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ORIGINAL ARTICLE

Behavioural responses of the Little Tern (*Sternula albifrons*) to different human disturbances

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Abstract

Human disturbances can have large impacts on wildlife and their behaviour. The extent of the effects of different kind of disturbances during different seasons is, however, less well known. Here, we assessed the impact of three different human disturbance types (a sole walker, two walkers talking, and a jogger) on the flight initiation distance (FID) and flight duration (FD) of a bird species that frequently breeds on coasts, the Little Tern (*Sternula albifrons*) during the breeding season. Our study was conducted in an area heavily utilised by tourists, the Alvor dunes in the Algarve in Portugal. We further assessed the effects of weather conditions and nest age on behavioural responses to disturbances. Although the sample size was limited (experiments were performed on 30 nests), we found that the jogger caused the largest FID, followed by the walker, and two walkers talking. The adult terns tended to return sooner to the nest when they were further along the incubation. The weather did not have any significant effect on the FID and FD in our study. These findings, along with other studies, emphasise the need for careful consideration of disturbance-free zones for coastal breeding birds. Furthermore, the FIDs and FDs cannot be generalised across bird species, time, space, and disturbance type.

Keywords Anthropogenic disturbance · Breeding success · Environmental stressors · Weather conditions · Tourism

Zusammenfassung

Verhaltensantworten von Zwergseeschwalben(*Sternula albifrons*) auf verschiedene anthropogene Störungen

Von Menschen verursachte Störungen können große Auswirkungen auf Wildtiere und ihr Verhalten haben. Wie sehr sich unterschiedliche Arten von Störungen zu verschiedenen Jahreszeiten auswirken, ist jedoch weniger gut bekannt. Wir untersuchten während der Brutzeit die Auswirkungen von drei verschiedenen Arten von Störungen (ein einzelner Spaziergänger, zwei Spaziergänger im Gespräch und ein Jogger) auf die Fluchtinitiationsdistanz (FID) und die Flugdauer (FD) der Zwergseeschwalbe (*Sternula albifrons*), einer Art, die weitverbreitet an Küsten brütet. Unsere Studie wurde in einem stark von Touristen frequentierten Gebiet durchgeführt, den Dünen von Alvor an der Algarve in Portugal. Wir untersuchten auch die Auswirkungen der Wetterbedingungen und des Nestalters auf die Reaktionen auf Störungen. Obwohl die Stichprobengröße begrenzt war (die Experimente wurden an 30 Nestern durchgeführt), stellten wir fest, dass der Jogger den stärksten FID verursachte, gefolgt von einem Spaziergänger und den zwei sich unterhaltenden Spaziergängern. Erwachsene Seeschwalben zeigten die Tendenz, schneller zum Nest zurückzukehren, wenn das Brüten schon weiter fortgeschritten war. Das Wetter hatte in unserer Untersuchung keinen signifikanten Einfluss auf die FID und FD. Diese Ergebnisse unterstreichen, wie auch

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andere Studien, die Notwendigkeit, störungsfreie Bereiche für Küstenbrüter gründlich zu erwägen. Darüber hinaus lassen sich die FIDs und FDs nicht über Vogelarten, Zeiträume, Räume und Art der Störung hinweg verallgemeinern.

Introduction

We are affecting wildlife through both consumptive (e.g. hunting) and non-consumptive activities (e.g. hiking, dog walking, and birdwatching) (Gaynor et al. 2018; Dertien et al. 2021). Coastal areas are heavily affected by these non-consumptive recreational activities because they provide services such as tourism (Cortés et al. 2021). Simultaneously, they also provide a crucial breeding habitat for shorebirds. The disturbances resulting from this overlap cause degradation of their habitat due to reduced foraging efficiency and opportunities to rest, which can eventually lead to altered behaviour and reduced survival and reproduction (Fitzpatrick and Bouchez 1998; Lafferty 2001).

A widely used measure to minimise effects of human disturbances is applying buffers or set-back distances, which are based on the assumption that with increasing distance the animal will respond less strong to the stimulus (Rodgers and Smith 1997; Glover et al. 2011; Schlacher et al. 2013). A practical method to measure the effect of human disturbances and estimate effective set-back distances is to measure the flight initiation distance (FID). The FID is the distance between the stimulus and the location where the individual animal will physically escape this potential threat (i.e. it is an indication of the tolerance to these disturbances; Guay et al. 2016). According to the optimal escape theory (Ydenberg and Dill 1986), an animal escapes a threat when the predation risk is equal to the cost of escape (Cooper et al. 2003). When a bird escapes too early, this might have a negative effect on the foraging efficiency or the physiology of the bird. However, leaving too late can increase predation mortality (Morelli et al. 2022). Based on FID data, an online tool has been created by Guay et al. (2016) for the management of birds. It will calculate the advised setback distances for multiple species and several types of disturbances, based on the user's preference (Guay et al. 2016).

In addition to FID, the intensity of the response can be measured by recording the flight duration (FD), which is defined as the time it takes for the bird to return to its initial location (e.g. a nest) after disturbance. It is an important response variable to measure when assessing the disturbance sensitivity of a bird (Collop et al. 2016). Bird species differ in their susceptibilities plus their response to a variety of stimuli, causing differences in their disturbance frequency and FD upon disturbance (van Der Kolk et al. 2020). The time a bird is away from the nest could also have energetic consequences. In combination with the frequency of disturbance, the bird could eventually reach a threshold where it cannot compensate for the increased energy costs (van Der Kolk et al. 2020).

