

Research

Why time-limited individuals can make populations more vulnerable to disturbance

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Oikos

130: 637–651, 2021

doi: 10.1111/oik.08031

Subject Editor: Silke Bauer

Editor-in-Chief: Dries Bonte

Accepted 13 January 2021



Individual variation in disturbance vulnerability (i.e. the likelihood that disturbance negatively affects an individual's fitness) can affect how disturbance impacts animal populations, as even at low disturbance levels some individuals could be severely affected and die. Individual variation in vulnerability can arise due to different responses to disturbance. We propose a new hypothesis that even when individuals respond similarly to disturbance, time-limited individuals are more at risk that their condition deteriorates since they have limited ability to extend their foraging time to compensate for disturbance. We investigate this 'time-limitation hypothesis' both empirically and mathematically by studying how individuals that differ in their average foraging time (presumably due to differences in foraging efficiency) are affected by disturbance. We used tracking data of 22 wintering Eurasian oystercatchers *Haematopus ostralegus* to compare time budgets between disturbed and undisturbed tidal periods. In three tidal periods with severe disturbance by transport airplanes, more than a third of the variation in additional flight time and foraging time loss was explained by individual differences. Inefficient individuals that foraged longer in undisturbed tidal periods experienced higher costs in disturbed tidal periods, since they lost more foraging time. We next used an analytical energy balance model to study how time-limited individuals differed in their maximum disturbance thresholds. Both our theoretical model and empirical study suggest that inefficient individuals in a time-limited environment may be unable to increase their foraging time to compensate for the effects of disturbance. Consequently, the magnitude of individual variation in time budgets strongly determines what proportion of the population is at risk that their condition deteriorates due to disturbance. Our hypothesis implies that, when assessing disturbance effects on a population, it is not only important to consider individual variation in disturbance responses, but also variation in time budgets that determine the consequences of disturbance.

Key words: disturbance, foraging time, individual variation, population, recreation ecology, shorebirds



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Introduction

The increasing number of human activities in nature is of concern for policy makers, since the resulting disturbance can heavily affect wildlife populations (Pirrotta et al. 2018). Human disturbances can elicit flight responses in wildlife (Stankowich 2008), which are often energetically costly and may have additional costs such as a loss of foraging time (Houston et al. 2012) or reduced intake rate (Rutten et al. 2010). If individuals are unable to compensate for the costs of disturbance, this can lead to deteriorating body condition (Amo et al. 2006), lower survival probabilities (Blanc et al. 2006, Goss-Custard et al. 2006), reduced reproduction (White and Thurow 1985) and thus lower fitness. Individual variation in disturbance vulnerability (i.e. the likelihood that disturbance will reduce an individual's fitness) can alter the effects of disturbance on wildlife populations. In populations where individuals vary in their disturbance vulnerability, the most vulnerable individuals are expected to suffer higher energetic losses when disturbance occurs and their condition may be affected even under low levels of disturbance (Rodríguez-Prieto et al. 2010, Griffin et al. 2017).

The conventional way of thinking about how individuals can vary in their disturbance vulnerability is through variation in their disturbance sensitivity, determining how strong they respond to disturbance ('disturbance sensitivity hypothesis' in Fig. 1). In experimental settings individuals differ consistently in their response to stressful stimuli that resemble disturbances, for example individual chaffinches showed consistent responses to model hawks (Quinn and Cresswell 2005). In the field, individual consistency in disturbance responses (often measured as the consistency in flight initiation distances) is also observed, but the extent varies strongly among species (Thiel et al. 2007, Ellenberg et al. 2009, Carrete and Tella 2013, DeVault et al. 2017). Individual variation in disturbance responses can be caused by personality (Ellenberg et al. 2009) and sex (Thiel et al. 2007, Ellenberg et al. 2009), but can also arise due to habituation (Runyan and Blumstein 2004, Ellenberg et al. 2009, Rodríguez-Prieto et al. 2010).

We propose a second pathway via which individual variation can affect how vulnerable individuals are to disturbance: differences in their ability to compensate for disturbance, for example by increasing foraging time (Urfi et al. 1996, Blanc et al. 2006, Houston et al. 2012), may also cause individual variation in disturbance vulnerability, even when disturbance responses are similar. In many populations, individuals differ in their foraging time budgets and thus in how time-limited they are (Pelletier and Festa-Bianchet 2004, Hamel and Côté 2008, Daunt et al. 2014, van der Kolk et al. 2020a). Time budget differences often arise from individual variation in foraging efficiency (Stillman et al. 2000, Cresswell et al. 2001, Lescroël et al. 2010). We hypothesize that time-limited individuals are less able to cope with disturbance than others since they have limited time to compensate

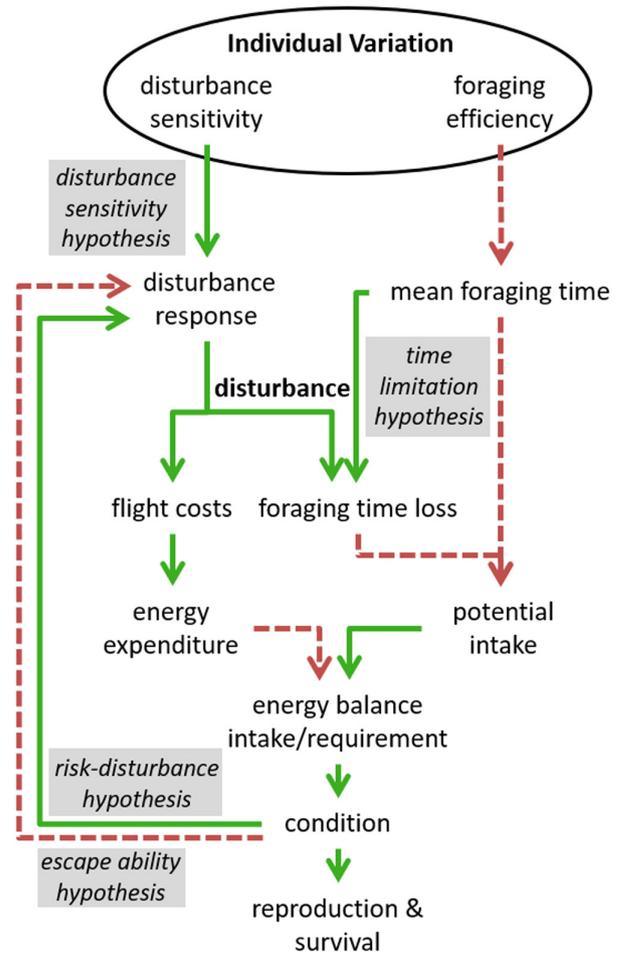


Figure 1. Proposed pathways via which variation among individuals in mean foraging time can affect how disturbance impacts condition. Green continuous arrows and red dashed arrows indicate positive and negative relationships, respectively. Four hypotheses discussed in the main text on how individual differences can alter disturbance impacts are marked inside grey boxes. The 'risk-disturbance hypothesis' and 'escape ability hypothesis' are explained in the discussion. Note that for simplicity, not all processes influencing disturbance responses (e.g. habituation) are included in the figure, as such processes are expected to be additive and not altering the hypothesized mechanisms.

for disturbance ('time-limitation hypothesis' in Fig. 1). Previous studies have shown that disturbance at foraging grounds has a larger predicted impact than disturbance outside foraging grounds, when animals could more easily compensate for disturbance costs (Pirrotta et al. 2019). However, no studies have explicitly quantified how disturbance costs differ among individuals that vary in their time budgets.

If for time-limited individuals their condition is more likely to deteriorate upon disturbance, then individual variation in time budgets is important to consider when quantifying disturbance impacts on a population. Many models have been developed to quantify disturbance impacts, ranging from relatively simple analytical models

(Houston et al. 2012), to complex individual-based models (Stillman and Goss-Custard 2010). Several modelling frameworks would allow to explore how individual variation could affect estimates of population impacts of disturbance (Stillman and Goss-Custard 2010, Pirotta et al. 2018), but no study has done this explicitly. A challenge therefore is to develop and parameterize such models with empirical data, in order to quantitatively assess the impact of individual variation in time budgets and thereby evaluate the importance of including such heterogeneity in population models.

