distribution of the birds within them. We also selected these areas on the basis of local knowledge of their differing distances from human populations, ease of access and resulting frequencies of human activities (such as walkers, dog-walkers, wildfowlers, bait diggers etc.) on the intertidal area and sea wall. Sites 1 to 3 can be characterized as areas of low disturbance, with a visitor frequency in the order of around three times per week; whereas the more easily accessible Site 4, on the eastern side of the Wash, had a comparatively high frequency of disturbance on a daily basis (M.G.Y. pers. obs.). Together the areas encompassed all shore levels and both regularly disturbed and undisturbed parts of the Wash, and so can be considered to be representative of the whole embayment.

Field experiments

All experiments took place during mid-December to late March of winters 2002/03, 2003/04, and 2004/05 and within the period of minimal tidal movement two hours either side of low water on spring tides, which on the Wash occur around midday. The intention was to survey all sites in all years, though circumstances dictated that Site 2 was not used in 2002/03 and

Site 3 was used only in 2003/04. Two observers worked together using binoculars to observe the birds and digital stopwatches were used to time the birds' behavioural responses to the nearest second.

The procedure was to mutually agree on a target bird, which remained unobscured from view for the duration of the observation, and then to walk side-by-side directly towards it at a comfortable pace on the soft substrate (approximately 2.5 km/h). The length of time for which the bird was visibly alert was noted and when the bird took flight both observers stopped walking. One observer timed the 'flight time' (the period from taking off to landing) and the 'latency time' (length of time between landing and the first attempt at feeding). Total time lost was calculated by summing alert time, flight time and latency time. The second observer kept their eyes on the place from which the bird had taken off and waited until the other observations had been completed before pacing out the FID. Distances were measured by counting paces which were later converted to metres after calibrating against a known distance in similar walking conditions. Isolated individuals of species that would normally be expected to feed in small groups or flocks were not selected for observation as their behaviour was considered unrepresentative of the usual behaviour of individuals of that species. Disturbance experiments took place on 38 separate survey days and the number of disturbances during each low tide survey period varied from three to 37 (median = 17.5; median for same species on same day = 3), depending on the number of birds present and how many experiments could be completed in the time available. Care was taken to ensure that the same birds were not disturbed more than once during a single survey, by searching for each target bird in a direction at least 90 degrees from that taken by the previous target bird when it flew off and landed. We also only selected birds that were at least 200 metres further away than the anticipated FID. Daily replicates were therefore well spread out in time and space so as to avoid order effects in the data.

In addition to the behavioural response parameters listed, a variety of environmental measurements were recorded relating to factors that may affect birds' responses; air temperature and wind speed (using a hand-held thermometer and anemometer) and the part of the shore at which each disturbance took place. This was assigned by dividing each site equally on a three-point scale from 'low' (1), through 'mid ' (2) and 'upper' (3) shore, as an indication of the relative proximity to the saltmarsh or sea wall (the most likely source of human disturbance) i.e. upper shore is closest. Shore width (distance between sea wall or marsh and the low tide mark) was approximately 2.5 km at Site 4 and 3-4.5 km at the other three sites. We also converted the date of each survey to the continuous variable 'winter day': with winter day 1 = 1 August.

Since warm bodies lose heat to the surrounding environment at faster rates when exposed to greater wind speeds (Williamson 2003), measurements of air temperature and wind speed from each disturbance experiment were converted to a wind chill equivalent temperature index (WCTI) using the following equation:

$$\mathrm{WCTI} = 13.12 + 0.6215\mathrm{T} - 11.37\mathrm{V}^{0.16} + 0.3965\mathrm{T}\cdot\mathrm{V}^{0.16}$$

where T is the air temperature in ˚C, and V is the wind speed in km/h (Williamson 2003, Osczevski & Bluestein 2005). We consider this to be a more appropriate independent variable, in relation to thermoregulation and energy budgets of birds, than records of air temperature alone (Wiersma & Piersma 1994).

Energy and time costs of responding to disturbance

To set birds' time-related responses in the context of daily energy requirements, we calculated energy cost per flight using the following equation from (Kvist *et al.* 2001):

$$Cost\ (kJ) = \frac{10^{0.39} \times M^{0.35} - 0.95}{1000} \times time\ spent\ in\ flight\ (s)$$

and used Nagy *et al.*'s (1999) equation for the birds' thermoneutral requirements:

$$Energy\ requirement\ (kJ) = 10.5 \times M^{0.681}$$

where M = body mass in grams.

We also estimated the number of disturbances that would result in a 1%, 5%, and 10% reduction in available feeding time based on our data for total time lost per disturbance (assuming that disturbance events do not overlap). Numbers are presented as a range based on the fact that birds are able to feed throughout the tidal cycle on neap tides, but not able to feed for two hours either side of high tide on spring tides (Goss-Custard *et al.* 1977). We used data from Goss-Custard *et al.* (1977) on how much of the available feeding time is used by each species during the winter as an indicator of their likely capacity to compensate for the costs of responding to disturbance. This is also presented as a range according to the spring-neap tidal cycle and reflecting the reduced number of daylight hours and increased thermoregulatory requirements of smaller species in mid-winter (Dawson & O'Connor 1996).