The FID and FD can vary due to multiple factors, such as species, body size, group size of approaching humans, speed of approach, nature and type of stimulus, stage of breeding, flock size and interacting factors, habituation, climatic conditions, level of urbanisation, and time of the year (e.g. Geist et al. 2005; Kerbiriou et al. 2009; Glover et al. 2011; Weston et al. 2012; McLeod et al. 2013; Amat et al. 2017; Lethlean et al. 2017; Bernard et al. 2018; Díaz et al. 2021; Hammer et al. 2022; Yin et al. 2023; Shuai et al. 2024). There are, however, many contradictory studies, suggesting that there are multiple species-dependent factors to be taken into account when studying disturbance behaviour in birds. Notwithstanding the relatively large number of studies on the subject, there are still relevant knowledge gaps concerning birds' behavioural responses to disturbances (Goodship and Furness 2022). First of all, most studies fail to assess the impacts of different stimuli on the FID and FD. The vast majority of papers have focussed on a sole walker as a stimulus and did not focus on other types of human activities (Lethlean et al. 2017; Bernard et al. 2018). Yet, those studies that did, regularly find different impacts of different types of stimuli (Cavalli et al. 2016a; Bernard et al. 2018; de Resende et al. 2024). Furthermore, behavioural responses to different stimuli may vary through time, i.e. the FID of a specific species to a specific stimulus may be different in the non-breeding season than in the breeding season due to different costs associated with escape in both seasons (Baines and Richardson 2007; Weston et al. 2012). Nevertheless, most studies on FID and FD distances have been conducted during the non-breeding season (Weston et al. 2012). Yet the breeding season is arguably more essential for the survival of both adults and chicks. The intensive reproductive efforts of birds during the breeding season can have large effects on their body condition (Sergio et al. 2019). The breeding season also coincides with increased numbers of tourists in many coastal areas which may further negatively affect chick survival and body condition (Müllner et al. 2004; Price 2008). A better knowledge on behavioural responses of birds to disturbances during the breeding season is therefore important. Furthermore, there is relatively little knowledge about differences in FIDs and FDs during the different stages in the breeding seasons (egg laying, incubation and post-hatching). FIDs may for instance be stable or unstable during the breeding season depending on the habitat type birds are located in (Cavalli et al. 2016b). Such knowledge is important if we are to provide effective conservation in areas highly exploited and used by tourists. Knowing when most protection is needed can aid the reconciliation of different purposes for an area.

Here, we studied the impacts of different stimuli on the FID and FD of the Little Tern (*Sternula albifrons*), during the breeding season in a coastal area highly utilised by tourists, the Alvor dunes in the Algarve in Portugal. This species often breeds in coastal areas. It is declining in numbers (BirdLife International 2021a) and in the region threatened by anthropogenic pressure, such as urbanisation and human recreation (Correia 2016). These anthropogenic threats are associated with reduced breeding success and declines in population numbers of the Little Tern in the area (Correia 2016). Published and available knowledge of the FID of this species would aid its conservation and may simultaneously benefit other coastal breeding birds in the area. Thus far, there are no data available on disturbance responses of the Little Tern in the breeding season. Here, we first obtained an indication of the type and frequency of the most common diurnal disturbances, both natural and anthropogenic, for the Little Tern in the region. Secondly, we determined the FID and FD responses of the Little Tern to different human disturbances—one walker, two walkers talking, and a jogger—during the breeding season (May, June and July) of 2023, accounting for environmental factors and nest characteristics. These three disturbances were selected as they were thought to best represent typical anthropogenic disturbances in an area heavily utilised by tourists, and partly due to logistic reasons related to availability of staff. Specifically, we addressed the following research questions:

1) What are the types and frequencies of the most common diurnal disturbances experienced by Little Terns in the region? We hypothesised that human-related activities, such as single walkers, and groups of walkers, would be the most frequent diurnal disturbances in the region.
2) How do the different disturbance stimuli affect the FID and FD of Little Terns? We hypothesised that the jogger treatment would have the largest impact on FID, compared to the single walker treatment, due to the faster movement and perceived threat (Cooper et al. 2006; Lethlean et al. 2017). We further hypothesised that two walkers talking would elicit a longer FID compared to a single walker due to increased visual and auditory stimuli (de Resende et al. 2024). For this reason, we also hypothesised that the two walkers talking would have the largest impact on the FD (van Der Kolk et al. 2020).
3) How do environmental factors, such as temperature, and nest characteristics, such as nest age, influence FID and FD? We hypothesised that FID would decrease with increasing temperature following findings by others (Dı́az et al. 2021). We further hypothesised that the FD would be negatively influenced by higher temperatures, as Little Terns are likely to minimise time away from the nest to reduce the risk of eggs and chicks overheating (Yasué and Dearden 2006). Also, the FD would decrease with nest age due to heightened parental defence behaviour as hatching approaches (Yasué and Dearden 2006).

Methods

Study species and area

The Little Tern is a migratory shorebird that breeds between May and July in either solitary pairs or in colonies (BirdLife International 2023). It usually breeds on sparsely vegetated beaches with less than 15% vegetation cover. Its diet consists of small fish, crustaceans, insects, annelid worms, and molluscs (Birdlife International 2023). The current breeding population in Europe is estimated to be around 12,800 to 18,700 pairs and has been declining with 9% over the course of 29 years (Birdlife International 2021a). In Portugal, the breeding population is estimated to be around 620 to 650 pairs, but data on its long-term population trend are lacking (BirdLife International 2021b).