Eurasian oystercatchers *Haematopus ostralegus* are a relevant model system to study the time-limitation hypothesis, as individuals vary greatly in their foraging efficiency (Goss-Custard and Durell 1983, Caldow et al. 1999) and foraging time (van der Kolk et al. 2020a), while they are strongly time constrained by the limited accessibility of intertidal feeding grounds (Zwarts et al. 1996). In fact, the average foraging time of an individual oystercatcher can be interpreted as a measure of the effort required to meet their energy requirements, and thus as a measure of how time-limited an individual is. Oystercatchers that forage on average shorter ('efficient foragers'; Glossary of terms used in Supporting information) forage likely more efficiently or have lower energetic costs. In support, individuals that forage shorter have a higher apparent winter survival in comparison to inefficient individuals that forage on average longer (van der Kolk et al. 2020a). Another reason why oystercatchers are a relevant model system is that they live in coastal areas that are also heavily utilized for a wide range of human activities that cause frequent disturbance (van der Kolk et al. 2020b). Disturbance is one of the potential causes of the current decline of the oystercatcher population that is insufficiently studied (van de Pol et al. 2014).

Here, we illustrate the potential implications of our time-limitation hypothesis by empirically and mathematically studying whether and how time-limited individuals are differently affected by disturbance than less time-limited individuals. We first use GPS-tracking of oystercatchers to assess individual variation in immediate flight responses and foraging time losses following three different disturbances by transport airplanes, which are rare but elicit strong flight responses (van der Kolk et al. 2020b). We test whether an individual's average foraging time in undisturbed tidal periods (a measure for how efficient individuals are) affects additional flight time and foraging time loss in disturbed tidal period. Next, we tested whether individuals compensated for disturbance costs in tidal periods following the disturbance. We then expanded and parameterized the analytical model developed by Houston et al. (2012), which predicts the maximum time animals can be disturbed while still meeting their energy requirements. We used the model to quantify disturbance thresholds for individuals that vary in their time budget, and illustrate how such variation could affect population impacts of disturbance for wintering oystercatchers, considering the observed distribution of average foraging times in the population at our study site.

Methods

Study system

Oystercatchers are long-lived shorebirds that winter in large numbers in the Wadden Sea. They forage on intertidal flats on shellfish (e.g. *Cerastoderma edule* and *Mytilus edulis*) and soft-bodied prey (e.g. *Polychaeta*) during low tide. During high tide, birds roost or can forage on alternative feeding areas where intake rates are lower, for example inland fields (Goss-Custard and Durell 1983). Most individuals show high site fidelity and return each winter to the same site. Most birds arrive in the winter areas in July and depart to the breeding areas in February.

The field study was conducted during the non-breeding season in the western Dutch Wadden Sea, on the barrier island Vlieland. The western half of the island is used as a military air force training area. Jets, helicopters and small civil airplanes frequently occur in the study area, but their disturbance impact is normally low, eliciting no or relatively short flight responses. In contrast, low-flying transport airplanes occur rarely (three times per year in 2017–2019) but evoke strong flight responses likely because of their exceptionally large size, even when the transport airplane flies far away (10 km) from the birds (van der Kolk et al. 2020b).

Data collection

Oystercatcher GPS data

Tidal foraging time and flight time of oystercatchers was quantified using solar powered UvA-BiTS GPS trackers (Bouten et al. 2013). Forty oystercatchers were equipped with GPS trackers on the Vliehors (53°23'N, 04°93'E): twenty non-local breeders were caught with mist nets in winter (December 2016–January 2017) and 20 local breeders were caught on the nest (May–July 2017). GPS fixes were taken in 5- or 60-min intervals and a 0.35 s sample (seven measurements) of a 20 Hz tri-axial accelerometer was taken at least every 10 min. We used a training dataset containing annotated accelerometer samples to train a Random Forest model (Breiman 2001) to classify foraging, flying and other (inactive and preening) behaviour (details in van der Kolk et al. 2020a). Using an independent testing dataset with 8178 samples, we confirmed the high prediction accuracy of the Random Forest model (precision: forage 98%, fly 98%, other 100%; recall: forage 99%, fly 95%, other 99%; Supporting information).

Aircraft and environmental data

Timings of transport airplane exercises were provided by the Royal Netherlands Air Force. The exact times when minimum and maximum water levels occurred at low and high tide, respectively, and water heights for every 10 min were provided for Vlieland harbour (53°29'5"N, 05°09'1"E) by Rijkswaterstaat (2019). A tidal period was defined as the period between two consecutive high tide maxima at Vlieland harbour (Rijkswaterstaat 2019). Each tidal period

thus included a single low tide and was approximately 12.4 h long. Timings of sunrise and sunset were obtained via the *sunrise.set* function in the *StreamMetabolism* package in R. Daily moon illumination values were obtained via the *lunar.illumination* function in the *lunar* package in R.

Empirical study: individual variation in additional flight time and foraging time loss

Data of GPS-tagged oystercatchers were used to empirically study how individuals (which varied in their average foraging time in undisturbed tidal periods) altered flight time and foraging time in response to disturbances. We first compared flight time and foraging time between disturbed tidal periods and undisturbed tidal periods. We then quantified whether individuals compensated for costs of disturbance by increasing their foraging time in subsequent tidal periods. All analyses were performed in R ver. 3.5.3 (<www.r-project.org>).

We studied three disturbed tidal periods on 9, 10 and 16 August 2017 (henceforth event 1, 2 and 3 respectively) with large disturbances by one Lockheed C-130 Hercules transport aircraft. The aircraft entered the study area 3, 5 and 6.5 h before low tide, respectively, and circled for approximately one hour in the study area (Supporting information). During the first two disturbance events, all GPS tagged oystercatchers present on the Vliehors were disturbed (i.e. took flight), whereas during the third event a subset of the birds were disturbed, which we confirmed by visual inspection of the GPS data. We collected data from 18 individuals during all three disturbed tidal periods, three individuals during two disturbed tidal periods and one individual during one disturbed tidal period ($n_{\text{bird}}=22$, $n_{\text{bird-disturbance}}=61$; Supporting information). Data from another 18 oystercatchers was not available because the tracker malfunctioned, the individual had died or the individual was outside the study area.

Tidal time budgets: flight time and foraging time

The total time spent flying, foraging or other behaviour was quantified for each bird for each tidal period. First, each annotated accelerometer measurement within a tidal period was weighed based on the time interval until the next annotated accelerometer measurement. This time interval was typically ten minutes, the default interval at which GPS trackers took accelerometer measurements, but sometimes longer if an accelerometer measurement was interrupted and could not be annotated. The time intervals from all annotated flight behaviours or annotated foraging behaviours within one tidal period were then summed to acquire the total tidal flight time or tidal foraging time in hours, respectively. To ensure sufficient accuracy, tidal flight and foraging time estimates were omitted if there were less than 70 behavioural measurements or if the maximum interval exceeded 20 min (van der Kolk et al. 2020a for more details).

Average foraging time

The average foraging time in undisturbed tidal periods and standard error was calculated for each individual over the

whole winter season (1 August 2017–31 March 2018). The tidal foraging time of 17 out of 22 individuals was measured during at least 100 tidal periods in this period (Supporting information). We used the average foraging time as explanatory variable in statistical models estimating the effect of disturbance on flight time and foraging time.

