

Frequency-dependent tolerance to aircraft disturbance drastically alters predicted impact on shorebirds

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Abstract

Anthropogenic disturbance of wildlife is increasing globally. Generalizing impacts of disturbance to novel situations is challenging, as the tolerance of animals to human activities varies with disturbance frequency (e.g. due to habituation). Few studies have quantified frequency-dependent tolerance, let alone determined how it affects predictions of disturbance impacts when these are extrapolated over large areas. In a comparative study across a gradient of air traffic intensities, we show that birds nearly always fled (80%) if aircraft were rare, while birds rarely responded (7%) if traffic was frequent. When extrapolating site-specific responses to an entire region, accounting for frequency-dependent tolerance dramatically alters the predicted costs of disturbance: the disturbance map homogenizes with fewer hotspots. Quantifying frequency-dependent tolerance has proven challenging, but we propose that (i) ignoring it causes extrapolations of disturbance impacts from single sites to be unreliable, and (ii) it can reconcile published idiosyncratic species- or source-specific disturbance responses.

KEYWORDS

avoidance, disturbance, disturbance map, habituation, impact assessment, population impact, recreation ecology, shorebirds, Wadden Sea, wildlife

INTRODUCTION

As the human population continues to grow, anthropogenic disturbance of wildlife is increasing globally, likely worsening human–wildlife conflicts (Dirzo et al., 2014; Gaynor et al., 2018). Consequently, a key challenge is to quantify the impact of disturbance for individuals and populations to new situations, such as for other areas (to create large-scale maps used to identify hotspots of disturbance impact) or for future changes in disturbance intensities (when plans for more recreation or traffic require evaluation). For this purpose, disturbance responses measured at one location (or one point

in time) typically are extrapolated and used to quantify population impacts (Goss-Custard et al., 2006) or energetic costs (van der Kolk, Allen, et al., 2020) for other locations (or future points in time for which we expect changing frequencies of disturbance source presence). However, if the behavioural response of animals towards disturbance sources depends on the frequency of disturbance source presence, then extrapolating responses to other situations where disturbance source frequencies are lower or higher may result in respectively underestimation or overestimation of impacts (when frequency-dependent responses are ignored). To predict the impact of disturbance in new situations, it is

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thus not only crucial to know how animals respond to a disturbance source but also whether and how strongly their tolerance of disturbance depends on the frequency of a disturbance source they have been exposed to. However, quantifying the strength of frequency-dependent tolerance (FDT) to disturbance is challenging. Furthermore, as far as we are aware, no studies to date have accounted for FDT in their large-scale predictions, nor have they assessed how much predictions that ignore FDT misrepresent disturbance impacts.

FDT to disturbance in wildlife populations can result from habituation and/or avoidance. Human activities can cause disturbance of animals by noise or visual cues (Francis & Barber, 2013; Steven et al., 2011). Most human disturbances in nature areas, specifically tourism and traffic, are non-lethal, allowing animals to learn that such human activities are non-threatening and consequently habituate (Blumstein, 2016; Geffroy et al., 2015). Habituation causes animals and populations to better tolerate disturbance sources that occur frequently, which reduces the impact of disturbance (Saltz et al., 2019; Vincze et al., 2016). An alternative non-mutually exclusive cause of increased population tolerance to frequent disturbance sources is that susceptible individuals avoid disturbed sites and may move away to non- or less disturbed sites, while less susceptible individuals stay in the area (Bejder et al., 2009; Carrete & Tella, 2013; Higham & Shelton, 2011; Sprau & Dingemans, 2017). Such an avoidance-driven redistribution of individuals will also result in populations in areas with more frequent disturbance sources having high tolerance.

Knowledge about FDT is not only important for reliably extrapolating to novel situations but also for interpreting differences in responses among studies. Specifically, when comparing the effects of multiple disturbance source types that differ in their frequency of occurrence among observational field studies. It is often unclear whether variation in disturbance responses is caused by actual differences in the disturbance potential among disturbance sources (as disturbance sources differ in size, shape, sound and movement), or by FDT, or both (Nordell et al., 2017; van der Kolk, Krijgsveld, et al., 2020). Figure 1 illustrates how in one location where different disturbance source types occur with different frequencies, it cannot be distinguished which mechanism causes the observed differences in disturbance impact. Similarly, differences in disturbance response among species may reflect intrinsic variation in how tolerant these species are but may also be a result of FDT if species differ in how much they are exposed to disturbance. Clarifying the role of FDT may thus improve our understanding of the differences observed among studies and species in disturbance responses and thereby lead to synthesis of a literature in which disturbance responses appear to be highly idiosyncratic.

Previous research provides evidence for the existence of (positive) FDT, but opposite patterns have also been observed. Such studies typically compared the responses of animals to the same disturbance source types in areas

with different levels of exposure (Baudains & Lloyd, 2007; Bötsch et al., 2018; González et al., 2006; Linley et al., 2018; Nordell et al., 2017; Saltz et al., 2019). For example, animals living in urban areas were shown to tolerate human disturbance more compared to conspecifics in rural areas (Díaz et al., 2013; Matsyura et al., 2015; Samia et al., 2015). However, if animals experience humans as a real threat (e.g. because poaching or collisions occur), an opposite relationship may exist where animals respond more to disturbance in areas with more frequent human activities (Manor & Saltz, 2005; Yamashita et al., 2018). The latter resembles a well-known concept in prey behaviour, where an animal's perception of predation risk can vary spatially ("landscape of fear"), induced by several factors including predator presence (Gaynor et al., 2019).

Behavioural responses towards disturbance result in physiological consequences. Disturbance will increase an animal's energy expenditure (sometimes expressed as a proportion of the normal daily energy expenditure, DEE; e.g. Regel & Pütz, 1997), but can additionally also reduce the amount of time available for foraging (Burger, 1994). If animals are not able to compensate sufficiently for increased energetic costs of disturbance by increasing their food intake, disturbance may cause deterioration of their condition and ultimately reduce their fitness (Miller et al., 1994; Goss-Custard et al. 2006).