The study took place at the nesting sites of the Little Tern on the southern coast of Portugal in the Faro district. The colony was located on the western part of the Alvor dunes (Fig. 1). The Alvor dunes are part of the Ria de Alvor estuary, which is both a Natura 2000 and a Ramsar site (Mateus et al. 2016; Ramsar 2016). The estuary has multiple functions, including acting as a stopover area for migrating birds and a breeding ground for several bird species (Mateus et al. 2016) including the Little Tern. The area surrounding the Ria de Alvor estuary is a popular tourism destination and has been subjected to urban development in the last few decades (Mateus et al. 2016). The part of the beach where the Little Terns are breeding is fenced off during the peak season with a simple rope fence. This conservation effort is led by the Portuguese Institute for Nature Conservation and Forests (ICNF) in collaboration with, amongst others, A Rocha Portugal (https://arocha.pt/en/), an organisation for nature conservation in the area. The western side of the Alvor dunes is the quietest part of these dunes. Early in the season (around the end of May), only a limited number of people will visit this part of the beach at a certain time point in the afternoon (ranging between five and ten). As time progressed, and especially in July, it was visited by substantially more people (ranging between ten and 40 people at any time point during the afternoon) (personal observation).

The study area was searched for nests of the Little Tern at the start of the breeding season in mid-May 2023. When nests were found, they were numbered. Nest locations were recorded with a GPS (Garmin GPSMAP 67) and marked using a permanent marker and wooden tongue depressors which were placed at least 40 cm away from the nest (Medeiros et al. 2007). Nest age of each individual nest was

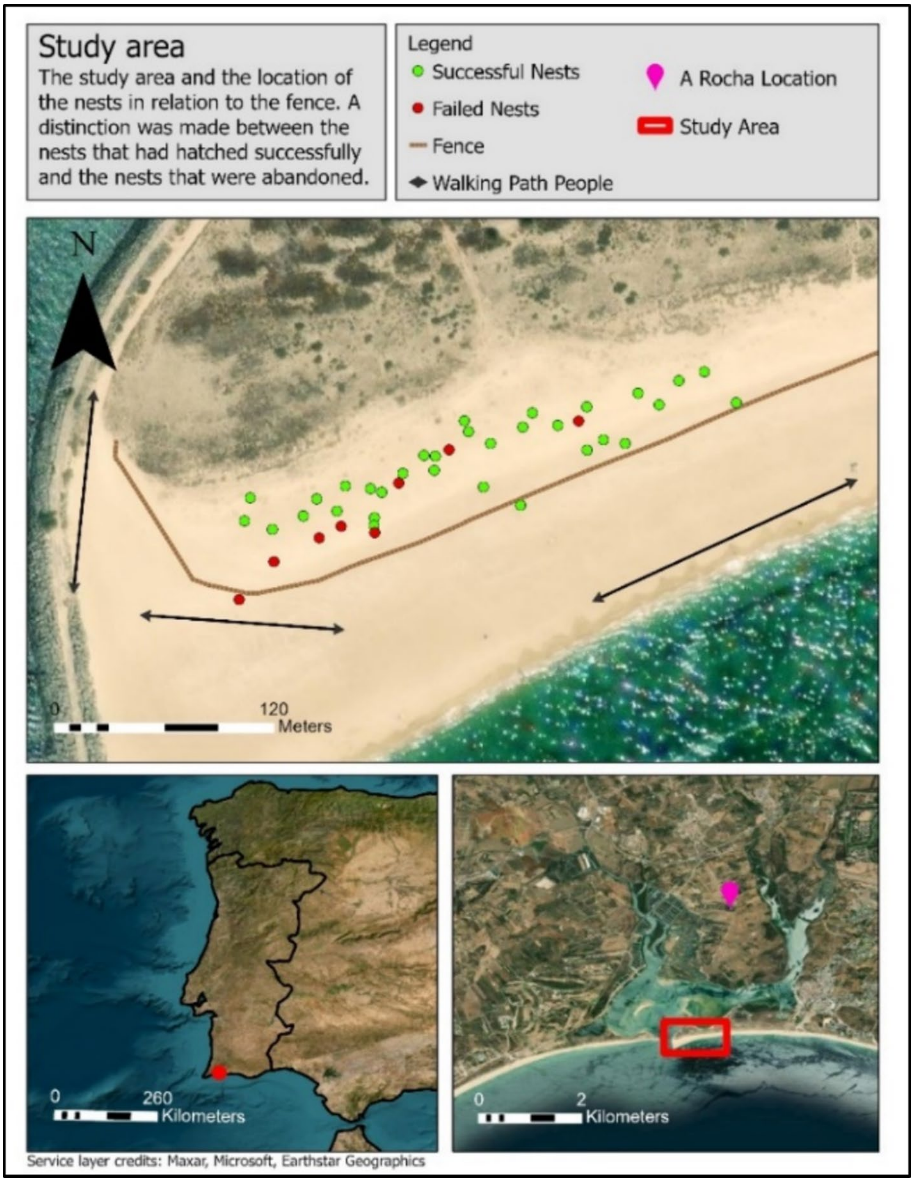

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Fig. 1 Study area, with all the nests found that hatched successfully (green dots) and the ones that did not (red dots), and the location where most people walked in relation to the fence. The location of the weather station from A Rocha Portugal is indicated in the right lower picture

determined by using the egg floatation method from Hays and LeCroy (1971) of the Common Tern (*Sterna hirundo*). Nest age was defined as the estimated number of days from when the first egg had most likely been laid to the day of the experiment. For nests first discovered after hatching, exact hatch dates could not be observed directly. Incubation ranges between 18 and 22 days (Cramp et al. 1988; Cheah and Ng 2008; Doyle et al. 2013). To estimate hatch dates in such cases, we assumed the average incubation period of 21 days and added one day for each chick that had already hatched when the nest was found. This approach provided a consistent and transparent rule for estimating ages while remaining within the known incubation range. Although this rule simplifies variation among clutches, it ensures comparability across nests and avoids over-estimating precision by selecting a narrower or arbitrary incubation value. Females usually abandon the nest when the chicks are 2 to 3 days old after which the chicks also leave the nest (Davies 1981).