Effects of disturbance on flight time and foraging time

Linear mixed effects models were used to analyse the effect of disturbance on tidal flight time and tidal foraging time. Tidal flight time and tidal foraging time between 1 August 2017 and 15 September 2017 were used as response variables. The model structure consisted of two parts (Eq. 1): 1) variables controlling for environmental conditions were estimated for all tidal periods. 2) Variables that were only estimated for disturbed tidal periods (the last part in Eq. 1 between parentheses). This structure was needed since we included average foraging time as explanatory variable for changes in flight or foraging time in disturbed tidal periods, but not for undisturbed tidal periods. Equation 1 shows the fixed structure of the model (for simplicity random effects are only described in the text).

$$\beta_0 + \beta_1 N + \beta_2 M + \beta_3 NM + \beta_4 A + D \times (\beta_5 E_1 + \beta_6 E_2 + \beta_7 E_3 + \beta_8 E_1 F + \beta_9 E_2 F + \beta_{10} E_3 F + \beta_{11} B) \quad (1)$$

where

β_0 – β_{11} = parameters estimated by the model

N = proportion of night-time (time between sunset and sunrise)

M = proportion of moon visibility (0 = new moon, 1 = full moon)

A = proportion of time water levels is below –10 cm Amsterdam Ordnance Datum and tidal flats are accessible for feeding

D = binary variable indicating whether it is a disturbed tidal period

E_1 – E_3 = binary variables indicating whether tidal period is disturbance event number 1, 2 or 3

F = average foraging time of an individual in undisturbed tidal periods

B = binary variable indicating whether an individual is a local breeder

For the first part of the model controlling for environmental conditions, the interaction between night (N) and moon stage (M) and intertidal flat accessibility (A) were used as explanatory variables (all mean-centred). Those tidal characteristics are important determinants of tidal foraging time (van der Kolk et al. 2020a) and were included in the model as confounding factors that affect flight time and foraging time. Bird individual was added as random intercept, and random slopes of night, moon stage and intertidal flat accessibility were fitted for individual birds as well, since individuals differ in how much foraging time is allocated to tidal periods with different environmental characteristics (e.g. some individuals

allocate more foraging time to day-time tidal periods than others; van der Kolk et al. 2020a).

For the second part of the model, a binary variable (D) was introduced such that the following variables were only estimated for disturbed tidal periods. For each of the three disturbance events (E_1 – E_3), the disturbance effect in interaction with average foraging time (F ; individual mean centred) was estimated. We expected that birds that had been breeding locally may respond less, given that they frequently encounter aircraft also in the breeding season. Breeding location of each individual was therefore included as an additional explanatory binary variable (B ; local breeder in study area, $n=14$ birds; non-local breeder, $n=8$ birds; Supporting information) for all disturbed tidal periods. We checked whether increased flight time and foraging time loss in disturbed tidal periods were affected by the distance at which birds were positioned from the centre of the military training area prior to disturbance by including it as an additional fixed effect in the disturbance part of the model. Since this effect was non-significant, this variable was not retained in the final models. We used the *nlme* function in R to estimate all twelve parameter values (β_0 – β_{11}) in the model. Visual inspection confirmed that the residuals of both models approximated a normal distribution (Supporting information).

To explore whether uncertainty in the average foraging time estimates affected the model estimates, we used bootstrapping to identify 95% confidence intervals of model estimates and p-values, by extracting average foraging times for each individual from a normal distribution based on their means and standard error ($n=1000$ iterations). We confirmed by visual inspection that foraging time estimates within individuals approached normal distributions. All parameters were robust to the uncertainty in individual average foraging times, except for the fixed slope of average foraging time on flight time during the 2nd disturbed tidal period (Supporting information). The interpretation of our results did, however, not depend on this one parameter being significant or not.

To quantify how consistent individuals' responses to disturbance were, 'additional flight time' (actual flight time minus expected flight time without disturbance) and 'foraging time loss' were calculated (expected foraging time minus actual foraging time). Expected flight and foraging times were predicted using only the estimates of the environmental variables in the models, reflecting flight and foraging times expected under these environmental conditions without any effect of disturbance. We then used additional flight time and foraging time loss as response variables in linear mixed models, including event number (1, 2 or 3) as explanatory factor and bird individual as random intercept. The proportion of variation explained by bird individual was calculated using the intra-class correlation coefficient (Nakagawa and Schielzeth 2010). We tested whether there was a (Pearson) correlation between additional flight time and foraging time loss.

Foraging time compensation after disturbance

We analysed whether birds compensated for disturbance by increasing their foraging time in tidal periods following

disturbed tidal periods. Additionally, we analysed whether an increase in foraging time was related to the costs of disturbance. For this purpose, we first calculated change in foraging time for these compensatory tidal periods (actual foraging time minus expected foraging time). The predicted required foraging time to compensate for disturbance (i.e. the total disturbance costs) was then calculated for each bird for each disturbed tidal period based on foraging time loss and the predicted foraging time required to compensate for flight costs:

$$\text{For}_{\text{comp}} = \text{For}_{\text{loss}} \frac{\text{Fly}_{\text{time}} \times \text{Fly}_{\text{cost}}}{\frac{\text{DEE}}{\text{For}_{\text{day}}}} \quad (2)$$

For_{comp} = change in foraging time required to compensate for disturbance costs (h)

For_{loss} = foraging time loss in disturbed tidal period (h)

Fly_{time} = additional flight time in disturbed tidal period (h)

Fly_{cost} = energetic costs of flight (kJ h^{-1})

DEE = daily energy expenditure (kJ)

For_{day} = daily foraging time of an individual (h)

To estimate the foraging time needed to compensate for flight costs, we assumed that flight costs (Fly_{cost}) were 135 kJ h^{-1} and daily energy expenditure (DEE) 734 kJ for all birds (Zwarts et al. 1996, Pennycuik 2008). We weighted flight costs by how efficient individuals acquired energy. Hence, flight costs were divided by the estimated individual foraging efficiency in kJ h^{-1} by dividing daily energy expenditure by the daily foraging time (where daily foraging time is twice the average tidal foraging time, provided that every day has approximately two tidal periods).

We used linear mixed models to determine whether change in foraging time in compensatory tidal periods was related to the required foraging time to compensate for disturbance costs. An interaction between disturbance event and required foraging time was added to the model. Bird identity was included as random intercept. We used two separate models to analyse compensation at two temporal scales: one and six tidal periods (roughly half a day and three days, respectively) following the disturbed tidal period. Since events 1 and 2 occurred on consecutive days, we merged their data for the analysis over six tidal periods.

Mathematical modelling of disturbance costs as a function of foraging time

We expanded the general analytical model developed by Houston et al. (2012) to assess how disturbance impacts the energy and time budget of individuals that vary in their foraging efficiency. The model of Houston et al. (2012) predicts the time an animal needs to forage in order to balance its energy budget over one day, while it is disturbed while foraging. From their model disturbance thresholds can be derived above which an animal cannot compensate for disturbance anymore and its condition will deteriorate. We modified

the model of Houston et al. in two ways. First, we explicitly divided the time budget into time during which an animal can forage and time that is not available for foraging. This allowed us to estimate disturbance thresholds for animals for which foraging time is restricted, for example by daylight or tidal patterns. Second, we modelled disturbance as a fixed duration instead of a proportion of the foraging time, to reflect that individuals can be disturbed independently of their behaviour. We do differentiate between disturbance during time when animals can forage (e.g. low tide) and time not available for foraging (e.g. high tide). This is necessary since only disturbance during available foraging time limits the potential maximum amount of time that can be spent foraging. Overall, our expansion of the Houston et al. model allowed us to investigate the differential compensation potential to disturbance in time-limited individuals and consequently quantify how individual variation in time budgets affects the proportion of the population in which condition may deteriorate.