To our knowledge, no study has explored how tolerance in animals towards aircraft disturbance depends on the frequency of air traffic. Aircraft can cause a lot of disturbance to animals (Lima et al., 2015), especially since they traverse large distances and can access remote areas (Miller et al., 1994). At the same time, aircraft disturbance is difficult to study since performing experiments is hardly feasible (but see Ward et al., 1999), and most studies rely on observations at sites where aircraft overflights are common (Blackwell et al., 2019; van der Kolk, Krijgsveld, et al., 2020). Many studies highlighted large differences in disturbance potential among aircraft types (Blackwell et al., 2019; Goudie, 2006; Komenda-Zehnder & Bruderer, 2002; Smit & Visser, 1993; van der Kolk, Krijgsveld, et al., 2020), but sometimes with contrasting rankings. For example, Komenda-Zehnder and Bruderer (2002) concluded that transport aircraft were less disturbing than jets, helicopters and small civil airplanes, whereas van der Kolk, Krijgsveld, et al. (2020) showed that transport aircraft had by far the highest disturbance potential among these same types of aircraft. Differences in aircraft overflight frequencies among study sites could potentially reconcile these contrasting results.

Here, we study FDT to aircraft disturbance by shorebirds. Using a comparative study of existing data from six locations along a gradient of aircraft overflight frequencies, we quantified how strongly the probability that various species took flight decreased with aircraft overflight frequency. Furthermore, we determined that responses varied widely among five aircraft types, but that most of this variation can be attributed to studies experiencing uncontrolled differences in disturbance exposure, rather than

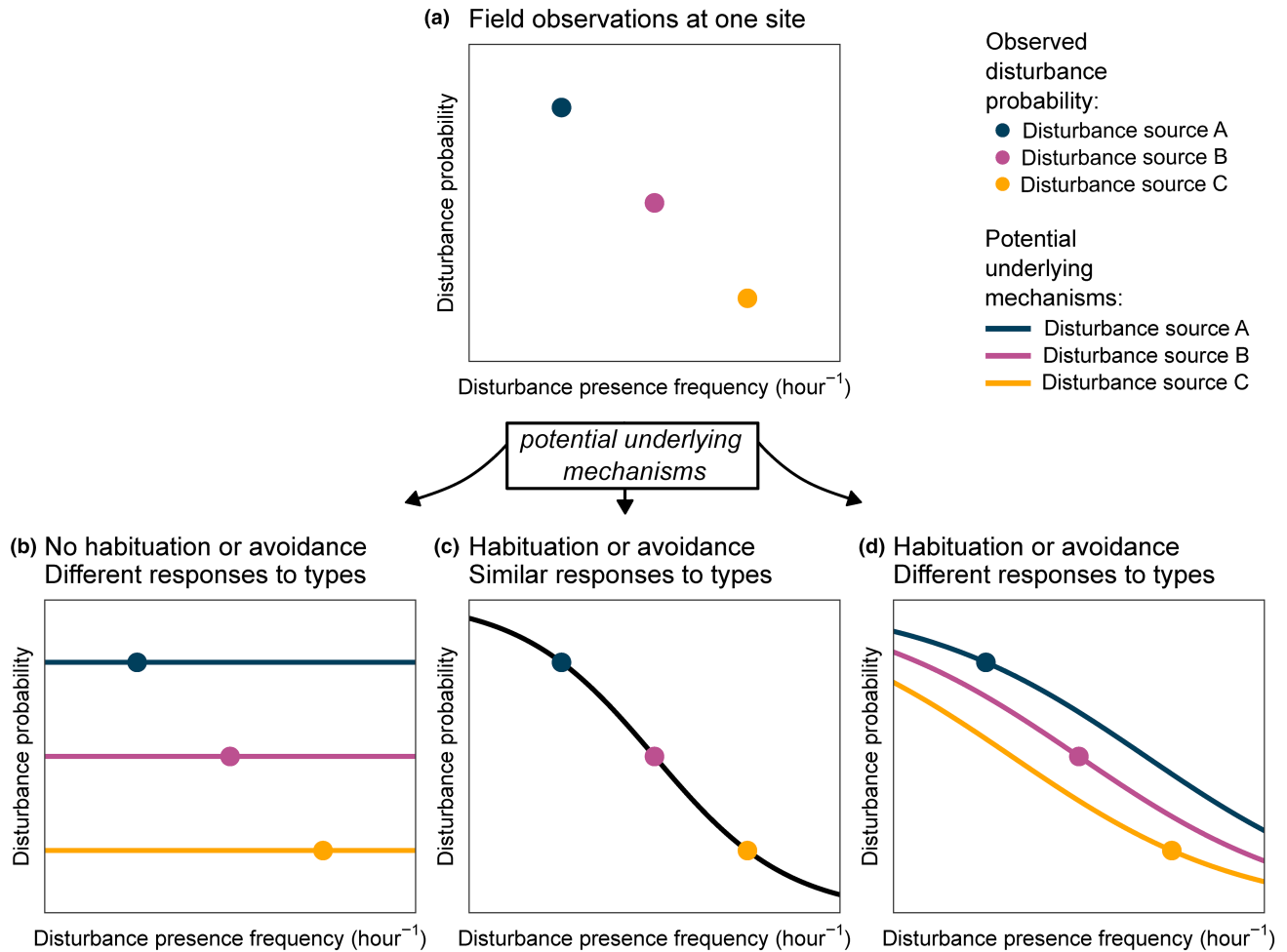


FIGURE 1 Hypothetical relationships between disturbance source presence frequency and the disturbance response (e.g. flight initiation distance or probability) for three different disturbance source types (Disturbance sources A–C). It can typically not be determined whether differential disturbance responses at a site are caused by differences in disturbance potential of different disturbance sources, or by different degrees of habituation or of avoidance. The panels illustrate this point by depicting an example where observed differences in the probability of disturbance response to three sources can be explained by different underlying mechanisms. In (b), disturbance responses are solely determined by disturbance source type, which may for example be caused by differences in sound, shape, size and behaviour between disturbance sources. However, by chance responses are associated with disturbance frequency, which may not be unlikely as studies often compare only a few disturbance sources. In (c), disturbance responses do not differ among disturbance source types but are shaped by habituation and avoidance and thus depend on the frequency of disturbance source presence. In (d) disturbance responses are shaped by a combined action of (b) and (c).

intrinsic differences. Finally, for the first time, we assess the importance of FDT for making reliable impact assessments for novel situations. Specifically, we quantify how accounting for overflight frequency alters the predicted energetic costs of airplane disturbance for wintering oystercatchers in the Wadden Sea world heritage area, by reconstructing large-scale disturbance maps from a previous study that ignored FDT (van der Kolk, Allen, et al., 2020).