Data collection

Observational and experimental data were collected between the 16th May and the 4th July 2023, usually between 11:00 and 18:00, when the birds were observed sitting on the nests most often. Some data (4% of the cases) were recorded earlier or later (electronic supplementary material S1) due to logistical constraints. Before each experiment to collect data on FID and FD started, there was a 15 min observation period of the bird sitting on a nest to account for potential short-term disturbances of the bird in focus due to external factors. In addition, this observation period allowed for the collection of diurnal disturbance data, which may not be representative for disturbances throughout the day, but do give an indication of the type and general frequency of disturbances in the area. This was done before each stimulus was applied to the nest. These observations were therefore also collected between 11:00 and 18:00. During these initial 15 min, the disturbance frequency, the cause of the disturbance, and the total time away from the nest after the disturbance were recorded. Both disturbances directly caused by humans (e.g. joggers, groups of people walking) and natural disturbances (e.g. gulls, heat) were recorded. A disturbance was classified as heat when the adults left the nest to go to the sea and wet their bellies and legs to cool themselves and their eggs down. This is a behaviour that is observed in a few other tern species as well (Sullivan et al. 2020). The experiments started after this initial observation period.

FID data were collected by applying three different experimental stimuli to each nest: a sole walker, two walkers talking, and a jogger. The distance at which a bird would take off from the nest was measured with a range finder (Nikon Forestry Pro accuracy ± 0.5 m when distance < 100 m). As the starting distance can affect the FID (Blumstein 2003), the starting distance from each nest was always approximately 80 m, which was determined with the use of the range finder. This distance was based on trial and error, because at this distance we could still easily see the bird sitting on the nest with binoculars and the bird itself did not seem to be bothered by our presence. Experiments only started when the birds were sitting on the nest. Nests were always approached from the south, or the southeast/southwest, because of the vegetated dunes that were right behind the colony on the northern side. Eye-contact with the bird was avoided and the nests were approached in a straight line. The three stimuli were applied in a random order on the same nest with a 1-h interval by the same observer. A second observer joined in the two walkers' talking approach. The observer(s) always wore the same non-conspicuous dark neutral coloured clothes. There were variations in people when applying the 'two walkers talking' stimulus because it was dependent on the availability of staff from A Rocha Portugal. The conversation started when the approach was initiated, and always consisted of small talk in a normal voice (e.g. 'How was your day?', and 'What are your plans for the weekend?'). The conversation stopped when the bird fled. The average speed of walking was 1 m/s, whereas the average speed of the jogger was 3 m/s (Glover et al. 2011). This was practiced beforehand. The FD was recorded by a second observer. This study complied with all current Portuguese laws and regulations. All data collected for this study were obtained using minimally invasive methods. Birds were not handled. They were habituated to the presence of humans, as the colony is situated in a heavily utilised tourist area.

Weather variables average wind speed, percentage cloud coverage, and ambient temperature were recorded before each experiment. Average wind speed data were measured over a 2-min period using an anemometer. Horizontal pictures of the sky were taken to visually estimate the percentage of cloud cover. Ambient temperature data were recorded with HOBO Data Loggers. These data loggers were placed on the dunes behind the colony, at a distance of approximately 5 m, out of reach for the general public. Daily wind direction data at 10:00 were taken from the weather station from A Rocha Portugal, which is located approximately 2.6 km away from the Alvor dunes (Fig. 1). The wind direction was divided into four categories for further analysis: north, east, south, and west. Unfortunately, due to logistic reasons, some data points were missing. As there is a positive relationship between relative humidity and cloud cover (Walcek 1994), linear regression was used to infer the two missing cloud cover data points using the complete data for relative humidity. Missing data on wind speed ($n = 11$) and wind direction ($n = 6$), were augmented with values recorded by the Portuguese Institute for Sea and Atmosphere (IPMA) in Portimão (data provided by Ricardo Deus of the climate department), which were recorded at Praia da Rocha located approximately 7 km away from the study area. There was no strong collinearity between the weather variables cloud cover and ambient temperature ($r = -0.432$) and cloud cover and relative humidity ($r = 0.521$).

As neighbouring birds may have an impact on the behavioural responses of the focal birds (Burger and Gochfeld 1988), nest density was determined by counting the number of nests within 46 m of the focus nests. The nest density was based on the FID measured after all experiments were completed. The buffer therefore had a diameter of 92 m and a radius of 46 m. This was used because nearby nests were very likely also affected by the observer's approach within that range of the focus nest. When a predator is approaching, many bird species will display alarm calls to other members of the same group, therefore affecting other birds (Suzuki 2011). This was done in *QGIS* version 3.28 (QGIS 2022) by creating buffers around each individual nest and overlapping these buffers with the nest layer to check which nests were intersecting the 46 m buffer. Only nests that were likely to be active during the day of the experiment of the focus nest were included, nests that were older than 21 days within the buffer zone were excluded from the analysis (Cheah and Ng 2008). As the strength of a behavioural response to a disturbance may vary based on habituation, the shortest distance with which each nest was situated from the fence was taken into account in the analyses. Distance to the fence was also calculated using *QGIS*. The average distance of the nests to the fence was 22.8 m. (min. 2.4 m, max. 44.8 m). As Little Terns are known to partake in so-called dreads or panic flights in which the entire colony all of a sudden takes flight for no apparent reason (Chabot et al. 2015); we paid close attention to this occurring in the colony. It did not occur during our experiments.