In our model, the energy budget is balanced over a certain period (T), for example one day or one tidal period. The model aim is to find the balance between the foraging time required to fulfil energy needs and the potentially available foraging time. The required foraging time depends on total energy requirements and foraging energy intake rate:

$$F_{\text{req}} = \frac{R}{g} \quad (3)$$

F_{req} = time that needs to be spent foraging to meet energy requirements (h)

R = total energy requirements (kJ)

g = foraging energy intake rate (kJ h⁻¹)

The energy requirements are determined by an individual's normal energy expenditure and additional costs due to disturbance. Disturbance can take place during time that is available for foraging (D_F) or during non-foraging time (D_N), and both cause increased energy expenditure:

$$R = (T - D_F - D_N) \times E_m + (D_F + D_N) \times E_d \quad (4)$$

T = time over which energy budget is balanced (h)

D_F = time disturbed during time that is available for foraging (h)

D_N = time disturbed during non-foraging time (h)

E_m = average energy expenditure throughout T (kJ h⁻¹)

E_d = energy expenditure during disturbance (kJ h⁻¹)

The potential foraging time F_{pot} is determined by the maximum time that can be spent foraging (e.g. the duration of low tide) and the reduction of that time due to disturbance (D_F):

$$F_{\text{pot}} = F_{\text{max}} - D_F \quad (5)$$

F_{max} = Maximum available foraging time when there is no disturbance (h)

By comparing F_{req} and F_{pot} it can be predicted whether an individual can forage sufficiently to meet its energy requirements, or whether it has a foraging time shortage leading to a reduced condition:

$$\text{if } F_{\text{pot}} \geq F_{\text{req}} : F_{\text{real}} = F_{\text{req}} \quad \text{Sufficient uptake to meet energy requirements} \quad (6)$$

$$\text{if } F_{\text{pot}} < F_{\text{req}} : F_{\text{real}} = F_{\text{pot}} \quad \text{Insufficient uptake and at risk of condition deterioration}$$

F_{real} = actual (realized) foraging time

From Eq. 3–6, we derived formulas of disturbance thresholds, for D_F (D_{F_crit} , assuming $D_N = 0$ h, Eq. S7 in the Supporting information), for D_N (D_{N_crit} , assuming $D_F = 0$ h, Eq. S8 in the Supporting information) and for D_F and D_N combined (D_{crit} , assuming $D_F = D_N$, Eq. S9 in the Supporting information). These disturbance thresholds represent the maximum duration of disturbance at which an individual can still fulfil its energy requirements (see the Supporting information for a more comprehensive model description).

The model is generally relevant for any species in which the available foraging time is restricted, but we parameterized and applied the model to wintering oystercatchers to predict disturbance thresholds and energetic losses due to disturbance. In the model, oystercatchers balance their energy requirements over one tidal period ($T = 12.4$ h), of which only the low tide period could be spent foraging ($F_{\text{max}} = 6.5$ h). Mean energy expenditure ($E_m = 30.6$ kJ h⁻¹) was derived from daily energy expenditure for an individual with a body mass of 550 g (Zwarts et al. 1996). During disturbance, birds typically take flight but also spend time being vigilant, which may not be energetically costly but further reduces the available foraging time. Energy expenditure during disturbance (E_d) was therefore composed of flight costs ($E_f = 135$ kJ h⁻¹; Pennycuik 2008) multiplied by the proportion of disturbed time spent in flight ($f = 0.333$, Collop et al. 2016), and energetic costs of being vigilant (E_v) multiplied by the proportion of time spent vigilant while disturbed (Eq. 7). For oystercatchers we lack data on the energetic cost of being vigilant and therefore assumed that $E_v = E_m$, as vigilance behaviour requires no additional physical activity.

$$E_d = f \times E_f + (1 - f) \times E_v \quad (7)$$

To explore the consequences of disturbance for individuals with different foraging times, we assumed a linear relationship between the foraging energy intake rate g and the average foraging time of an individual. For individuals that ranged in their foraging time from 3.0–6.5 h per tidal period (equivalent to $g = 58$ – 126 kJ h⁻¹ when assuming $E_m = 30.6$ kJ h⁻¹

and $T=12.4$ h), we derived disturbance thresholds for low tide disturbance, high tide disturbance and combined low and high tide disturbance. To assess impacts of disturbance on individuals with varying time budgets, we calculated the realized foraging times (F_{real}) in one tidal period under six disturbance scenarios: one, two or three hours of disturbance during either low tide or high tide. If birds were unable to fulfil their energy requirements, we calculated the energetic loss (E_{loss}) in one tidal period (Supporting information).

Finally, we used the observed distribution of foraging times of wintering oystercatchers at our study site to illustrate how variation in time budgets could impact the effect of disturbance on a population. We used GPS data to determine average foraging times of 85 individuals between 2016 and 2019 (Supporting information and van der Kolk et al. 2020a). We estimated the proportion of the population for which condition may deteriorate as a function of disturbance duration (in h per tidal period), by comparing disturbance levels with the population distribution of critical disturbance thresholds (D_{crit}). This assumes that imposed disturbance levels reflect

the average disturbance level over an extended period. To show how populations can be differentially impacted by heterogeneity in time budget, we repeated the calculations for simulated populations in which we increased or decreased the amount of observed individual variability in average foraging time by 10%.

Results

Empirical flight and foraging time responses to disturbance

Individual differences in disturbance responses

Disturbance by transport airplanes caused an increase in tidal flight time and a reduction in tidal foraging time. Flight time increased on average more than half an hour in the first two disturbed tidal periods and by about 15 min in the third disturbed tidal period (Fig. 2a, Table 1). Foraging time was on average significantly reduced by 1.7 h and 1.3 h in the first

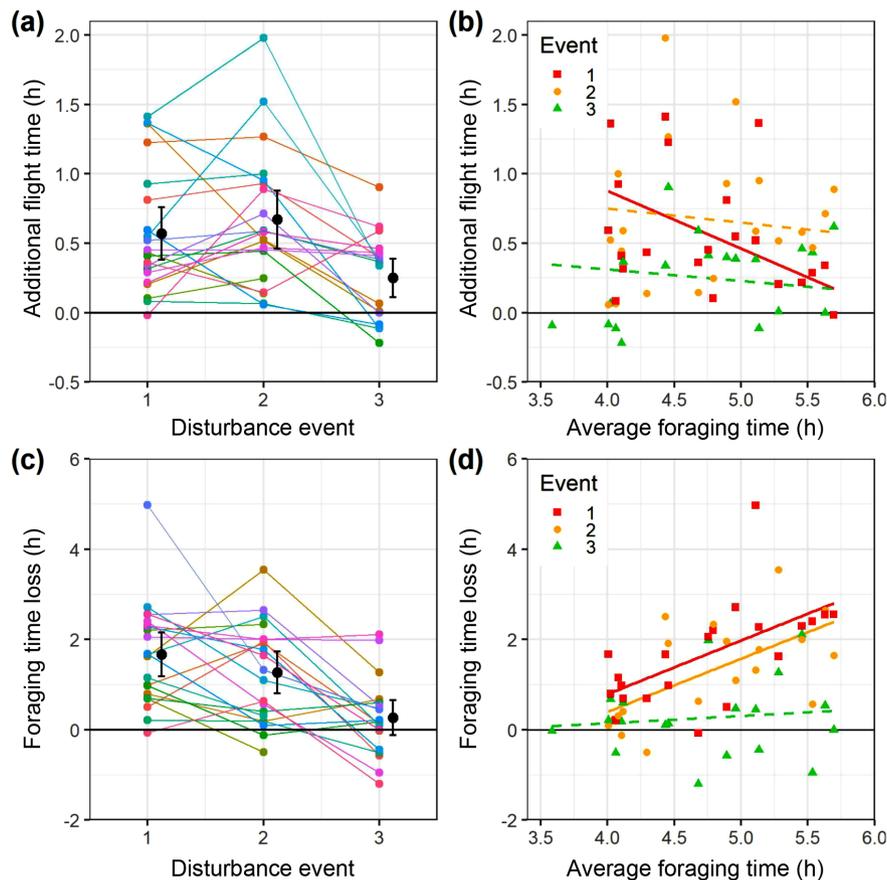


Figure 2. Additional flight time (a–b) and foraging time loss (c–d) in disturbed tidal periods compared to undisturbed tidal periods. In (a) and (c) the responses during each event are depicted, where dots from the same individual are connected and the black dots and error bars represent the means and 95% confidence intervals. In (b) and (d) the relationships between the average foraging time of an individual and additional flight time or foraging time loss for the three disturbed tidal periods are depicted. Values above zero indicate birds flew more (a–b) or lost more foraging time (c–d) than expected based on environmental conditions. Twenty-two individuals were measured, of which three were measured during two events and one during one event ($n_{\text{bird-disturbance}}=61$). Regression lines in (b) and (d) are derived from the model in Table 1.