METHODS

Data collection

The study was conducted in the western part of the Wadden Sea, a UNESCO world heritage site that is an important stop-over and wintering site for

millions of shorebirds in the East Atlantic Flyway (Reise et al., 2010). We combined and standardized previously collected data from six locations with different intensities of air traffic (Figure 2). Two study sites were used as an air force training area (Vliehors and Noordsvaarder), and consequently military helicopters and jets were common. Helicopters were also frequent at two study sites located near an airport used by military and civil helicopters (Kuitje and Kooyhoekschor). Four study sites (Vliehors, Kuitje, Kooyhoekschor and Borkum) were located near civil airports, and consequently high frequencies of small airplane overflights were recorded. Variation in aircraft frequency varied by at least one order of magnitude across sites for each aircraft type, except for medium-sized civil airplanes. At one study site (Rottum) all aircraft types were rare.

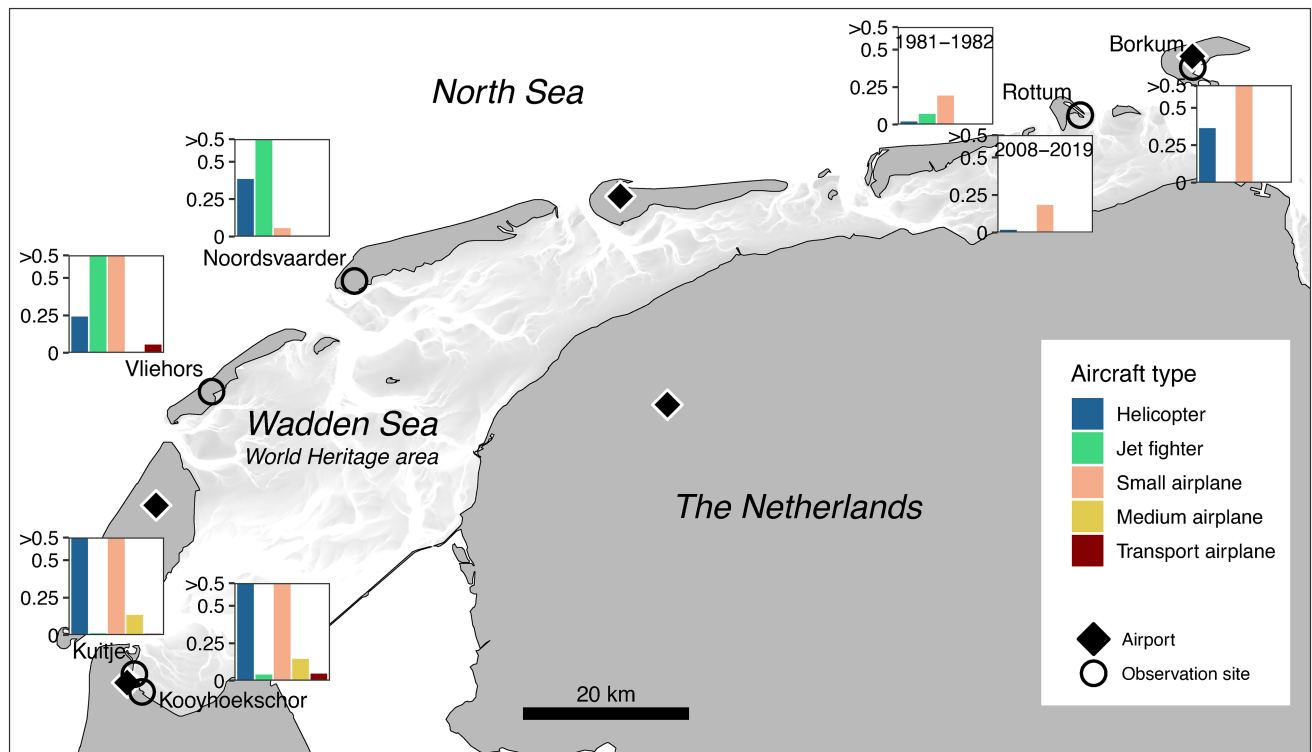


FIGURE 2 Map of the study area showing the locations where shorebirds and aircraft were observed. Inset histograms show the overflight frequencies (hour^{-1}) of each aircraft type per location.

All observation protocols aimed to record all aircraft overflights (at some sites also other types of disturbance sources were recorded) and whether they caused disturbance. We grouped the data in five aircraft types that differ in their shape (helicopter vs. airplane), size (small sports-plane vs large transport airplanes) and flight movements (small sports-plane vs. jet fighter): (1) helicopters (including both civil and military helicopters), (2) jet fighters, (3) small airplanes, (4) medium-sized airplanes and (5) large transport airplanes. Flight height was not recorded, but aircraft generally flew at a height of $\leq 450\text{m}$, and generally lower on sites where aircraft were more frequent (i.e. military training areas and nearby airports). The frequency of aircraft overflights was derived by dividing the total number of observed overflights (per aircraft type) by the total observation time (in hours).

A disturbance was defined as an occasion when at least 1% of the observed flock took flight upon aircraft overflight; this 1% threshold was chosen to exclude cases where only one or very few birds took flight for reasons possibly other than disturbance. Observations on the Vliehors and Noordsvaarder focussed on bartailed godwits (*Limosa lapponica*), curlews (*Numenius arquata*), oystercatchers (*Haematopus ostralegus*) and gulls (flocks with several gull species, mostly black-headed gull (*Chroicocephalus ridibundus*), European herring gull (*Larus argentatus*) and common gull (*Larus canus*), only observed on Vliehors). Bird species were not specified in the other sites and were therefore classified as mixed

species, but all observations applied to non-breeding shorebirds in intertidal areas. Since the species observed at Vliehors and Noordsvaarder are common throughout the whole Wadden Sea, they were likely also often included—and even abundant—in observations in the other sites. Observations on Vliehors and Noordsvaarder focussed on roosting shorebirds, whereas in the other studies both roosting and foraging shorebirds were observed. Shorebirds on Rottum were observed during two distinct time periods, 1981–1982 and 2008–2019, that differed slightly in aircraft frequency (Figure 2) and also given the large time gap, were treated as two different sites in the analysis. Over 2000 hours of observations were conducted across all six sites; for more details on characteristics and data collection at each of the sites, see Supplementary Text S1.