Statistical analysis

ArcGIS Pro version 2.9.5 (ESRI 2023) and *QGIS* version 3.28 (QGIS 2022) were used for visualisation and distance and density calculations. As data were collected on weekdays ($n = 13$) and in weekends ($n = 3$) and differing numbers of tourists may be expected during these parts of the week, we tested for significant differences between median diurnal disturbances during these parts of the week using a Mann–Whitney U test. Generalised linear mixed models (GLMMs) were used to identify possible effects of the collected variables on the FID and FD, using *R* in *RStudio*® (Posit 2023), with the *lme4* package (Bates et al. 2023). FD was log-transformed due to non-normality and heteroscedasticity. There was no multicollinearity amongst the predictor variables (all variance inflation factors < 5; *car* package; Fox and Weisberg 2019). Predictor variables (all weather variables, nest age, nest density, distance to the fence, stimulus type and the order of the treatment) were first tested in univariate models with FID as a response variable and nest ID as a random factor. Date and time had no effect (all $p > 0.1$) and were excluded. Various interaction terms were tested for significance; wind direction × wind speed, diurnal disturbance frequency x disturbance duration, ambient temperature × nest age. For categorical predictors, ANOVAs and post hoc test with 'sidak' adjustment were used to test for overall significance (*car* package; Fox and Weisberg 2019; and *emmeans* package; Lenth 2025). If the variable was found to be significant on a 0.1 level, it was selected for multivariate models. The order of the treatment was always included. Final model selection was based on the Akaike information criterion (AIC), keeping the most parsimonious model when ΔAIC was < 2. Model fit was evaluated with *r.squaredGLMM* function from the *MuMIn* package (Barton 2023).

Results

We found a total of 40 Little Tern nests during the fieldwork period between the 16th May and the 4th July 2023 on the western side of the Alvor dunes. The experiments were performed on 32 of these nests, of which eight had hatched chicks (electronic supplementary material S1). The remaining eight nests were already empty. Two of the nests included in the experiment failed due to abandonment for unknown causes, the remaining 30 nests were successful (Fig. 1).

Types and frequencies of diurnal disturbances

The most common recorded diurnal disturbance was a natural disturbance, heat, which accounted for 54.5% of all the disturbances observed in a total period of 8 h. Other common disturbances were caused by groups of people (more than one person) (14.4%), gulls (10.6%), sole walkers (7.6%), groups of people with a dog (3.8%), and off leash dogs (3.8%) (Fig. 2). There was no significant difference between the median diurnal disturbance frequency on weekdays and weekend days (Mann–Whitney U test: $W = 900$, $p = 0.205$).

Effects of disturbance stimuli and environmental factors on the FID and FD

The FID was on average 45.7 ± 11.7 m and was affected by stimulus type (Table 1, Fig. 3). None of the other predictor variables nor interaction terms significantly affected the FID. The most parsimonious model with the lowest AIC (694.1) was the model with stimulus type as the only fixed factor and the nest identification as random factor. The model with treatment order as additional fixed factor had a lower AIC (693.4) but ΔAIC was 0.7 and treatment order itself did not significantly affect the FID ($p = 0.183$). The variance explained by the model was 0.308 excluding the random factor and 0.498 including the random factor (nest identification). Of the stimulus types, the jogger caused the largest effect. The birds left the nest significantly sooner when it was confronted with a jogger (average FID 54.4 m ± 8.9 m) than when it was confronted with a sole walker (44.7 m ± 9.6 m) or with two walkers talking (38.2 m ± 10.8 m) (Fig. 3). Compared to the two walkers talking, the FID was 15.9 m longer for the jogger (SE = 2.015, $df = 60.365$, $p < 0.001$), and 6.1 m longer for the sole walker (SE = 2.011, $df = 60.368$, $p = 0.003$). All of the group levels differed significantly from each other (Table 1).

The average FD was 58 ± 60 s and was affected by age of the nest (Table 1, Fig. 4). None of the other predictor factors, including stimulus type (Fig. 5), nor interaction terms significantly affected the FD. The most parsimonious model with the lowest AIC (203.7) was the model with nest age as the only fixed factor and the identification of the nest as random factor. The variance explained by the model was 0.158 excluding the random factor and 0.322 including the random factor (nest identification). Adult terns with older nests returned sooner to the nest; the response time decreased with 4.8% per day.

Discussion

Obtaining a better understanding of the behavioural responses of birds, and the magnitude of the responses to disturbances is essential for the right implementation