Model selection and data analysis

We used general linear models in a multi-model inference approach (Symonds & Moussalli 2011, Pap *et al.* 2013) to find variables with high explanatory power for our three different response variables (FID, flight time and total time lost). Preliminary analyses showed no effect of winter year, so the data from all three winters were combined (Supplementary Online Table S1). When deciding on the global models to be tested for each response variable, we initially included all biologically plausible two-way interactions in addition to the potential explanatory variables as main effects. Interactions that were found to be non-significant were subsequently excluded from the candidate model set, as recommended by Schielzeth (2010). In situations where the Akaike weight of the best AIC_c-ranked model in the candidate set was considerably higher than that of the next best model, inferences were made based on that model alone (Symonds & Moussalli 2011). However, if this was not the case, model averaging was undertaken using all models with $\Delta_i < 4$ to estimate the relative importance of the predictor variables under consideration. This involves summing the Akaike weights for each model in which that variable appears (Symonds & Moussalli 2011). The larger the sum of the Akaike weights (up to a maximum value of 1), the more important the variable is relative to the others in the global model (Burnham & Anderson 2002). Burnham and Anderson (2002) suggest ranking variables according to their relative importance, so in our analyses variables with a relative importance value greater than 0.9 were considered to have high explanatory power, those with values between 0.6 and 0.9 were considered moderate and variables with relative importance less than 0.6 were considered to have low explanatory power.

The candidate models that we tested included 'site' as a fixed factor, with 'shore level', 'wind chill index', 'winter day' and 'species mass' in grams (using Wash-specific data from Johnson 1985) as covariates. We also included two binary variables indicating whether the species was an Oystercatcher or not, or whether it was a plover or not, since these species are in different families to the others (Haematopididae and Charadriidae, respectively as opposed to Scolopacidae) and have different feeding ecologies (Goss-Custard *et al.* 2006). Before carrying out the analyses we centred and standardized the input variables (following Gelman 2008 and Grueber *et al.* 2011) to facilitate interpretation of the relative strength of parameter estimates, particularly where interaction terms were involved. The three response variables were $\log_e$-transformed, which helped to achieve a better distribution of the model residuals in relation to the assumptions of the statistical tests used.

To assess the relationships between our different response variables we used Spearman's rank correlation tests along with visual inspection of the bivariate scatterplots. We visually inspected diagnostic plots of the residuals for the statistical tests performed, as recommended by Zuur *et al.* (2010). This showed no issues with lack of normality, heterogeneity of variance, collinearity or undue leverage; however, as is often the case with ecological studies, the assumption of independence was not met. Therefore inferences beyond the sample space are made with care, and we will discuss the possibility that this could be an indication that an important covariate was not measured (Zuur *et al.* 2010). Details of preliminary data exploration and statistical tests not reported in the main text can be found in the supporting information. Analyses were carried out in R (R Core Team 2015) using functions available in 'arm' (Gelman & Su 2015) to standardize model predictors, and the multi-model inference package 'MuMIn' (Barton 2015) for model selection and averaging; plots were produced using 'ggplot2' (Wickham 2009) and 'PerformanceAnalytics' (Peterson & Carl 2014). Means are presented ± 1 SE.

RESULTS

We approached waders a total of 677 times and the birds' responses to the experimental disturbances are summarized in Table 1. During the survey period, the wind chill index ranged from -4.74 ˚C up to a maximum of 14.27 ˚C, which is within the range of typical winter temperatures for the area after accounting for wind speed (Met Office 2016).

Following Frid and Dill (2002), we predicted that all measures of response to disturbance would be correlated with each other and Fig. 2 shows that this was well supported by our data. Flight time and latency time were strongly positively correlated both with each other and with total time lost, although alert time was not significantly correlated with flight time or latency time and was only weakly correlated with total time lost. Individuals that exhibited greater FIDs spent longer in flight and took longer to resume feeding (particularly at FIDs below 200 m) and consequently lost more time in total. However, there was no correlation between FID and alert time.

Mean FID for all species was 89.7 m ± 3.1 (5–570 m, $n = 677$), but was significantly different between species ($F_{9,667} = 122.1$, $P < 0.001$). There was also a significant difference between species in flight time ($F_{9,667} = 20.9$, $P < 0.001$) and total time lost ($F_{9,677} = 29.5$, $P < 0.001$). Model selection and ranking by AIC_c (Table 2) revealed clear support for the top model, with all potential predictors included, when explaining both FID and time spent in flight (each with a model weight (ω_i) > 0.8). In the case of total time lost, the top model only had a model weight of 0.727, though the cumulative model weight of the top two models (acc ω_i) was 0.993, setting them well apart from the lower ranked models in the candidate set. Standardized and model averaged parameter estimates are shown in Table 3, and with all the coefficients being positive for 'species mass' and 'wind chill', these results support expectations that FID, time spent in flight and total time lost increase with body size (Fig. 3), and that response magnitude decreases under harsher environmental conditions (i.e. lower values of wind chill equivalent temperature; Fig. 4). There is also support for the expectation that responses vary both between sites and over time; a mixture of positive and negative coefficients indicates differences in birds' responses between sub-sites (Fig. 5) and negative coefficients for the relationships with 'winter day' indicate that response magnitude decreases as the season progresses, although the 95% confidence interval for FID includes zero. In addition to the between-site differences in response we also found within-site differences, with the negative coefficients for 'shore level' indicating a trend for greater response magnitudes when birds were feeding closer to the low water mark.