Analysis

Although observation protocols differed among sites, all data sets were standardized such that the response variable was the probability that aircraft overflight caused at least 1% of birds to take flight, and the explanatory variable the frequency of aircraft overflights. This probability of disturbance was analysed using a logistic mixed regression model, with data points based on the number of observed aircraft overflights that caused disturbance over the total number of overflights for each combination of site, species and aircraft type

($n=44$). Aircraft overflight frequency (log-transformed), aircraft type and bird species (five categories: bar-tailed godwit, curlew, oystercatchers, gull species and mixed-species) were included as fixed explanatory variables. An interaction was added between aircraft overflight frequency and aircraft type. Site was included as a random intercept, to account for differences in methodologies and sites that could cause differences in estimated disturbance probabilities. The Akaike Information Criterion (AIC), marginal R^2 and conditional R^2 of models with all combinations of fixed variables were compared (10 models in total, including a null model with no fixed factors). This comparison was done to explore the variation that could be explained by aircraft overflight frequency or aircraft type alone in comparison with models that included both factors. The AIC is a measure of the relative fit of a model, where models with lower AIC values are better supported by the data than models with higher AIC values (Burnham & Anderson, 2004). We considered models with >2 units AIC higher than the top model to be significantly less supported. The marginal R^2 and conditional R^2 are estimates of the explained variation by fixed factors only and by fixed and random factors combined, respectively (Nakagawa & Schielzeth, 2013). The model assumptions were met, that is, absence of multicollinearity, absence of overdispersion or underdispersion, and coefficients of the random variable being normally distributed. A post-hoc Tukey test was used to detect significant differences among aircraft types in a model with aircraft overflight frequency (log-transformed), aircraft type and bird species as fixed factors (no interactions). All analyses were performed in R (R Core Team, 2016).

Implication for predicting energetic costs of disturbance at a large scale

To determine how FDT can alter the predicted energetic costs of disturbance, we re-analysed predictions of the energetic costs of small civil airplanes for wintering oystercatchers across the whole Dutch Wadden Sea area (3000 km²) from a previous study in which we did not account for FDT (van der Kolk, Allen, et al., 2020). We used GPS data from small civil airplanes from July to September 2018, the months in which oystercatchers have already returned from their breeding areas and small civil airplane activity peaks. In the previous study, we derived disturbance probability from the distances between aircraft and birds by combined tracking of aircraft and oystercatchers on the Vliehors. We applied those distance–response relationships to the civil aircraft GPS data to calculate disturbance frequencies and energetic costs expressed as additional daily energy expenditure over the whole Dutch Wadden Sea, resulting in a disturbance heat map. This map assumed that disturbance probability was fixed (i.e. frequency

independent) over the whole Wadden Sea area, and equal to the observed probability at Vliehors: 0.14 for a straight overflight of a small civil airplane at a height of 450 m (van der Kolk, Allen, et al., 2020).

Here, we modified these calculations in two ways. First, while in the previous study we extrapolated from an area with low disturbance probability by small airplanes (Vliehors, disturbance probability of 0.14 and overflight frequency of 0.40 h⁻¹), we now also extrapolated a disturbance map from a single study site with high disturbance probability (Noordsvaarder, disturbance probability of 0.80 and overflight frequency of 0.02 h⁻¹) as a reference (Visser, 1986). This analysis thus still did not account for FDT, but because values were extrapolated from a study where disturbance probabilities were higher, an overall higher estimate of the disturbance impact is expected, illustrating the extent to which extrapolations can depend on the choice of reference study.

Second, we implemented the estimated relationship between disturbance probability and aircraft overflight frequency (for small airplanes for oystercatchers) in our model to construct a disturbance impact map that specifically accounts for FDT. For all three assessments, we calculated the additional daily energy expenditure (DEE; see van der Kolk, Allen, et al. (2020) how these were derived) caused by small civil aircraft on oystercatcher high-tide roost sites. Oystercatcher high-tide roost locations and averages of counts for July to September 2014–2018 were provided by Sovon Dutch Centre for Field Ornithology and were per roost expressed as the percentage of the total population (ca. 100,000 individuals). The costs were considered low if below 0.1% DEE, intermediate if between 0.1% and 0.5% DEE and high if above 0.5% DEE. Although in general only disturbance costs above 1% DEE are considered problematic (van der Kolk, Allen, et al., 2020), it should be considered that birds experience additional disturbance due to other disturbance sources on top of disturbance by the small civil airplanes focused on here.

RESULTS

Relationship between aircraft overflight frequency and disturbance probability

There was a strong negative relationship between aircraft overflight frequency and the probability that an aircraft caused disturbance (Table S1; Figure 3): Disturbance probabilities were around 80% when aircraft were rare (<0.01 overflights per hour) but as low as 7% when aircraft were common (>3 overflights per hour; Figure 3). Aircraft overflight frequency alone explained 37.4%, while aircraft type alone explained 26.4% of the variation in disturbance probabilities (Table S1). Because these predictors were partly confounded (e.g. transport aircraft were uncommon at all sites), the fixed factors in a model