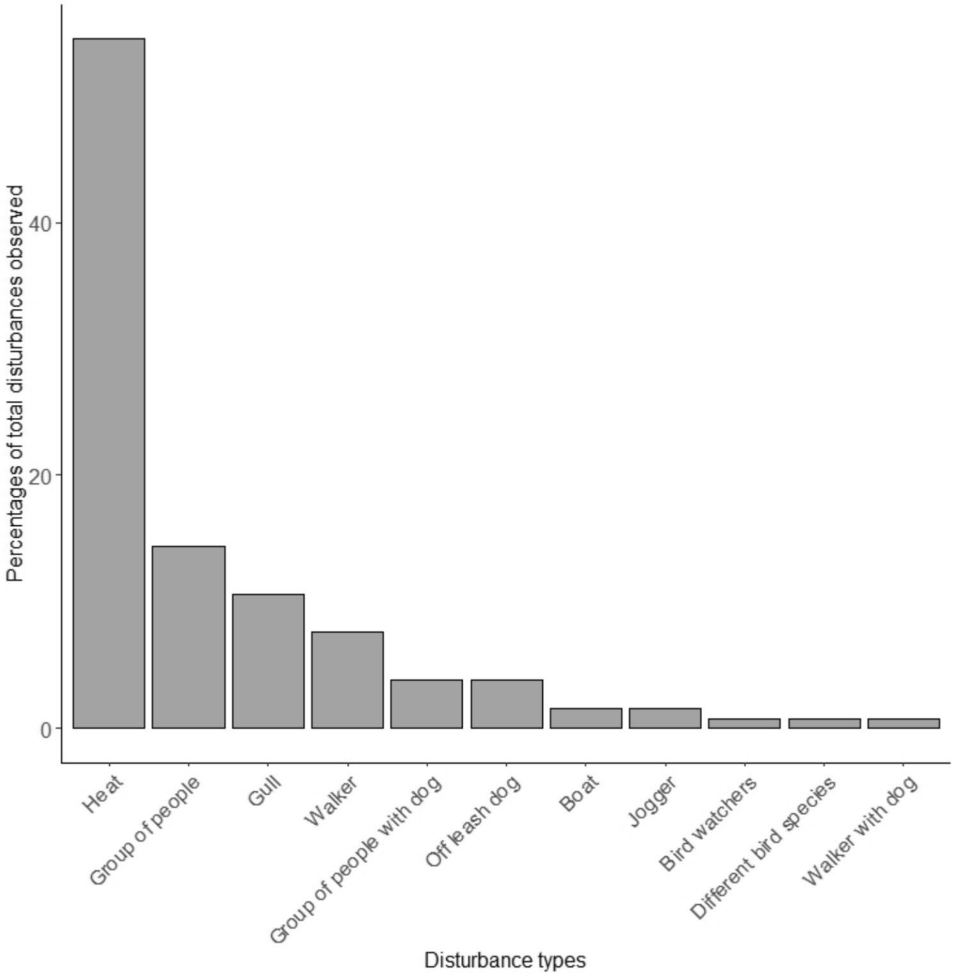


Fig. 2 Frequencies of the disturbances observed

Table 1 Results of the GLMM for FID, Sidak posthoc test for FID per stimulus type, and GLMM for FD

Model	Response	Variable/contrast	Coefficients	SE	*df*	*t*–value	*p*
GLMM	FID	Intercept	38.228	1.728	79.683	22.122	< 0.001
		Stimulus type 'Jogger'	15.847	2.101	60.776	7.542	< 0.001
		Stimulus type 'Walker'	6.512	2.081	60.323	3.129	0.003
Sidak Posthoc	FID	Two walkers talking – jogger	−16.030	2.140	61.300	−7.508	< 0.001
		Two walkers talking – walker	−6.740	2.120	61.100	−3.177	0.007
		Jogger – walker	9.290	2.150	60.500	4.315	< 0.001
GLMM	FD	Intercept	3.753	0.081	30.119	46.182	< 0.001
		Nest age	−0.292	0.081	30.128	−3.476	0.001

of conservation measures. Especially for species that are already threatened by anthropogenic activities such as the Little Tern (Correia 2016). We need to have a good knowledge of the distances at which different types of disturbances may cause disruptions, like leaving the nest, and how long those disruptions maintain to reconcile effective conservation of coastal species with tourist activities occurring in the same region. Here we found that the most frequent diurnal disturbances for the Little Tern in the area were heat, (groups of) people, gulls, and people with (off-leash) dogs. Behaviour of Little Terns after these disturbances was, however, not recorded. Regarding the disturbance experiments, we found that stimulus type had a significant impact on the FID of the Little Tern but not on the FD. The weather and other external factors did not have a significant effect on the FID and FD, but for nest age which had a significant impact on the FD. Adults returned sooner to the nest when eggs were nearing hatching time or when eggs were already hatched.