Inclusion of the two bnary variables indicating whether the specis was an Oystercatcher or a plover demonstrated additional between-species differences over and above the species mass relationship described. With positive and negative coefficients, respectively, plovers had larger magnitude responses than expected for their size; and Oystercatchers were relatively more tolerant, exhibiting shorter FIDs and spending less time in flight, although any relationship was poorly supported for total time lost (Table 3: relative importance = 0.267, and the 95% confidence interval includes zero).

Using our data on mean flight time and mean total time lost, we looked in more detail at the energetic consequences and the lost feeding opportunity costs of responding to disturbance for each species (Table 4). A 5% reduction in birds' daily available feeding time would be expected to result from responding to between 38 and 162 separate disturbance events (depending on species and tidal stage). The mean cost per individual flight response represented less than a tenth of a percent of each species' daily energy requirements: Fig. 6 shows there was no significant relationship between body mass and energetic cost of responding to a single disturbance when expressed in this way ($F_{1,675} = 0.565$, $P = 0.45$).

DISCUSSION

Our study provides data for 10 species of wader on FID, flight time and total time lost, along with associated energy costs, when birds flee an approaching pedestrian during the non-breeding season. Based on the findings of other studies from around the world (Urfi *et al.* 1996, Stillman & Goss-Custard 2002, Blumstein *et al.* 2003, 2005, Ikuta & Blumstein 2003, Glover *et al.* 2011, Lin *et al.* 2012), we identified four expectations about how birds' responses to disturbance vary: all four were supported by our results. Waders show a great deal of variation in their responses and much of that variation can be explained by species, body mass, environmental conditions and site differences on both small and larger spatial scales.

Relationships between response measures

With the exception of alert time, all of the time- and distance-related measures of response that we recorded were inter-correlated. This supports the expectation that disturbance avoidance behaviour depends on the relative costs of fleeing and remaining (Frid & Dill 2002): when starvation risk is lower, birds fly from further away (FID), flee further (longer flight time) and spend more time being vigilant (alert and latency time). The lack of a strong relationship between alert time and the other variables could be due to the fact that this was more difficult to record accurately, especially at greater distances. Alternatively, it may be that alert time is simply not a useful measure of response to disturbance in this case, since it is likely to be related to speed of approach, which was approximately constant in our experiments.

Between-species differences

Larger species had greater FIDs, spent more time in flight, and lost more feeding time overall than did smaller species. Møller *et al.* (2013) suggest that longer FIDs in larger species are due to the aerodynamic cost of large body size: this explanation may work for FID, but does not explain the additional body mass relationships with flight time and total time lost. Another explanation could be that since smaller birds generally spend a greater proportion of the available time feeding (Goss-Custard *et al.* 1977) and have proportionally lower body fat reserves upon which they can rely if they are unable to meet their daily intake requirements (Piersma & Vanbrederode 1990), they have less capacity to compensate for the costs of responding to disturbance. Indeed, the trade-off becomes apparent when the energetic cost per flight response is expressed as a percentage of the species' daily requirements, and the body mass relationship disappears.

Effect of environmental conditions

One prediction of the risk-disturbance hypothesis is that 'fleeing probability and FID increase when… environmental conditions are mild' (Frid & Dill 2002), because when birds are able to meet their daily energetic requirements easily, the balance in the trade-off between avoidance of starvation and predation shifts towards greater FIDs. We found this to be the case: birds also spent significantly longer in flight and lost more time overall when conditions were milder (i.e. higher wind chill equivalent temperatures).

Within- and between-site differences

The magnitude of all three measures of response varied on both small and larger spatial scales; birds responded less strongly to disturbance when feeding further from the low water mark and at the site with easiest access, closest proximity to residential areas, and highest frequency of potential disturbers. The site effect may thus be attributable to habituation. However, it is not possible to rule out alternative explanations without detailed knowledge of the differences between sites and individual birds, which we unfortunately do not have. For example, if birds feeding on high disturbance sites are in poorer condition they will prioritize feeding more than higher quality birds feeding on low disturbance sites. Or with any differences between sites in food availability and competitive ability of birds, birds feeding at lower quality sites would be expected to be more tolerant of disturbance because of a lack of alternatives (Frid & Dill 2002). Similar arguments and explanations relating to habitat quality and individual differences could also apply to the observed relationship with shore level. Whilst it was also beyond the scope of this study to collect detailed information on types and frequencies of human activities, we suggest that future studies consider using an objective measure of disturbance (such as number of visitors per day) which lends itself better to comparisons between sites and shore levels.

Costs of responding to disturbance

In addition to the energetic costs of flight, responding to disturbance reduces birds' available feeding time. Feeding intensity data (Goss-Custard *et al.* 1977) show that most birds on the Wash are likely to be able to cope with at least a 5% reduction, which we calculate would be caused by between 38 and 162 separate disturbance events per day depending on species and tidal stage. Curlew, Oystercatcher, Bar-tailed Godwit and Grey Plover may even be able to cope with a more serious reduction of 10% (caused by between 77 and 184 daily disturbance events). While objective data on visitor frequencies and distribution across the intertidal habitat in our study area are lacking, we believe from experience that current levels on most parts of the embayment are well below these values, especially at lower shore levels (in the order of around three visitors per week; M.G.Y. pers. obs.), though perhaps with the exception of the more easily accessible eastern area around site four on busier weekend days. As an example, the popular RSPB Titchwell Marsh Nature Reserve (7 km east of Site 4) receives on average 217 visitors per day (Visit England 2015), and as few as 10% of visitors might cause disturbance events (Liley & Fearnley 2012). We suggest, therefore, that wintering wader populations on the Wash are not currently significantly negatively impacted by human disturbance during the intertidal foraging period.