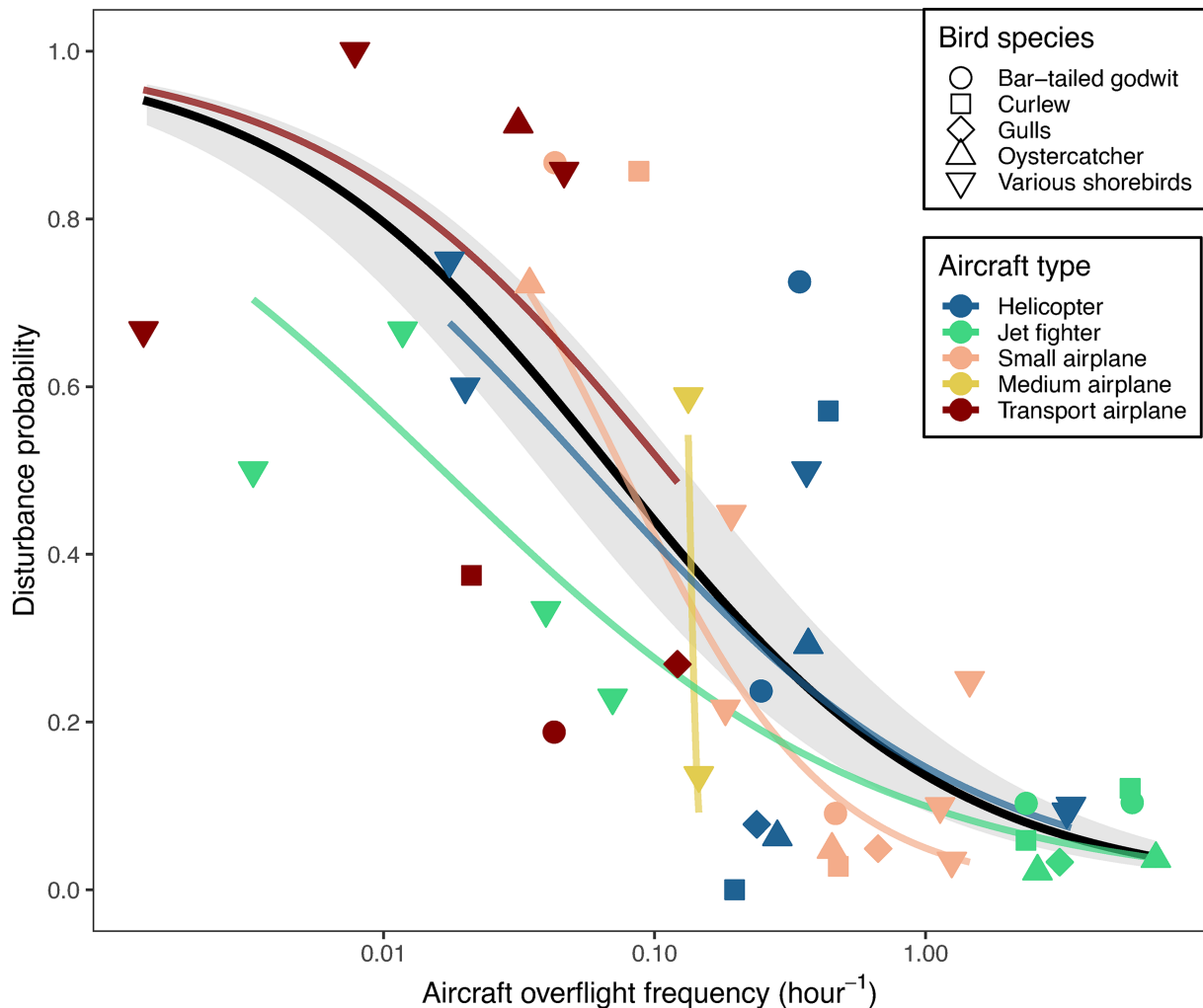


FIGURE 3 Frequency-dependent tolerance in shorebirds, as evidenced from the relationship between aircraft overflight frequency and disturbance probability for different aircraft types. Every dot represents a unique site-aircraft type-bird species combination. Black line (with shaded 95% confidence interval) shows overall relationship, coloured lines relationships for each aircraft type, derived from the model presented in [Table S2](#). Note the log transformed x -axis.

including both aircraft overflight frequency and aircraft type explained little more of the variation in disturbance probabilities than the model with aircraft overflight frequency alone (39.1% vs. 37.4%). The top model included an interaction between aircraft overflight frequency and aircraft type, and was much better supported than the second performing model that lacked this interaction ($\Delta AIC=29.9$; [Tables S1 and S2](#)). The top model also included a species effect, with oystercatchers and gull species being least likely to be disturbed ([Table S2](#)).

How frequency-dependent tolerance clarifies differences in disturbance response among aircraft types

When not accounting for differences among sites (i.e. a model including only aircraft type as explanatory

variable), the observed disturbance responses varied greatly among aircraft types with jets only eliciting responses by birds on average 5% of the time, while medium-sized airplanes caused responses in 68% of overflights ([Figure 4](#)). However, as these observations were done at locations that varied in the aircraft overflight frequencies, accounting for FDT (i.e. a model including only aircraft type in interaction with overflight frequency) removed much of the variation in bird responses to different aircraft types. The probability of a response to disturbance now varied between 20% (small airplanes) and 47% (transport airplanes; [Figure 4](#)). Notwithstanding, after correcting for aircraft overflight frequency and bird species, transport airplanes, medium-sized airplanes and helicopters had a significantly higher probability of causing disturbance than small civil airplanes ([Figure 4](#)).

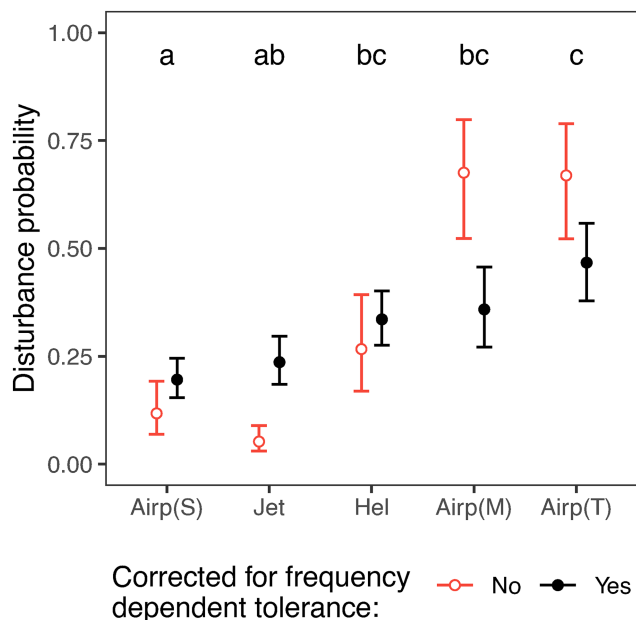


FIGURE 4 Differences in disturbance probabilities among aircraft types, with and without accounting for frequency-dependent tolerance (i.e. with and without including aircraft overflight frequency as predictor in the model). Letters indicate significant differences among aircraft types when accounting for frequency-dependent tolerance. Error bars show standard errors around the mean estimate.

Implication for predicting energetic costs of disturbance at a large scale

Accounting for FDT substantially modifies predictions of disturbance costs at large spatial scales. Linear extrapolation of disturbance responses to sites with different air traffic intensities (when disturbance probability is assumed to be independent of aircraft overflight frequency) will generally underestimate disturbance frequencies in areas with few aircraft, but overestimate disturbance frequencies in areas with many aircraft. The magnitude and direction of the error in the predicted disturbance impacts depends on the initial site where responses were measured: When disturbance responses were measured in an area with many aircraft, a low disturbance probability would be recorded (Figure 5a), which would generally lead to an underestimation of the disturbance impact when extrapolating to areas with intermediate aircraft presence (Figure 5c). Conversely, when disturbance responses were measured in an area with few aircraft, a high disturbance probability would be recorded (Figure 5b), which would generally lead to an overestimation of the disturbance impact when extrapolating to areas with intermediate aircraft presence (Figure 5d).

To assess the importance of FDT for real-world decision tools, we reconstructed a disturbance map of the predicted costs of small airplane disturbance for the Dutch Wadden Sea, using a FDT function instead of a fixed response probability. When accounting for

FDT, the predicted impact of small civil airplane was more homogenous across the Wadden Sea (Figure 6c vs. Figure 6a), being higher in most parts of the Wadden Sea, that is, in those areas where aircraft overflight frequencies were lower than the reference site Vlieland from which we extrapolated (Figure 6c vs. Figure 6a). In a few areas, especially near airports, where aircraft overflight frequencies were higher than the reference site, FDT caused costs to be lower (Figure 6c vs. Figure 6a). When disturbance impacts were instead extrapolated based on the high disturbance probability measured at the Noordsvaarder reference site, including FDT in the model resulted in disturbance impacts being lower at most sites, as most sites experienced higher amounts of air traffic than Noordsvaarder (Figure 6c vs. Figure 6b).