Fig. 3 Flight initiation distance per stimulus type

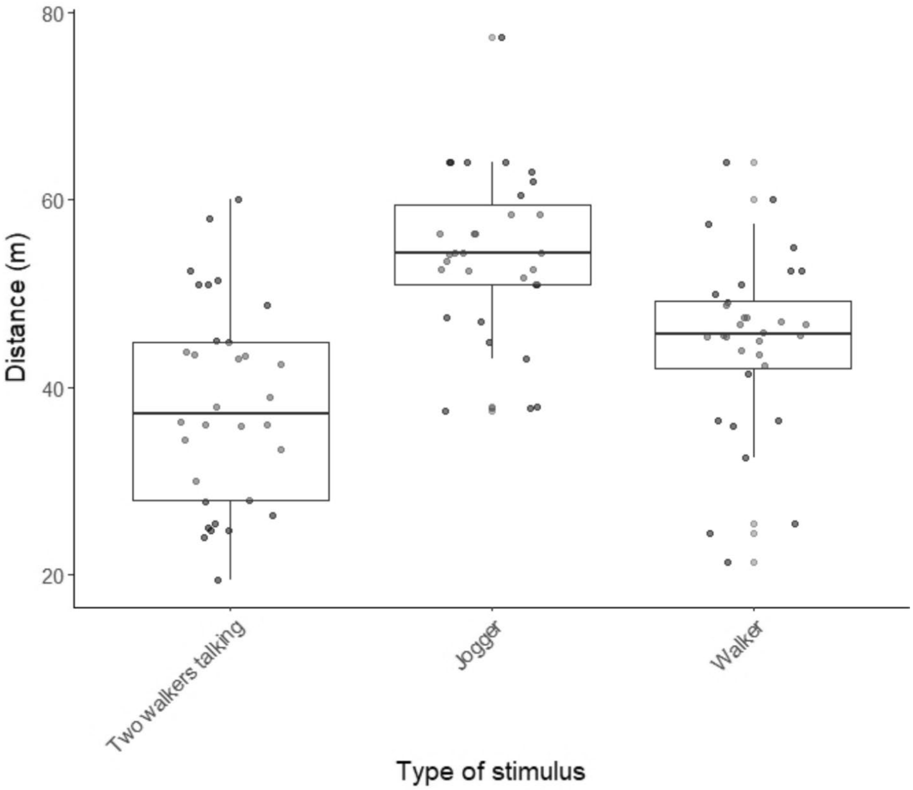
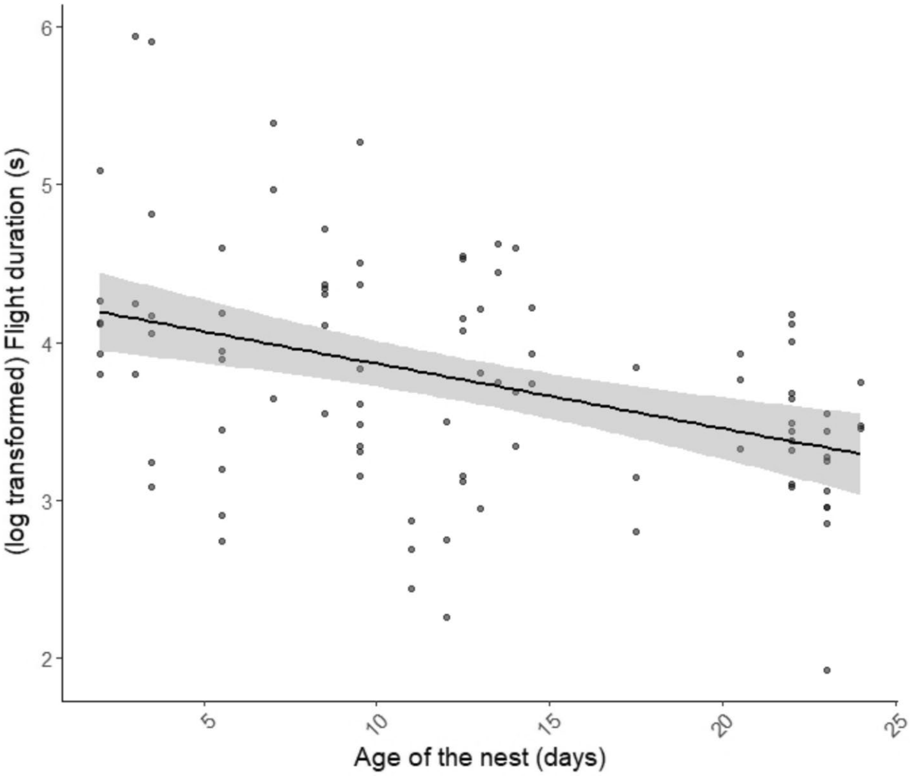


Fig. 4 Flight duration (Log transformed) as a function of nest age in days



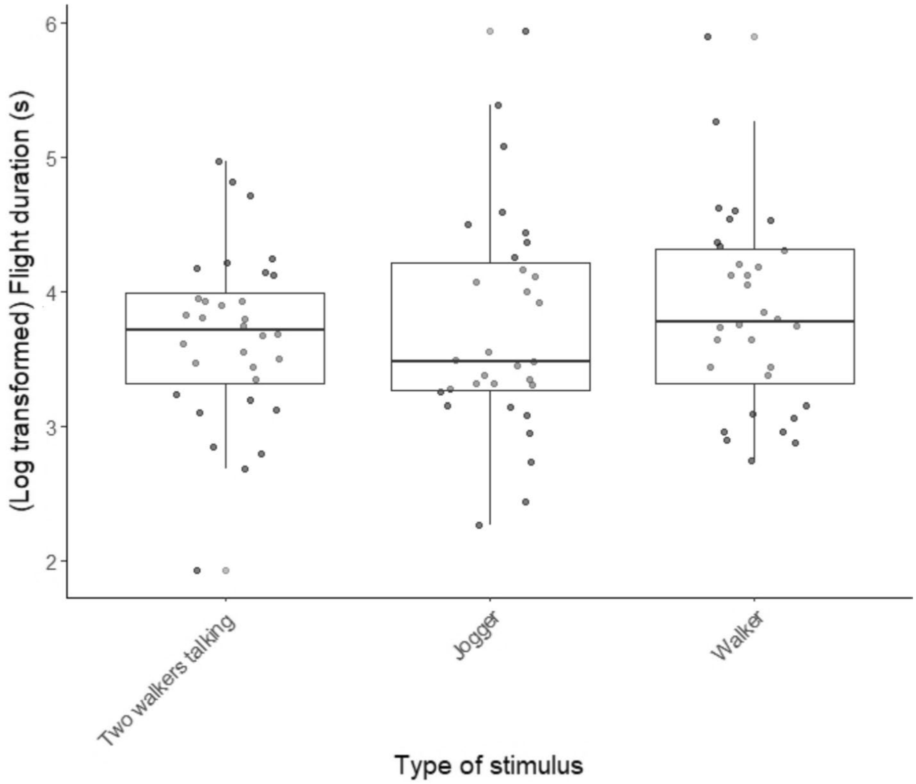


Fig. 5 Flight duration (log transformed) per stimulus type

Types and frequencies of diurnal disturbances

We hypothesised that human-related activities would be the cause of most frequent diurnal disturbances. Even though human-related activities did cause frequent disturbance, heat stress was the cause of over 50% of the diurnal disturbances in our study region. Heat stress caused birds to leave the nest to wet their bellies and legs to cool themselves and their eggs. We however do not know if the level of disturbance observed here was abnormal in comparison to earlier years and other regions. As we only recorded diurnal disturbances for short periods before the experiments, we cannot give daily estimates either. Notwithstanding, climate change is expected to come with an increased frequency of extreme heat events. This may lead to a more frequent display of such behaviours and can also have negative consequences for the reproductive success of birds, especially in hot and arid environments (Sharpe et al. 2021). Heat events can cause catastrophic chick mortality due to higher ground and air temperatures (Salzman 1982). It can also alter the behaviour of a bird. In addition to heat stress, people, be it in groups or alone or with or without dogs, were, as expected, reasons of frequent disturbance for Little Terns in our study region throughout the week. This is a consequence of the region being popular among tourists.