Further work to quantify disturbance of high tide roosts would complement this study and allow a more confident assessment of the overall impacts of disturbance (or lack thereof) on wintering waders on the Wash. As well as requiring suitable high tide refuges upon which to rest and preen (Rogers *et al.* 2006), some species are known to rely on supratidal habitats for foraging when they are not able to meet their energy requirements during the intertidal exposure period, for example due to increased requirements for thermoregulation during extreme cold weather or reduced intertidal exposure during storm events (Goss-Custard 1969, Milsom *et al.* 1998, Smart & Gill 2003). In such situations, the time and energy costs associated with responding to disturbance could be particularly problematic, especially if birds are forced to fly long distances to alternative roost or foraging sites (Rehfisch et al. 1996).

The data that we present here do not take account of the potential additional energetic costs of physiological responses (increased heart rate, stress hormones etc.) that may be incurred even when birds do not flee, and which can last longer than visible response behaviours (Ackerman *et al.* 2004, Elliott *et al.* 2016). More research is needed in this area; however Ackerman *et al.* (2004) found that the largest increase in heart rate occurs during the period immediately before and after initiation of flight, so we expect that that the contribution made by physiological changes not associated with flight is small compared to that due to the costs of flight and lost feeding time.

Conclusions

The few published studies with comparable data to ours show that there can be considerable between-estuary variation in responses (Smit & Visser 1993, Urfi *et al.* 1996, Fitzpatrick & Bouchez 1998, Laursen *et al.* 2005), as well as the within-estuary variation that we observed. We would therefore caution against making direct inferences from our data about the magnitude of birds' responses to disturbance at other sites if those sites do not also have large areas of intertidal habitat that are relatively inaccessible (for humans), where the width of the shore tends to be much greater than our largest observed FID, and where potentially disturbing activities are largely restricted to the upper shore. Similarly, given the influence of environmental conditions, it is important to note the temperature range over which experiments take place – for example, during an abnormally cold winter FIDs would be lower than those exhibited under more commonly experienced conditions. Our study on the Wash adds to the suite of available data from a range of sites, providing more options for informed comparisons with new sites.

Finally, greater emphasis is needed on recording time-related measures of responses to disturbance – to understand better the constraints on birds' time and energy budgets – rather than simply reporting FID. Doing so would also add value by providing the information necessary for parameterizing simulation models for understanding population-level impacts of different levels of disturbance and to predict the effectiveness of proposed management options (e.g. Blumstein *et al.* 2005, Stillman 2007).

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TABLES

Table 1. Mean, maximum and minimum responses to an approaching pedestrian for each species. Species are presented in order of decreasing body size. FID = flight initiation distance; FlightTime = time spent in flight; TotalTimeLost = time taken to resume feeding after becoming alert, flying and landing.

Species	**Mass(g)**	***n***	**FID(m)**				**FlightTime(s)**				**TotalTimeLost(s)**			
			mean	**SE**	**min**	**max**	**mean**	**SE**	**min**	**max**	**mean**	**SE**	**min**	**max**
Curlew (CU)	751	39	340.33	18.23	88	570	34.20	2.35	11.7	78	75.27	4.8	28	163
Oystercatcher (OC)	500	147	97.28	2.97	30	228	21.17	0.94	6	61	59.86	2.0	21	136
Bar-tailed Godwit (BA)	297	92	84.36	3.93	32	225	20.07	1.20	5	53	47.03	2.4	14	118
Grey Plover (GV)	215	55	132.27	6.81	35	251	22.82	1.65	6	56	58.22	3.4	19	154
Redshank (RK)	143	53	79.83	5.95	28	187	17.44	1.67	4	58	45.16	3.4	11	120
Knot (KN)	134	78	71.83	3.92	20	240	19.58	1.26	6	59	43.71	2.6	15	125
Turnstone (TT)	105	40	31.50	3.00	5	75	12.84	1.49	2	41	32.79	2.8	7	85
Ringed Plover (RP)	64	30	41.07	2.55	20	74	12.35	1.16	4	32	36.15	2.7	11	72
Sanderling (SS)	54	26	25.00	2.65	9	51	10.08	1.27	3	34	26.69	2.6	10	72
Dunlin (DN)	48	117	43.93	2.68	9	194	13.61	0.69	3	41	32.05	1.4	8	85

Table 2. Model selection tables – top five AIC$_c$-ranked models in each candidate set. Δ_i = difference in AIC$_c$ between model and top model. ω_i = Aikaike model weight. acc ω_i = cumulative model weight. SpMass = species mass (g); WindChill = wind chill equivalent temperature (˚C); IsItOC = Oystercatcher vs other species; IsItPlover = plover vs other species.

a) Global model = log(FID)~SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover+Site:WinterDay