Table 1. Linear mixed effect model details for tidal flight time and tidal foraging time. Environmental variables and average foraging time were mean-centred prior to analysis. *D* is a binary variable indicating whether it is a disturbed tidal period (1) or not (0). Non-local breeder was used as reference category. Bold numbers indicate significant effects ($p < 0.05$). $n = 1724$ tidal periods for both models.

	Tidal flight time			Tidal foraging time		
	Estimate	SE	p	Estimate	SE	p
Variables correcting for environmental conditions						
Intercept	0.251	0.019	0.000	4.49	0.14	0.000
Night	-0.009	0.023	0.692	-1.79	0.29	0.000
Moon	0.004	0.014	0.748	0.32	0.09	0.001
Night \times Moon	0.073	0.041	0.075	0.75	0.26	0.004
Intertidal flat exposure	-0.527	0.091	0.000	-0.81	0.47	0.087
Variables estimated for disturbed tidal periods						
D \times Event 1	0.271	0.049	0.000	-1.65	0.31	0.000
D \times Event 2	0.375	0.049	0.000	-1.25	0.31	0.000
D \times Event 3	-0.050	0.051	0.329	-0.25	0.32	0.424
D \times Local breeder	0.448	0.051	0.000	-0.02	0.32	0.957
D \times Average For. Time \times Event 1	-0.417	0.065	0.000	-1.19	0.41	0.004
D \times Average For. Time \times Event 2	-0.101	0.065	0.123	-1.18	0.41	0.004
D \times Average For. Time \times Event 3	-0.083	0.063	0.190	-0.16	0.40	0.685
Random intercepts						
$\sigma^2_{\text{residuals}}$	0.157			0.982		
σ^2_{BirdID}	0.089			0.652		
Random slopes among BirdIDs						
σ^2_{Night}	0.069			1.296		
σ^2_{Moon}	0.026			0.232		
$\sigma^2_{\text{Intertidal flat exposure}}$	0.354			1.693		

and second disturbed tidal period, respectively, but was not significantly affected in the third disturbed tidal period when the disturbance occurred earlier in the tidal period around high tide (Fig. 2c, Table 1). There was a positive correlation between additional flight time and foraging time loss ($r = 0.27$, $p = 0.038$, $n = 61$; Supporting information).

Individual differences accounted for a substantial proportion of the variation in response to disturbance. After correcting for the tidal period, bird identity accounted for 35.8% and 35.2% of the variation in additional flight time and foraging time loss, respectively (Fig. 2; Supporting information). This was significantly higher than what would be expected when randomly assigning Bird IDs to additional flight time (95% CI: 0–24.3%, 5000 iterations) and foraging time loss (95% CI: 0–23.5%, 5000 iterations).

Inefficient foragers increased their flight time less in the first disturbed tidal period, but not in the second and third disturbed tidal periods, compared to efficient individuals that foraged on average shorter (Table 1, Fig. 2b). Contrary to our expectations, individuals that had been breeding locally increased flight time more than non-local breeders (Table 1).

In support of the time-limitation hypothesis, foraging time loss in disturbed tidal periods was significantly larger for inefficient foragers (Table 1, Fig. 2d). Foraging time losses in disturbed tidal periods one and two increased with respectively 1.19 h and 1.18 h for individuals that foraged on average 1 h longer in undisturbed tidal periods (Table 1, Fig. 2d). During these disturbed tidal periods, inefficient foragers lost foraging time at the start of the tidal period and did not compensate for that later in the tidal period (Fig. 3). Efficient foragers did lose no or little foraging time, since also under normal conditions they would not have started foraging yet. During the

third event, the disturbance took place well before the start of the low tide (Fig. 3) and consequently foraging time losses were not apparent and not significantly related to the average foraging time (Fig. 2d).

Foraging time compensation after disturbance

Change in foraging time in the tidal period following the disturbed tidal period was positively related to the required foraging time to compensate for disturbance (Fig. 4a; Supporting information). Thus, individuals who experienced larger costs of disturbance lengthened their foraging time more than individuals for which costs of disturbance had been less. Notwithstanding, foraging time increased little in tidal periods following events 1 and 2 and was according to our calculations insufficient to compensate for the costs of disturbance.

Over a longer time span of three days, after disturbance events 1 and 2 individuals did not significantly increasing their foraging time (Fig. 4b; Supporting information). Only following event 3, birds increased their foraging time sufficiently to compensate for the costs of disturbance (Fig. 4). It is important to note that after event 3 less compensation was required, as the costs of disturbance were relatively low compared to events 1 and 2 (Fig. 4).

Mathematical modelling of disturbance costs as a function of foraging time

Using our analytical model parameterized with field and literature data from our model species, we explored disturbance thresholds, energetic costs and potential population consequences of disturbance for varying amounts of individual