Most importantly, the extrapolation that accounted for FDT had reduced variation across the region and roosts in disturbance costs, compared to both extrapolations using a reference site. This is reflected in the distribution of the predicted costs per high-tide roost site: the maximum impact at a roost site and the variation among roost sites was larger for when either Vlieland (max=0.40% DEE, var=0.0043; inset Figure 6a) or Noordsvaarder (max=2.3% DEE, var=0.14; inset Figure 6b) were used as a reference site, compared to when the impact was assessed while accounting for FDT (max=0.14% DEE, var=0.00081; inset Figure 6c). FDT homogenizing the disturbance impact landscape thus means that there will be fewer roosts with very high aircraft disturbance costs (hotspots of high costs are generally of most concern for conservation and policy). For example, when using Noordsvaarder as a reference site, the number of roosts experiencing impacts exceeding 0.5% of their daily energy expenditure was reduced from 14% (10 out of 73 roost sites) to 0% after accounting for FDT (red zones in inset Figure 6b vs. Figure 6c). However, if relatively low levels of disturbance are reason for concern, then accounting for FDT may also result in many more sites exceeding a threshold (e.g. a threshold of 0.01% DEE, Figure 6c. vs. Figure 6a), since the predicted costs increase on the sites with low disturbance intensities.

DISCUSSION

Our comparative study provides evidence for very strong FDT, with birds virtually always responding when aircraft were rare, while rarely fleeing from these same aircraft types when common. Most of the variation in responses to different aircraft types was artificial and due to aircraft types being observed at different overflight frequencies. To our knowledge this is the first study that outlines how extrapolating impacts of disturbance from single sites to a wider area yields unreliable results under the common practice of ignoring FDT: FDT drastically alters the disturbance impact landscape, here leading to fewer disturbance hotspots for shorebirds in the Wadden Sea World Heritage Area.

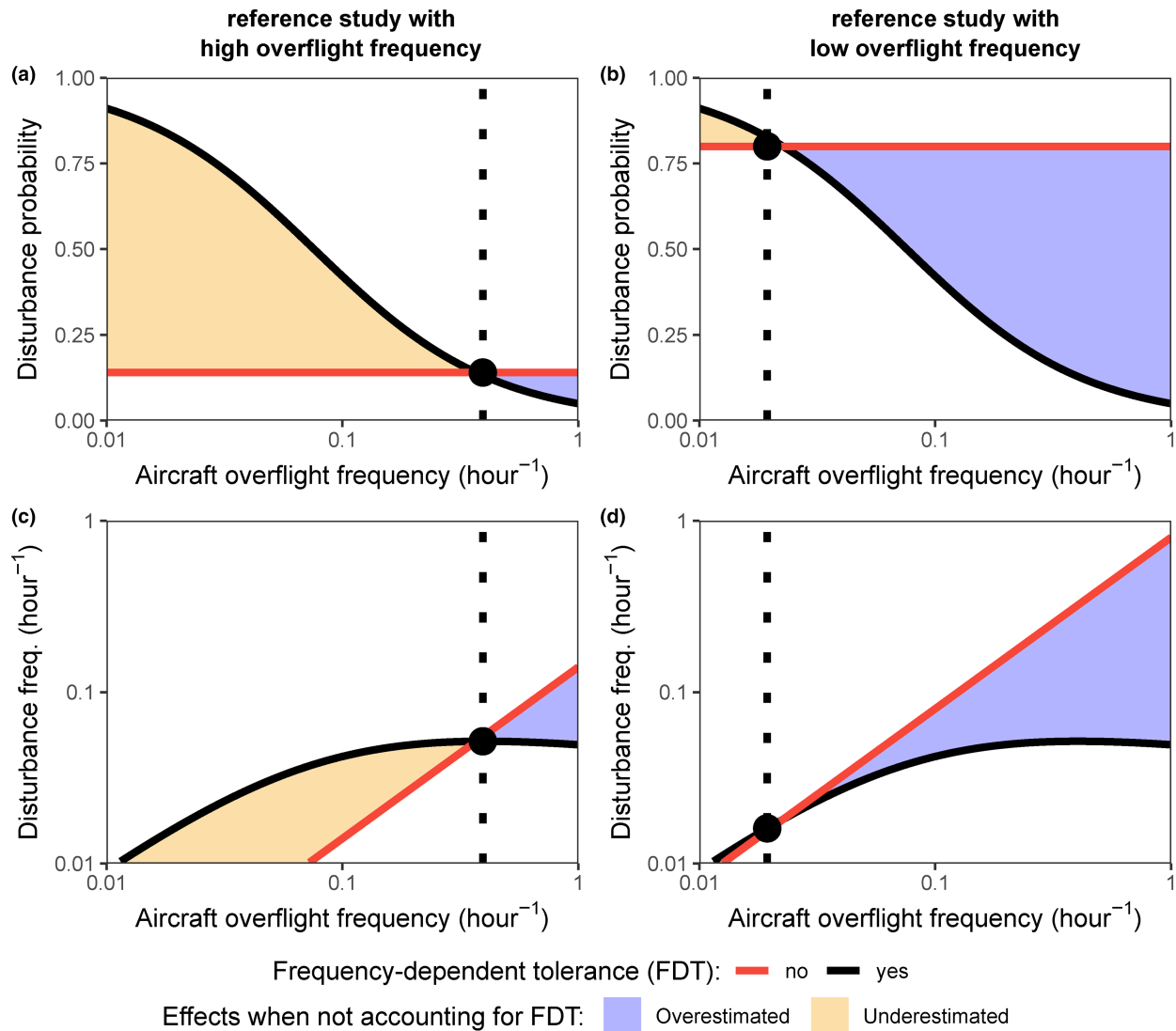


FIGURE 5 Relationships between aircraft overflight frequency and disturbance probability (a, b) or disturbance frequency (c, d) with and without considering frequency-dependent tolerance. The disturbance frequency is calculated by multiplying the aircraft overflight frequency with the disturbance probability. (a, c) show relationships for a reference study where aircraft were common and disturbance probability low (0.14; i.e. small civil airplanes at Vlieland 2017–2018), whereas (c, d) show relationships for a reference study where aircraft were rare and disturbance probability high (0.8; i.e. small civil airplanes at Noordsvaarder 1980–1984). The black circle and dashed line show the aircraft overflight frequencies of the reference studies.