	Candidate models	**adjR^2**	**AIC$_c$**	**Δ_i**	**ω_i**	**acc ω_i**
1	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover+Site:WinterDay	0.66561	971.232	0	0.916	0.916
2	SpMass+Site+ShoreLevel+WinterDay+IsItOC+IsItPlover+Site:WinterDay	0.66083	976.398	5.166	0.069	0.985
3	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover	0.65683	980.328	9.096	0.010	0.995
4	SpMass+Site+ShoreLevel+WinterDay+IsItOC+IsItPlover	0.65371	982.901	11.669	0.003	0.997
5	SpMass+Site+ShoreLevel+WindChill+IsItOC+IsItPlover	0.65325	983.581	12.348	0.0019	0.999

b) Global model = log(FlightTime)~SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover+Site:WinterDay

	Candidate models	**adjR^2**	**AIC$_c$**	**Δ_i**	**ω_i**	**acc ω_i**
1	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover+Site:WinterDay	0.29671	1107.022	0	0.892	0.892
2	SpMass+Site+ShoreLevel+WindChill+IsItOC+IsItPlover	0.28098	1112.770	5.749	0.050	0.943
3	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover	0.28106	1114.778	7.757	0.018	0.961
4	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItPlover+Site:WinterDay	0.28326	1115.192	8.170	0.015	0.976
5	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+Site:WinterDay	0.28268	1115.627	8.605	0.012	0.988

c) Global model = log(TotalTimeLost)~SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover+Site:WinterDay

	Candidate models	**adjR^2**	**AIC$_c$**	**Δ_i**	**ω_i**	**acc ω_i**
1	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItPlover+Site:WinterDay	0.39716	860.499	0	0.727	0.727
2	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover+Site:WinterDay	0.39724	862.515	2.016	0.265	0.993
3	SpMass+Site+ShoreLevel+WindChill+IsItPlover	0.37560	871.248	10.749	0.003	0.996
4	SpMass+Site+ShoreLevel+WindChill+IsItOC+IsItPlover	0.37590	873.077	12.578	0.001	0.998
5	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItPlover	0.37566	873.266	12.767	0.001	0.999

Table 3. Standardized parameter estimates and confidence intervals for eight potential predictors of waders' responses to disturbance. Dependent variables have been natural log transformed. See Tables 1 and 2 for parameter abbreviations.

		logFID[a]				**logFlightTime[a]**				**logTotalTimeLost[b]**				
	Predictor	**Estimate**	**SE**	**95% confidence interval**		**Estimate**	**SE**	**95% confidence interval**		**Relative importance**	**Estimate**	**SE**	**95% confidence interval**	
				Lower limit	**Upper limit**			**Lower limit**	**Upper limit**				**Lower limit**	**Upper limit**
	Intercept	4.430	0.035	4.361	4.499	2.915	0.039	2.839	2.991		3.796	0.032	3.732	3.859
1	SpMass	1.263	0.050	1.165	1.361	0.564	0.055	0.456	0.673	1	0.512	0.039	0.435	0.589
2	WindChill	0.109	0.041	0.029	0.189	0.163	0.045	0.075	0.252	1	0.163	0.038	0.089	0.237
3	ShoreLevel	-0.165	0.040	-0.244	-0.086	-0.164	0.044	-0.251	-0.077	1	-0.154	0.037	-0.226	-0.081
4	Site[c]									1				
	Site2-Maretail	-0.093	0.210	-0.506	0.320	-0.245	0.232	-0.702	0.211	-	-0.111	0.194	-0.492	0.270
	Site3-Breast Sand	0.098	0.126	-0.150	0.345	0.208	0.140	-0.066	0.482	-	0.237	0.116	0.009	0.464
	Site4-Stubborn Sand	-0.361	0.042	-0.445	-0.278	-0.257	0.047	-0.350	-0.165	-	-0.137	0.039	-0.214	-0.061
5	WinterDay	-0.101	0.073	-0.244	0.042	-0.229	0.080	-0.386	-0.071	1	-0.222	0.067	-0.354	-0.091
6	IsItOC[d]	-0.533	0.060	-0.651	-0.416	-0.211	0.066	-0.340	-0.081	0.267	0.004	0.029	-0.054	0.061
7	IsItPlover[d]	0.487	0.061	0.367	0.606	0.219	0.067	0.087	0.351	1	0.330	0.056	0.220	0.440
8	Site:WinterDay[e]									1				
	Site2-Maretail:WinterDay	-0.228	0.333	-0.882	0.426	-0.072	0.368	-0.795	0.652	-	-0.099	0.308	-0.703	0.504
	Site3-Breast Sand:WinterDay	-	-	-	-	-	-	-	-	-	0	0	0	0
	Site4-Stubborn Sand:WinterDay	0.298	0.087	0.127	0.469	0.324	0.096	0.135	0.514	-	0.321	0.080	0.163	0.479

[a] Based on top model only. [b] Results of model averaging top two models.

[c] Reference category is 'Site1-Wrangle Flats'. [d] Reference category is 'No'. [e] Reference category is 'Site1-Wrangle Flats:WinterDay'.

Table 4. An assessment of the time and energy costs incurred by waders per disturbance response, and the number of disturbances that would be expected to reduce available feeding time by 1%, 5% and 10%. See text for a description of the calculations involved. Data reproduced from Goss-Custard *et al.* (1977) give an indication of birds' likely capacity to compensate by extending their feeding time.