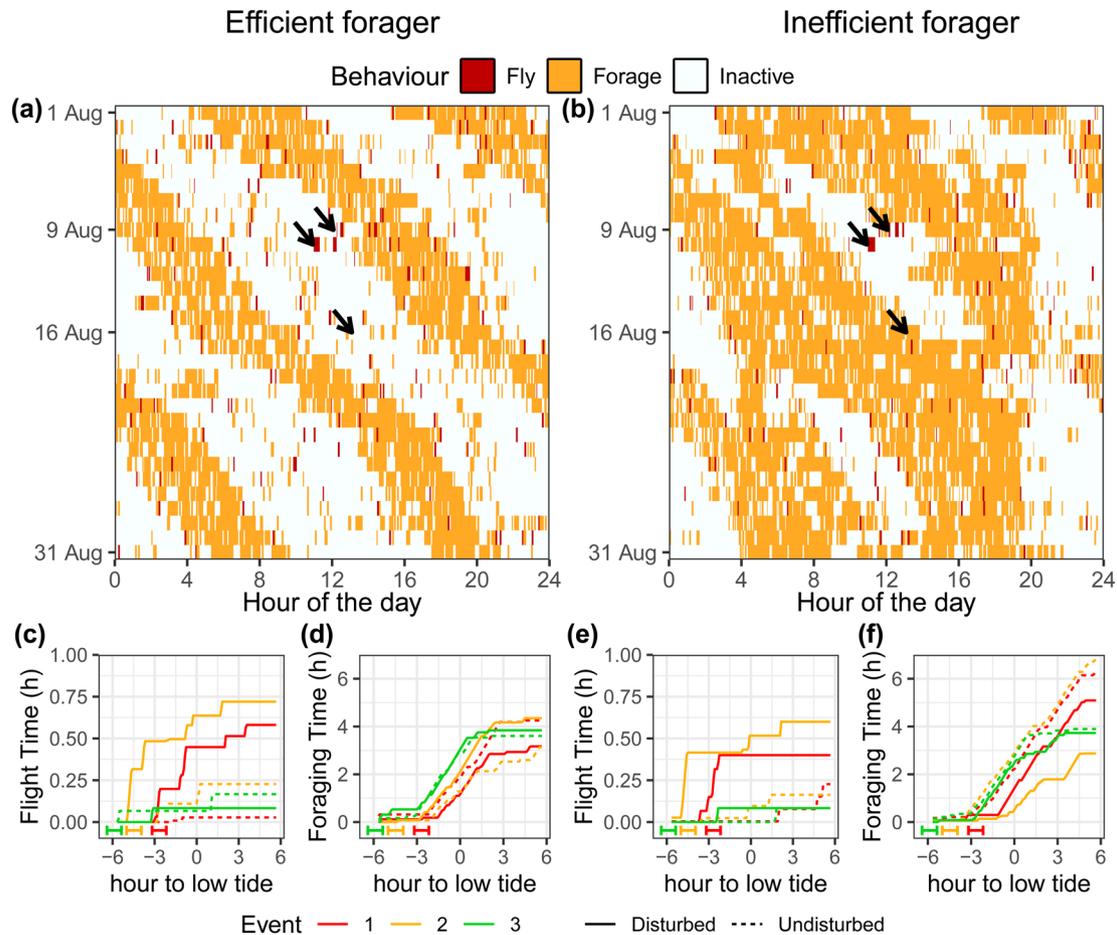


Figure 3. Illustrative time budgets, cumulative flight time and cumulative foraging time for an example efficient (a, c, d) and inefficient (b, e, f) individual. (a) and (b) show time budgets from 1 August 2017 to 31 August 2017 with flying, foraging and inactive (including preening) behaviour. In (c–f), disturbed tides are plotted together with undisturbed tides (tidal periods two days before (events 1 and 2) or one day before (event 3) the disturbed tidal periods) for comparison for visual reasons only. The moments of disturbance are indicated with arrows in (a–b) and with bars in the bottom of the plots in (c–f). In (a–b) note that foraging is synchronized with the timing of low tide that shifts each day due to the lunar cycle.

variation in time budgets. Efficient foragers had a higher disturbance threshold, particularly when disturbance occurred during high tide, as then disturbance does not limit available foraging time (Fig. 5a). If individuals cannot compensate for disturbance, it is expected that they maximize their foraging time (Fig. 5b). A lack of time to compensate for disturbance (i.e. when individuals cannot further increase their foraging time) may explain why we did not find a clear increased foraging time in the field across all individuals following disturbance events 1 and 2, when the costs of disturbance were largest. In the model, inefficient foragers lost energy under most disturbance scenarios, whereas efficient foragers were able to deal with higher levels of disturbance without energetic losses (Fig. 5c).

Using average foraging time estimates of 85 GPS-tracked individuals (Fig. 6a), our model estimated that a typical wintering oystercatcher could compensate for 2.4 h disturbance per tidal period, assuming that disturbance pressure is similar during high and low tide. The large individual variation

($SD=0.70$ h), however, implies that some individuals can only compensate for low levels of disturbance (Fig. 6b). When oystercatchers are disturbed for half an hour in each tidal period, the model predicted that 0.27% of the population would not be able to compensate for disturbance and was at risk that their condition would deteriorate. To illustrate that small changes in the distribution of the population affect this estimate, Fig. 6c shows that the part of the population at risk was more than halved (0.10%) or doubled (0.53%) when individual variation in average foraging time would be 10% smaller or larger, respectively.

Discussion

Our field study shows that upon disturbance inefficient foragers lose most foraging time. Using an analytical model, we further show how inefficient foragers may lack the time to compensate for disturbance. Consequently, these results

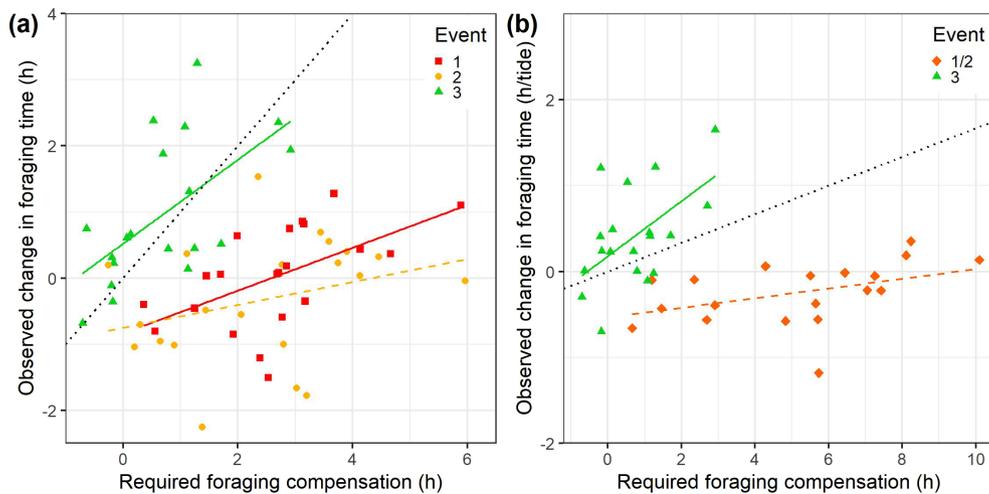


Figure 4. Relation between predicted foraging time required to compensate for disturbance costs (h) and the actual observed change in foraging time (in h per tidal period) in (a) one or (b) six tidal periods (3 days) following disturbance (7 tidal period for events 1 and 2 combined, 6 tidal periods for event 3). Events 1 and 2 were combined in (b) since they occurred on consecutive days, and compensation effects over three days could thus not be measured separately. Dotted lines indicate the relationship if individuals would increase their foraging time sufficiently to compensate for the costs of disturbance.

support our newly proposed hypothesis that time-limited individuals are more likely to experience negative consequences from disturbance (e.g. condition reduction due to reduced food intake). Ultimately, variation in how time-limited individuals are can affect the proportion of the population that is at risk from their condition deteriorating upon disturbance. In combination, these empirical and analytical results support the biological relevance of the time-limitation hypothesis and thereby offer a novel perspective on the causes and consequences of individual variation in vulnerability to disturbance. We discuss how our hypothesis is complementary to prevailing ideas by exploring 1) the mechanisms that determine individual differences in vulnerability to disturbance, 2) potential feedback loops between an individual's condition and its response to disturbance that can alter individual vulnerability to disturbance and 3) the implications of our findings for population studies.

Individual variation in vulnerability to disturbance

Individuals that live in the same area and encounter the same exposure to disturbance sources can experience different costs from disturbance. In accordance with previous studies (Carrete and Tella 2013), we show that there is individual consistency in disturbance responses, i.e. the increased flight time of oystercatchers following transport aircraft disturbance. These differences in responses may be caused by an individual's personality (Quinn and Cresswell 2005) or previous experiences with disturbances (Conomy et al. 1998). Contrary to our expectations, however, oystercatchers that had bred locally responded more fiercely and increased flight time more than non-local breeders. Although local breeders may be more used to jets and small civil aircraft, the frequency of occurrence of other human disturbance sources is limited

(van der Kolk et al. 2020b). Non-local breeders mostly nest in inland farmland areas, where they may encounter a larger range and higher frequency of human disturbance sources and thus may be more used or more tolerant to a range of (unusual) disturbance sources. Such differences among populations has been shown in song sparrows *Melospiza melodia*, where individuals in urban areas respond less to disturbance compared to conspecifics in rural areas (Evans et al. 2010).

The consequences of disturbance also differ for individuals that vary in their time budget. Individuals within a population can differ greatly in their foraging time and when they are active (Hertel et al. 2017, van der Kolk et al. 2020a). In general, individuals that forage longer, for example because they are less efficient foragers, are more likely to lose foraging time following disturbance. The costs of disturbance are thus expected to be higher for inefficient individuals.