Mechanisms of frequency-dependent tolerance to disturbance

FDT is potentially a common phenomenon in many species and for a variety of disturbance source types (González et al., 2006; Nordell et al., 2017). Two non-mutually exclusive hypotheses can explain why shorebirds are more tolerant to aircraft in areas where aircraft overflights are common. First, shorebirds in those areas may have habituated to aircraft overflights. In support, naïve American black ducks (*Anas rubripes*) held in an enclosure habituated to military aircraft overflights and thereby reduced their response from 38% to 6% after 2 weeks (Conomy et al., 1998). Alternatively, susceptible individuals may avoid sites where aircraft overflights

are more frequent, such that in the most disturbed areas only the least susceptible individuals are present. Such non-random distribution of ‘personalities’ was suggested to exist in great tits (*Parus major*) in urban areas with varying degrees of human activities (Sprau & Dingemanse, 2017) and in burrowing owls (Carrete & Tella, 2013; owls may habituate as well, see Cavalli et al., 2018). In the Wadden Sea, shorebird numbers are high in the few areas with high levels of aircraft disturbance (Folmer et al., 2022), suggesting that these areas are not avoided and thereby pointing towards habituation as the underlying mechanism. Strong direct tests of habituation require experimentally introducing new disturbance sources to animals while following individual's responses over time, but in many parts of the world

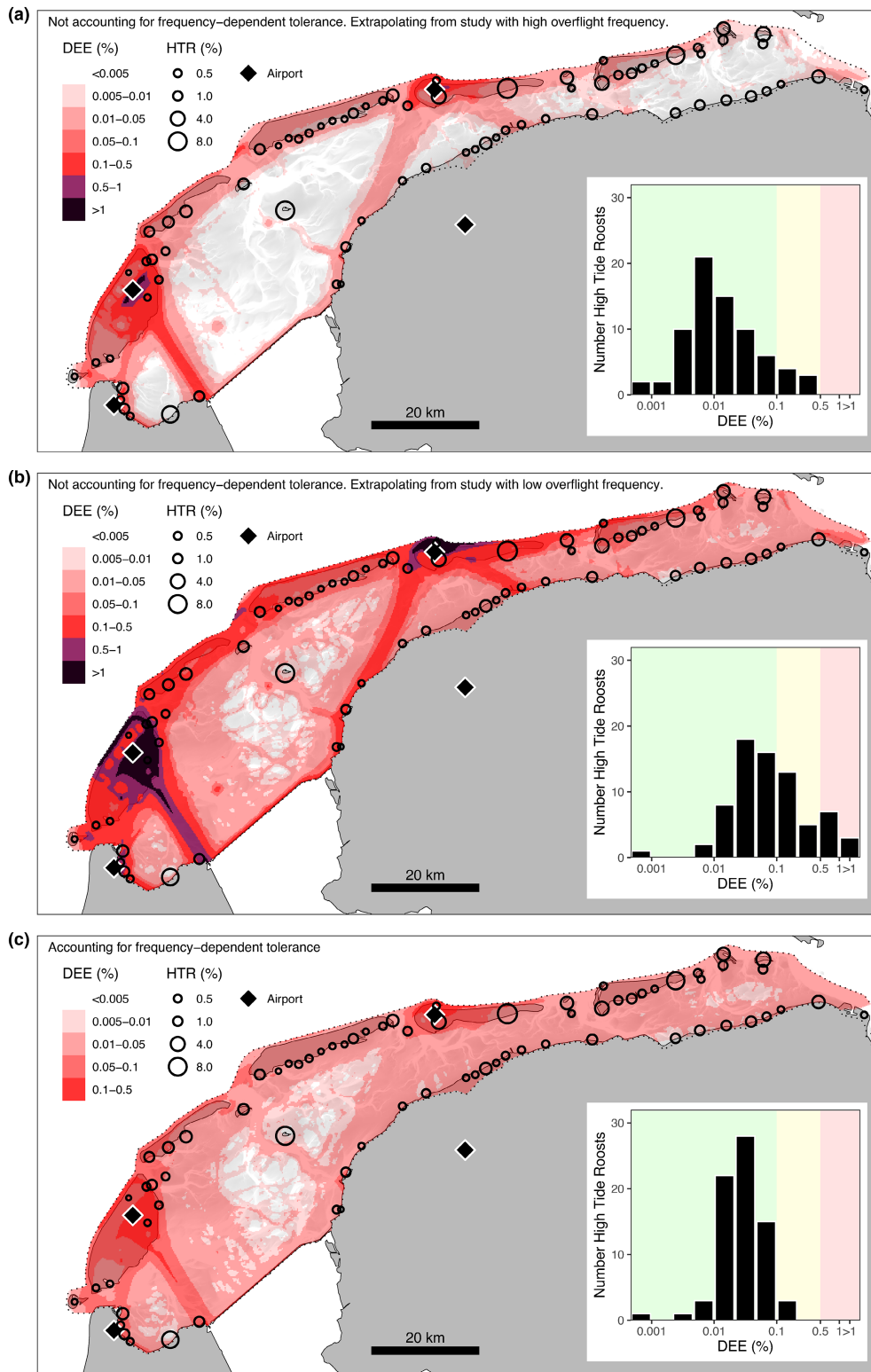


FIGURE 6 Maps of disturbance impact due to flight costs (% additional daily energy expenditure; DEE) by civil airplanes for wintering oystercatchers in the Dutch part of the Wadden Sea World Heritage Area. Shown are situations not accounting for frequency-dependent tolerance and extrapolating from a reference study from an area with a high (a) or low (b) overflight frequency and respectively low and high disturbance probability (based on red curves in Figure 5c,d) and (c) with accounting for frequency-dependent tolerance (based on black curves in Figure 5c,d). Black ring-size indicates the percentage of the oystercatcher population roosting at high-tide roost sites (HTR; total population = 100,000 oystercatchers). The insets present the distribution of energetic costs across the roost sites, where coloured zones indicate low costs that are unlikely to have an impact (green, additional DEE < 0.1%), intermediate costs that may have an impact (yellow, additional DEE 0.1–0.5%) and high costs that are likely to have a significant impact (red, additional DEE > 0.5%), for example, on the condition and survival of birds. The dotted line encloses the area which is used for roosting and foraging by wintering oystercatchers and for which calculations were done. Panel (a) is modified from van der Kolk, Allen, et al. (2020).

it will be challenging to find naïve animals in the wild (or determine their history of exposure to disturbance; Bejder et al., 2009).