Species	Cost per flight response (kJ)[a]	Thermoneutral daily energy requirement (kJ)[b]	Cost per flight as % of daily intake requirement	Number of disturbances that would reduce available feeding time (day and night) by:			% available daylight time spent feeding in winter[c]
				1%	5%	10%	
Curlew	0.820	953.89	0.086	8-11	38-57	77-115	50-80
Oystercatcher	0.437	723.08	0.060	10-14	48-72	96-144	50-70
Bar-tailed Godwit	0.342	507.15	0.068	12-18	61-92	122-184	70-85
Grey Plover	0.345	406.99	0.085	10-15	49-74	99-148	70-80
Redshank	0.227	308.30	0.074	13-19	64-96	128-191	90-100
Knot	0.248	294.95	0.084	13-20	66-99	132-198	97-100
Turnstone	0.148	249.82	0.059	18-26	88-132	176-263	not recorded
Ringed Plover	0.118	178.32	0.066	16-24	80-120	159-239	not recorded
Sanderling	0.090	158.84	0.057	22-32	108-162	216-324	not recorded
Dunlin	0.117	146.59	0.080	18-27	90-135	180-270	95-100

[a] using cost per second of flight from Kvist *et al.* (2001)

[b] using Nagy *et al.*'s (1999) allometric equation

[c] as observed by Goss-Custard *et al.* (1977)

FIGURE LEGENDS

Figure 1. The intertidal areas of the Wash on which disturbance observations were made in winter and early spring of 2002/03, 2003/04 and 2004/05. Site 1-Wrangle; Site 2-Maretail; Site 3-Breast Sand; Site 4-Stubborn Sand. Reproduced from Ordnance Survey map data by permission of Ordnance Survey © Crown copyright 2013.

Figure 2. Correlation matrix for all recorded measures of birds' responses to experimental disturbance. Bivariate scatterplots are presented with a fitted line, and Spearman's rank correlation coefficients, along with stars to indicate significance level.

Significance codes: '***' 0.001 '**' 0.01 '*' 0.05.

Figure 3. Relationship between species mass and three measures of responses to disturbance. Dependent variables have been $\log_e$-transformed.

Figure 4. Relationships between wind chill equivalent temperature and measures of response to disturbance, adjusted relative to the mean response of each species. Regression lines with 95% confidence intervals.

Figure 5. Variation between sub-sites in birds' responses to disturbance, adjusted relative to the mean response of each species. Site codes: 1 = Wrangle; 2 = Maretail; 3 = Breast Sand; 4 = Stubborn Sand.

Figure 6. Relationship between species body mass and energetic costs of flight in response to disturbance.

FIGURES

Figure 1.

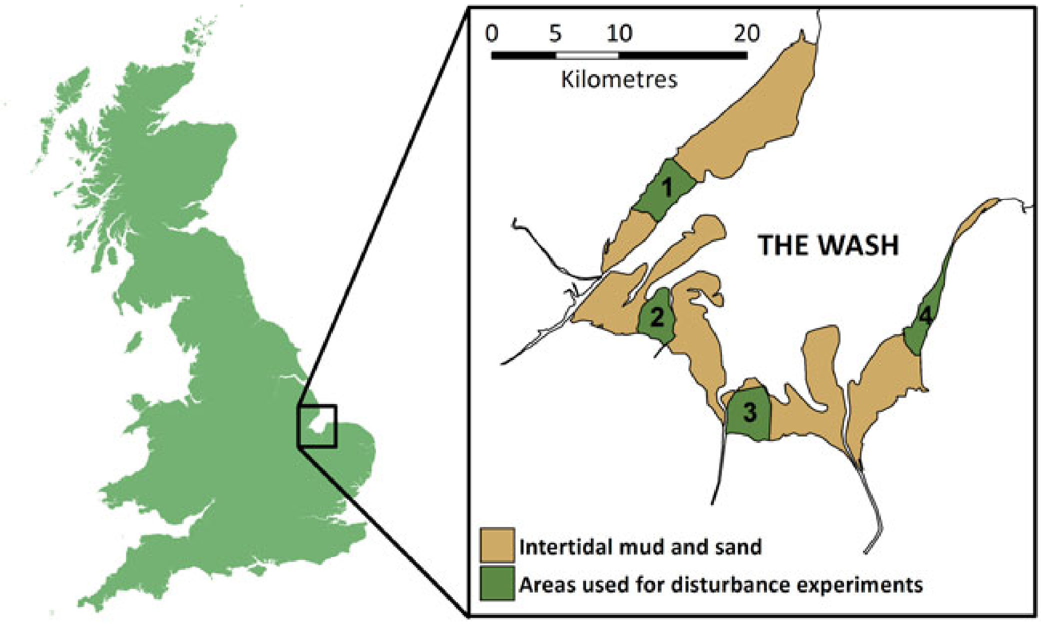

Figure 2.