Whether or not disturbance results in actual condition reductions may well depend on the ability of the individual to compensate for disturbance (Blanc et al. 2006, Selman et al. 2013). Individuals can compensate for disturbance by increasing foraging time after disturbance (Urfi et al. 1996, Urfi 2011). In our study, only after the third event foraging time was sufficiently prolonged in subsequent tidal periods to compensate for disturbance. A lack of compensation is not necessarily surprising, since foraging time is restricted by the tidal pattern and many individuals may be unable to increase foraging time after disturbance. Alternatively, individuals may increase their foraging efficiency to compensate for disturbance (Swennen et al. 1989, Iason et al. 1999). Oystercatchers can also increase their intake efficiency by decreasing the handling time of prey, but they are not likely to do so as this increases the risk of bill damage (Swennen et al. 1989). Whether or not individuals can compensate will not only depend on how time-limited they are,

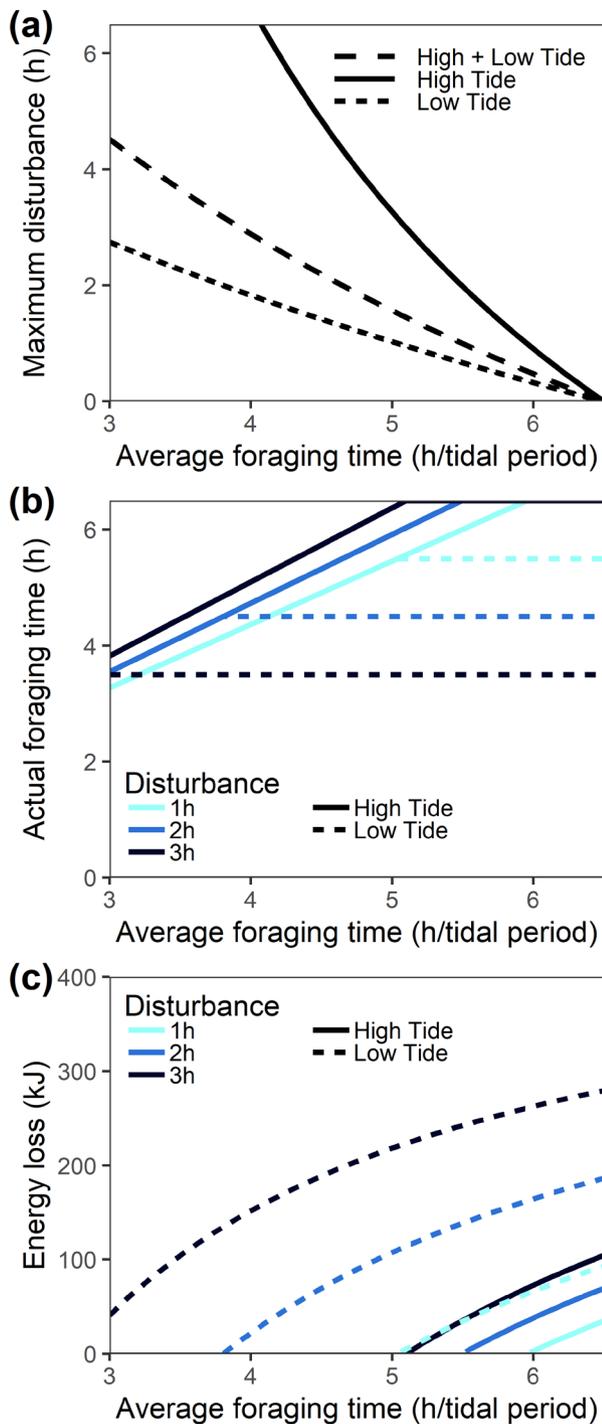


Figure 5. Model predictions of disturbance thresholds, foraging time and energetic losses of individuals when there is 1, 2 or 3 h disturbance during either high tide, low tide or both tides, as a function of their average foraging time. (a) Maximum duration of low tide ($D_{F_{crit}}$, Eq. S7 in the Supporting information), high tide ($D_{N_{crit}}$, Eq. S8 in the Supporting information) and combined low and high tide (D_{crit} , Eq. S9 in the Supporting information) disturbance an individual is predicted to be able to compensate for. (b) Predicted tidal foraging time (F_{real} , Eq. S6 in the Supporting information) for different disturbance scenarios. (c) Predicted energetic losses (E_{loss} , Eq. S10 in the Supporting information) in one tidal period for different disturbance scenarios.

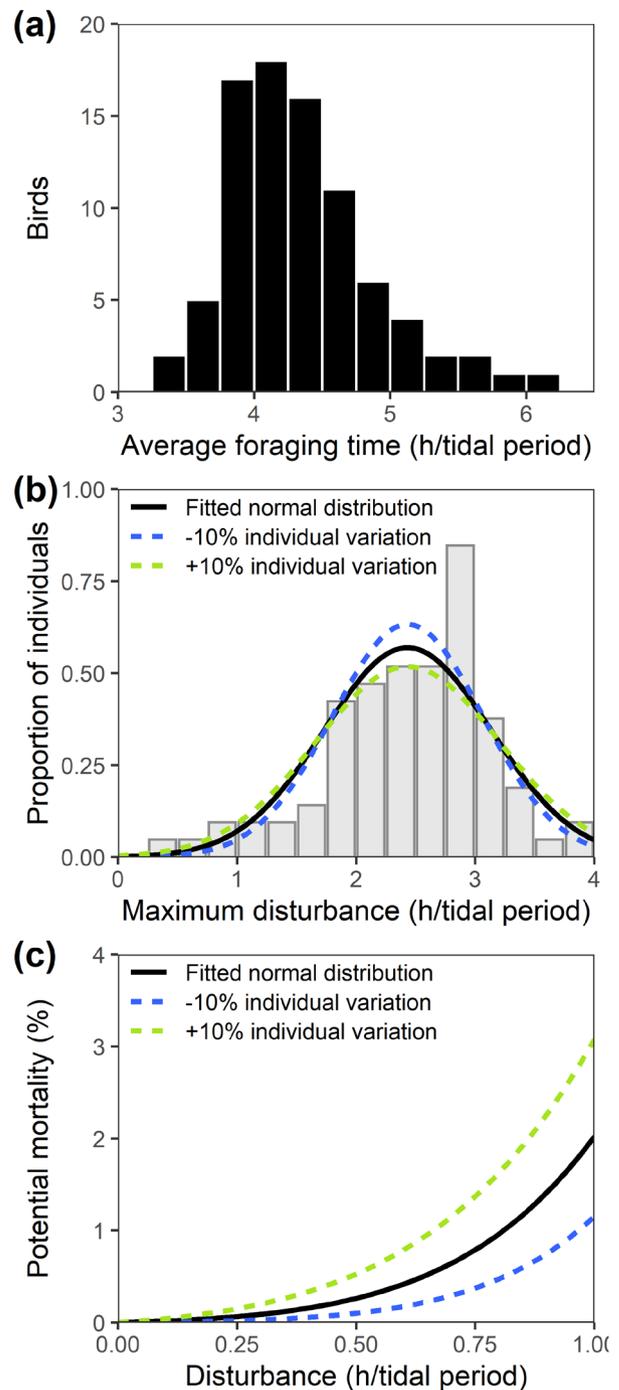


Figure 6. (a) Average intertidal foraging time of 85 GPS tagged individual oystercatchers that were measured during at least 25 tidal periods (see the Supporting information for details). (b) Distributions of maximum disturbance (D_{crit}) for which individuals can compensate (Fig. 5a). Grey bars indicate the observed distribution from which the normal distribution (black line) was derived. (c) Percentage of the population that is at risk of starving due to disturbance, assuming that disturbance levels are maintained over extended periods and exceeding disturbance threshold will therefore lead to deadly condition reductions. In (b) and (c) functions are also displayed when the individual variation in foraging time observed in (a) would be 10% smaller or larger than the observed distribution.

but also on the environmental conditions, such as food availability (Iason et al. 1999).

There seems to be a twofold cost of disturbance for less efficient individuals: Firstly, since they spend more time foraging they are more likely to be disturbed while foraging and, secondly, they have less spare time to compensate for disturbance. It is important to note, however, that those are often two sides of the same coin, since both these aspects act via limiting the potential maximum foraging time. Notably, the potential maximum foraging time is also limited upon disturbance for efficient foragers. Since efficient foragers do not utilize all available foraging time, disturbance will not affect their behavioural pattern if it takes place when those individuals were not foraging, even though they could have potentially been doing so. In our field study, for example, all individuals were limited in their potential foraging time following the disturbances, but realized foraging time was only affected in individuals that would utilize that time to forage under normal conditions.

In many populations, individuals differ not only in how long they forage but also in when they can or prefer to forage, which is due to individual differences in feeding strategy or specialisation (Hertel et al. 2017, van der Kolk et al. 2020a). In these situations, disturbance may only affect the foraging time of a part of the population. For example, in a population where some individuals feed during the night and others during the day, day-time disturbance will only reduce foraging time of day-time foragers.