Identifying the behavioural mechanism causing tolerance is crucial to determine the disturbance impact. Both avoidance and habituation reduce direct costs due to fewer responses to disturbances. However, avoidance could lead to substantial additional costs by individuals moving to suboptimal habitat, increasing commuting distances and increased competition on the few remaining undisturbed sites. The impacts of avoidance are hard to quantify, but nevertheless very important to consider in projects where new disturbance sources are introduced (e.g. the airport development in Tagus estuary in Portugal; Nightingale et al., 2023), especially since it is impossible to research these effects after the new disturbance source has been introduced. Habituation does not have such additional indirect costs, since animals do not move away but learning not to react to non-threatening disturbance sources, but habituation could also be costly if it makes animals more vulnerable to predators (Geffroy et al., 2015). However, animals can distinguish between non-threatening human activities and predators. For example, birds can distinguish between different shapes and behaviours of aerial disturbance sources, and were shown to react more and habituate less to aircraft and drones that do resemble bird of prey (McEvoy et al., 2016; Storms et al., 2022).

Implications for synthesizing the disturbance literature

The literature consists of many highly idiosyncratic source-specific disturbance responses, sometimes with studies reporting completely opposite results about which type of aircraft is most disturbing (Komenda-Zehnder and Bruderer (2002) vs. van der Kolk, Krijgsveld, et al. (2020)). At first glance, there were large differences in shorebird responses to different aircraft types in our study. However, after accounting for FDT and the fact that our comparative analysis involved responses from studies that varied widely in their air traffic frequency, the variation in responses to different aircraft types was largely reduced. Notably, in the disturbance literature there is no standardization of the frequency at which disturbance sources occur, and thus accounting for FDT has the potential to (i) explain much of the published variation among studies and (ii) clarify that much reported variation is due to methodological rather than biological reasons.

Species also differ in their responses to the same disturbance source type (Blumstein, 2016; Blumstein et al., 2003). FDT could similarly explain part of these species-differences if one would account for the different disturbance source frequencies used in the various studies on different species. Accounting for FDT could

help in synthesizing much of the idiosyncratic source- and species-specific disturbance responses, and a meta-analysis that relates a species' response to the disturbance source frequencies of that published study could be a logical first step to investigate this further.

Implications for predicting costs of disturbance

Disturbance impact assessments have not been considering FDT. However, a strong increase in tolerance with increasing levels of human disturbance implies that observed disturbance responses at one location cannot be extrapolated reliably to another location without considering variation in levels of human disturbance. From a conservation perspective we are typically most concerned about the high-impact locations and ignoring FDT will generally overestimate costs for wildlife at the most impacted sites. This is especially relevant for assessments in areas where disturbance source presence will increase in the future (e.g. build of new infrastructure). If the response of animals is measured in the current situation (i.e. with low frequencies of disturbance source presence) and then extrapolated to the future situation, this would overestimate the future impact of the planned activity when ignoring FDT.

However, the opposite can also happen. Many studies on disturbance are conducted at sites with a high frequency of disturbance source presence, as that is often an incentive to study disturbance impacts. This implies that when the costs are then extrapolated to other sites, for example as part of large-scale disturbance map (van der Kolk, Allen, et al., 2020), that these other sites will mostly have lower disturbance frequencies, and thus ignoring FDT will then underestimate the predicted impact at all but the busiest locations. Whether this is problematic or not depends on the exact threshold of the costs where wildlife will start to suffer (lose mass, increase mortality). In our study, we showed that the number of roosts that experience a cost of 0.5% daily energy expenditure decreased after accounting for FDT. However, if a much lower daily energy expenditure threshold would affect avian performance (e.g. 0.01%), more roost sites would be above this threshold when accounting for FDT (Figure 6c vs. Figure 6a). When doing large-scale assessments, accounting for FDT can thus dramatically change the conclusions drawn on whether disturbance is harmful for wildlife.

In our study, we only considered disturbance probability, while also the intensity of a behavioural response may vary with levels of human disturbance. Previous work in shorebirds showed that flight time following disturbance was higher in response to rarer aircraft types (van der Kolk, Allen, et al., 2020; van der Kolk, Krijgsveld, et al., 2020). When this is generally the case,

ignoring the frequency-dependent nature of responses will further over- or underestimate the average daily energetic costs of disturbance. It also implies that the overall costs of rare and common aircrafts can be quite similar: rare types cause occasionally large additional costs since birds are likely to react and flee far, whereas frequent disturbance sources repetitively cause low additional costs, since birds only react occasionally and spend little energy in their short flight (van der Kolk, Allen, et al., 2020). In general, we aimed to showcase the concepts of FDT and therefore presented predicted costs of disturbance as model estimates without considering precision. When using such models as actual decision tools, we also recommend quantifying model precision to determine how certain locations are below or above a certain threshold. Finally, aircraft impacts may differ from disturbance sources on land (e.g. walkers), since aircraft fly over and do not occupy space on land and physically displace animals. Disturbance sources on land may more easily permanently force away animals if they become too frequent, which is known to lead to avoidance in shorebirds (Martín et al., 2015; van der Kolk et al., 2022).

CONCLUSION

Very few studies have managed to quantify FDT, but our results show that the frequency-dependent effect can be very strong and that clear reasons exist for it to be common. Given that FDT can (i) cause existing extrapolations of disturbance impacts to be unreliable, and (ii) reconcile published highly idiosyncratic species- or source-specific disturbance responses, we argue that studies on disturbance and disturbance impact assessments should consider FDT. Given that it will be hard to standardize disturbance frequencies across studies in the wild, more effort is therefore needed to quantify disturbance responses across a range of disturbance frequencies, even if it involves many hours of observation to observe sufficient responses at low disturbance frequency sites. Furthermore, to make studies more comparable, studies should focus on similar wildlife disturbance response variables (flight initiation distance, disturbance probability, fleeing time) and provide quantitative metrics of the disturbance frequency they encountered (rather than qualitative proxies like urban vs. rural areas). Finally, despite its logistical challenges, experimental approaches may be most meaningful to determine the behavioural mechanisms underlying tolerance and to identify how we can utilize these behavioural mechanisms to reduce the impact of disturbance (Coetzee & Chown, 2016).

AUTHOR CONTRIBUTIONS

All authors designed the study. HK and CS gathered the data. HK performed the analysis. HK and MP

wrote the manuscript, with all authors contributing to revisions.

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DATA AVAILABILITY STATEMENT

All data and R code to replicate the analyses and to reproduce the figures are deposited at Zenodo (<https://doi.org/10.5281/zenodo.10101231>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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