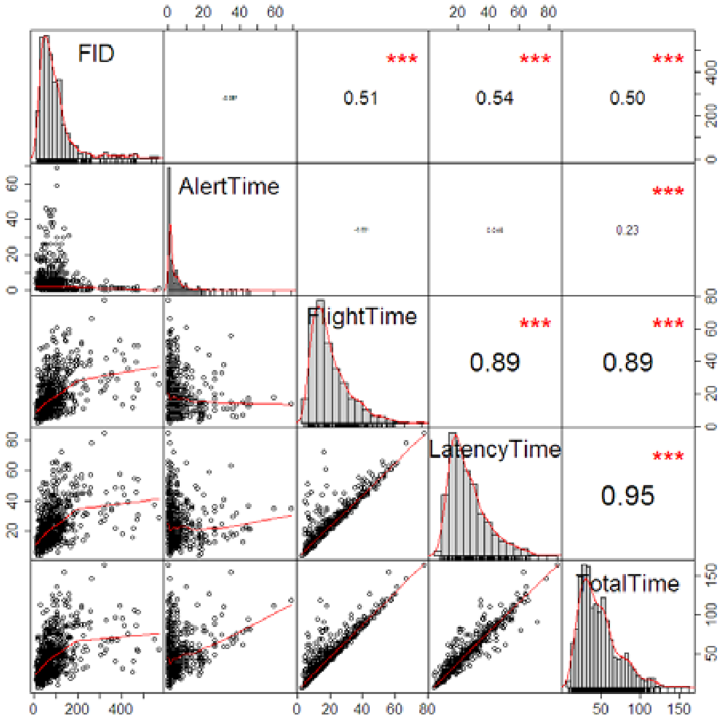

Figure 3.

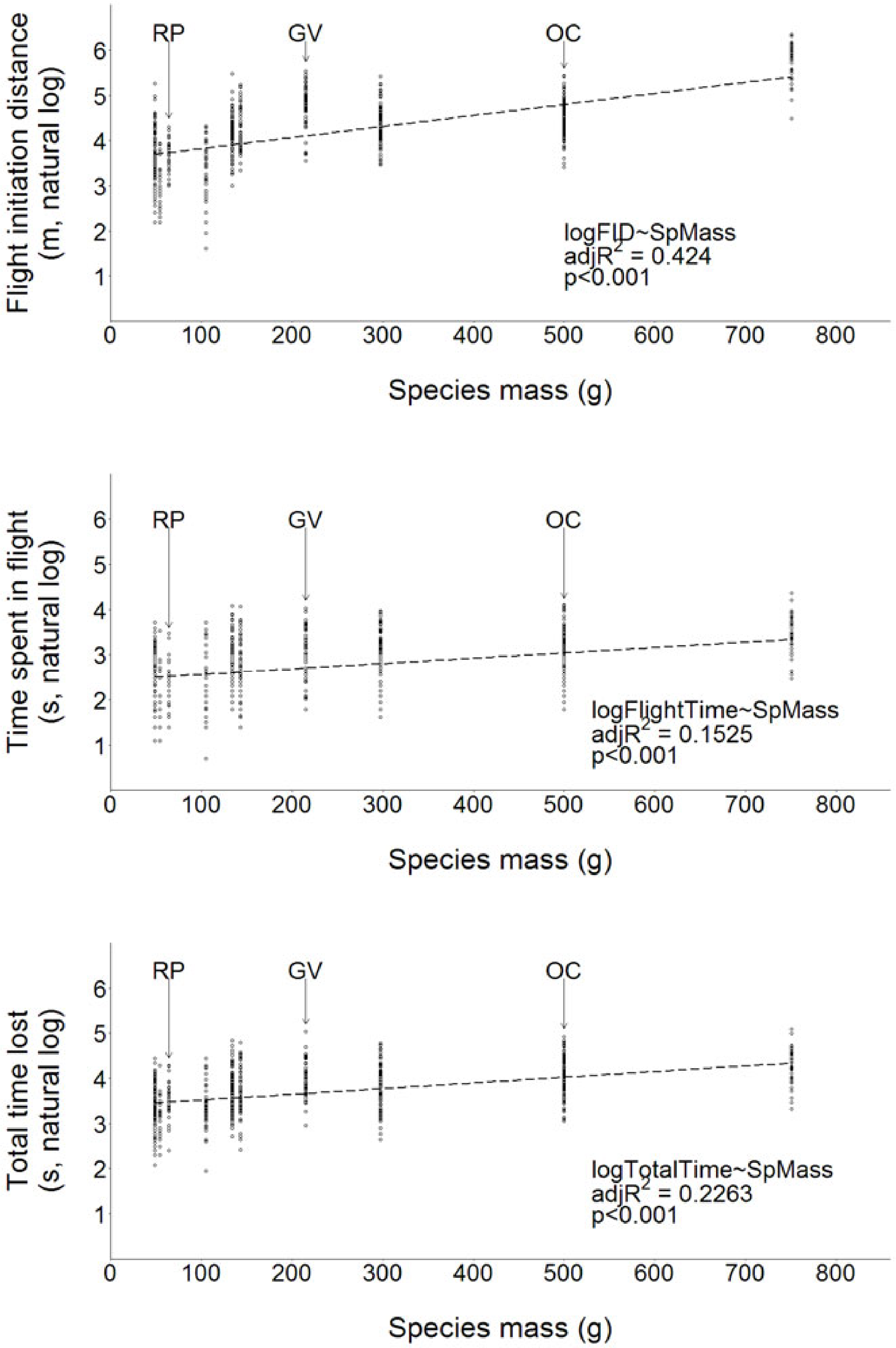
RP
GV
OC
Flight initiation distance (m, natural log)
1
2
3
4
5
6
0
100
200
300
400
500
600
700
800
Species mass (g)
logFID~SpMass
adjR^2 = 0.424
p<0.001
RP
GV
OC
Time spent in flight (s, natural log)
1
2
3
4
5
6
0
100
200
300
400
500
600
700
800
Species mass (g)
logFlightTime~SpMass
adjR^2 = 0.1525
p<0.001
RP
GV
OC
Total time lost (s, natural log)
1
2
3
4
5
6
0
100
200
300
400
500
600
700
800
Species mass (g)
logTotalTime~SpMass
adjR^2 = 0.2263
p<0.001

Figure 4.