We empirically studied how individuals vary in their response to disturbance by taking advantage of large disturbances by transport aircraft. Such disturbances are rare and consequently we could only study three of such events (possibly their rarity also explains the strong response). Although higher sample sizes are preferred, it is challenging to study many disturbances similarly for a high number of individuals: Studying individual variation in responses to disturbance requires a study setup in which all individuals experience strong disturbances in the same way. Disturbances that have a large impact and significantly affect foraging time are, however, difficult to mimic experimentally and generally rarely occur 'naturally'. Note, however, that our hypothesis also applies to small disturbances, such as recreational disturbances that affect many species in many areas, since also weak disturbances are expected to impact time-limited individuals more than others. However, it is challenging to test our hypothesis by studying small disturbances since the direct effects are 1) likely to be too small to accurately measure differences among individuals (e.g. foraging time loss) in the field, and 2) smaller natural disturbances typically only elicit responses at short distances, meaning that individuals that are even several hundreds of meters apart are disturbed in different ways by the same event and cannot be meaningfully compared.

Feedback loops between condition and disturbance responses

Individuals that are inefficient and spend more time foraging have been shown to be in a worse condition (black-legged

kittiwakes *Rissa tridactyla*; Angelier et al. 2007), have lower breeding success (European shags *Phalacrocorax aristotelis*; Daunt et al. 2014) and have lower apparent survival (Eurasian oystercatchers; van der Kolk et al. 2020a). Feedbacks between an individual's condition and disturbance response could modulate the impact of both individual variation-pathways on condition reductions (Fig. 1). Individuals balance the energy investment that they put into the disturbance response against the perceived predation risk (Frid and Dill 2002; risk-disturbance hypothesis in Fig. 1). Animals that are in a worse condition are generally willing to take more predation risks while foraging (Bachman 1993, Sinclair and Arcese 1995, Sweitzer 1996), and were also suggested to invest less energy in responding to disturbance (Stankowich and Blumstein 2005). Since human disturbances are generally non-lethal, this feedback between condition and disturbance response could reduce the impact of individual variation on condition reductions. In support of this hypothesis, turnstones *Arenaria interpres* that received supplementary food responded at a larger distance and flew further when approached by walkers in comparison to turnstones that were not fed (Beale and Monaghan 2004). Also, shorebirds respond less to disturbance later in the winter season and with colder temperatures, so under conditions when it is more difficult to meet their energy requirements (Stillman and Goss-Custard 2002, Collop et al. 2016). Alternatively, individuals that are in a worse condition may need to respond equally or earlier as their conspecifics to disturbances when their escape ability is negatively affected by a lower body or health condition (Alzaga et al. 2008; escape ability hypothesis in Fig. 1). Predators may target the weakest individuals, and therefore it is important for weak individuals not to stand out in comparison to conspecifics. This is supported by studies that show that healthier individuals respond less to predatory cues (López et al. 2005, Martín et al. 2006). For example, it was shown that yearlings of the collared flycatcher *Ficedula albicollis* with a shorter flight initiation distance take longer to catch in an aviary, indicating they were in a better condition (Jablonszky et al. 2017).

In our study, inefficient foragers are expected to be in a worse condition than efficient foragers, which may explain why they tended to increase their flight time less upon disturbance. However, the overall costs of disturbance were still higher for inefficient foragers than for efficient foragers, since they lost more foraging time (Supporting information). In flocking species, such as oystercatchers at high tide roosts, individuals may need to respond simultaneously as group-members to not stand out (Hilton et al. 1999). Following disturbance, all individuals may thus be similarly affected independent of their condition, which may explain why the total costs of disturbance were still higher for inefficient foragers.

If environmental conditions are mild, time-limited individuals may be able to take in sufficient energy to maintain their body condition and are then not necessarily in a worse condition than conspecifics. However, when this is the case, time-limited individuals are the first individuals to be

negatively affected once disturbance occurs, since they are less able to compensate. Overall, our time-limitation hypothesis thus offers an additional and complementary view on how non-lethal human disturbances may negatively affect an animal's condition (Fig. 1).

Implications for predicting population consequences of disturbance

Predicting the population consequences of disturbance is important in conservation research to define effective mitigation measures (Stillman and Goss-Custard 2010, Pirota et al. 2015, 2018, Hertel et al. 2017). Understanding individual behaviour can be crucial for predicting population processes (Stillman and Goss-Custard 2010, Pirota et al. 2015). When modelling population effects of disturbance, our study suggests that it is important to include individual variation in immediate responses to disturbance as well as variation in individual's time-budgets. Our hypothesis implies that variation in how time-limited individuals are strongly influences the proportion of the population that is at risk that their condition deteriorates due to disturbance. This is true even under low levels of disturbance and under normal winter conditions: The estimated disturbance thresholds for the 1% most vulnerable part of the population are threefold lower than for the mean individual (Fig. 6).

Individual variation in time budgets is currently not included in many of the models that study the effects of disturbance on populations (New et al. 2014), although many existing modelling frameworks would allow inclusion of individual variation (Pirota et al. 2018). In individual-based models, however, the effect of individual variation in time budgets on disturbance vulnerability is often already implicitly incorporated. For example, individual-based models that simulate wintering populations of shorebirds do include individual variation in foraging efficiency (Goss-Custard et al. 2006, Stillman and Goss-Custard 2010). In such models, individuals with a low foraging efficiency (or individuals that forage on poor sites) will forage on average longer, and therefore also suffer more from disturbance since they have less spare time in which they can compensate for disturbance costs.

Finally, disturbance may target the same individuals within a population as harsh weather conditions and poor food stocks: with increasing disturbance, harsher weather conditions and lower food availability, the condition of the most time-limited and least efficient individuals will deteriorate first, ultimately impacting the survival of the population. The impact of disturbance, food stocks and weather are thus likely to interact, and models that aim to predict disturbance impacts should ideally consider the synergistic effects of individual variation in time limitation on all these environmental factors combined.

Data availability statement

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.r7sqv9sbf>>. (van der Kolk et al. 2021).

Acknowledgements – We thank the numerous volunteers involved in catching and tagging of oystercatchers, the Royal Netherlands Air Force for providing logistical support and Staatsbosbeheer for providing accommodation.

Funding – Funding was provided by the Applied and Engineering Sciences domain of the Netherlands Organisation for Scientific Research (NWO-TTW 14638) and co-funding via NWO-TTW by Royal Netherlands Air Force, Birdlife Netherlands, NAM gas exploration and Deltares. We acknowledge the feedback provided by ecologists working at these organisations during half-yearly meetings. The authors declare that they have no competing interests. UvA-BiTS studies are facilitated by infrastructures for e-Science, developed with support of the NLeSC (<www.esciencecenter.com>), and carried out on the Dutch national e-infrastructure with support of SURF Cooperative.

Conflicts of interest – The authors declare that they have no competing interests.

Permits – Tagging of oystercatchers was done under license of the Dutch Flora and Fauna Law (FF/75A/2013/038), the Natuurbeschermingswet (Province of Friesland, 801233) and approved by the Dutch Ethical Committee (Sovon AVD25002015200-001).

Author contributions

Henk-Jan van der Kolk: Conceptualization (lead); Formal analysis (lead); Investigation (equal); Methodology (lead); Writing – original draft (lead). **Bruno J. Ens:** Conceptualization (supporting); Supervision (equal); Writing – review and editing (equal). **Magali Frauendorf:** Investigation (supporting); Methodology (supporting); Writing – review and editing (equal). **Eelke Jongejans:** Supervision (equal); Writing – review and editing (equal). **Kees Oosterbeek:** Investigation (equal). **Willem Bouten:** Methodology (supporting); Writing – review and editing (equal). **Martijn van de Pol:** Conceptualization (supporting); Formal analysis (supporting); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal).

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