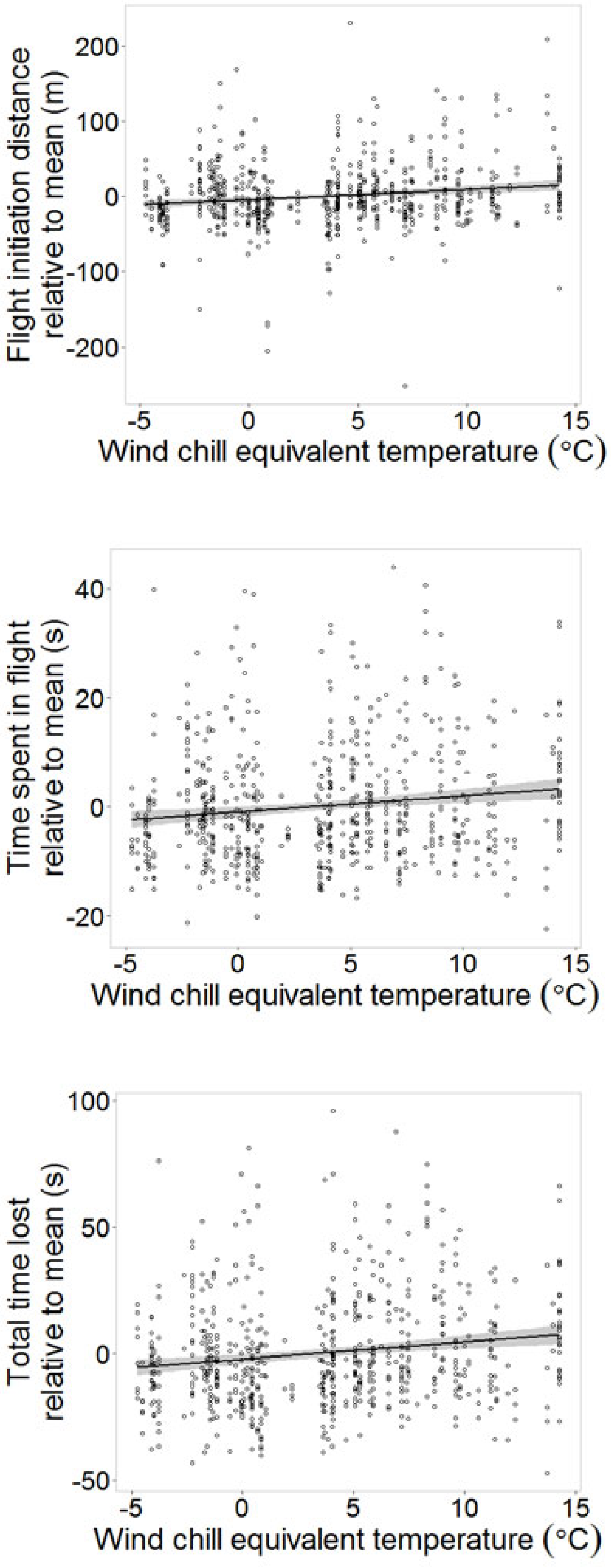
Flight initiation distance relative to mean (m)
200
100
0
-100
-200
-5
0
5
10
15
Wind chill equivalent temperature (°C)
Time spent in flight relative to mean (s)
40
20
0
-20
-5
0
5
10
15
Wind chill equivalent temperature (°C)
Total time lost relative to mean (s)
100
50
0
-50
-5
0
5
10
15
Wind chill equivalent temperature (°C)

Figure 5.

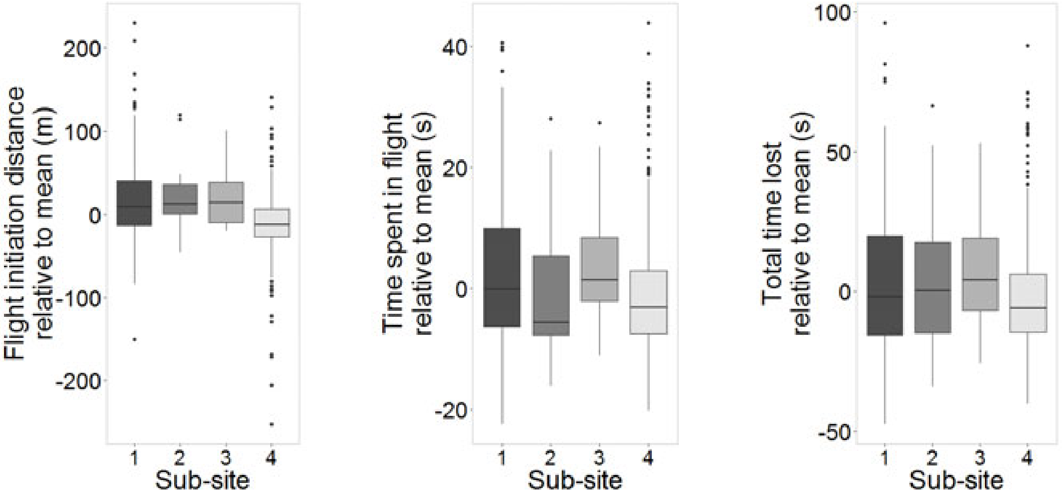

Figure 6.