Effects of disturbance stimuli on the FID and FD

The relatively large frequency of human-related activities can cause large disturbances of birds. We hypothesised that the jogger treatment would have the largest impact on FID followed by the two walkers talking, and that the single walker would have the smallest impact. We further hypothesised that the two walkers talking would have the largest impact on the FD. We indeed found that the mode with which people approached breeding Little Terns had a significant impact on the FID, but not on the FD. Birds left the nest significantly earlier when a jogger approached than when a sole walker approached, a finding corroborated by earlier work (Lethlean et al. 2017). The faster rate of change in the size of the threat in the bird's view and the higher level of noise caused by joggers may be important reasons for these differences (Lethlean et al. 2017). However, contra to our expectation, Little Terns generally allowed a closer approach when they were confronted with two walkers talking compared to a sole walker and a jogger. This is also contradictory to findings by Geist et al. (2005), who found that the Pied Currawong (*Strepera graculina*) did not show a difference in FID when confronted with one walker and two people walking. This emphasises that the response to a certain threat is species-specific (Glover et al. 2011) and may depend on life history traits (Geist et al. 2005). That

Little Terns in our study did show a significant different response to the sole walker than to the two walkers talking may be explained by the focus on the bird. American Robins (*Turdus migratorius*) are for instance able to assess whether approaching humans are looking directly at them or not; they have shorter FIDs when the focus is not on them (Eason et al. 2006). Further research is needed to study the effect of focus (i.e. looking versus not looking at the bird) and potentially auditory cues, such as talking versus not talking, on the Little Tern.

Effects of environmental factors on the FID and FD

Environmental factors may also have large impacts on the responses of birds to stimuli (Amat et al. 2017; Díaz et al. 2021; Hammer et al. 2022). We hypothesised that FID and FD would decrease with increasing temperatures. We, however, did not find any significant effects of weather conditions on the FID and FD of the Little Tern. The fact that the majority of data was collected during the hottest part of the day (between 11:00 and 18:00) when the Little Terns were most often seen incubating the nests, may explain that temperature did not have significant effects on behavioural responses of Little Terns. Studying impacts of ambient temperature on the FID and FD may therefore need to take place during a larger part of the day to cover a larger range of ambient temperatures.

We further hypothesised that FD would decrease with nest age. We indeed found that nest age had a significant impact on the FD. Birds returned earlier to the nest when they had eggs that were close to hatching or chicks in the nest. This contradicts findings for e.g. the Malaysian Plover (*Anarhynchus peronii*) (Yasué and Dearden 2006). These different findings again suggest that behavioural responses to disturbances are species-specific and findings for one species cannot easily be transferred to other species. Every bird species can show different risk-taking behaviours, such as returning earlier to the nest, which can for instance be dependent on body size (Oteyza et al. 2021). The defence strategy of a species may also play a role. Small waders such as the Malaysian plover will try to lead the predator away from the nest in a distractive display. Returning quickly to the nest would not be optimal in this case. The Little Tern, however, is a very aggressive bird and will start mobbing potential predators by diving repeatedly at the threat (McManus 2018), and quickly returning to the nest would therefore not be such an issue. This risk-taking behaviour of a bird may change with nest age as well. Eggs that are near hatching or have already hatched might increase the nest defence behaviour compared to the recently laid eggs since they have a higher probability of making it to the reproductive stage (Thys et al. 2019). The type of predator that caused the initial disturbance may also influence the nest return time and the risk-taking behaviour of a bird (Yasué and Dearden 2006; Thys et al. 2019). The Little Tern likely responds differently to a human predator than to e.g. a gull or snake.

Limitations to the study

An important limitation to our study is that we were only able to conduct experiments on 30 nests, due to not more nests being available in the study area. However, with this small dataset, we were still able to uncover some significant findings. A larger dataset would likely find similar, and perhaps even stronger effects. Yet another limitation was that we did not have accurate hatching days for every nest and had to resort to making some assumptions regarding the age of the nest. This may have affected our conclusions to some extent. As we found a limited number of nests in the area and were limited by logistic constraints, we were also unable to do more disturbance experiments (e.g. effect of a larger group of people or of a dog walker). Effects of different anthropogenic disturbances on the FID and FD on the Little Tern therefore remain unknown. Furthermore, factors like the sex of the bird and age may also affect the behavioural responses of birds to disturbances (Weimerskirch et al. 2002; Møller 2014). We unfortunately were unable to take that into account as the Little Tern is a monochromatic bird species. The level of camouflage of the eggs may also affect the FID of some bird species. Birds with poorly camouflaged eggs against the background can for instance have longer FIDs than birds with better-camouflaged eggs due to the higher costs of bad camouflage if the nest is discovered at shorter distances (Wilson-Aggarwal et al. 2016). If this holds for the Little Tern remains an open question as we did not assess the level of camouflage. Another potential factor determining the FID of birds that we did not take into account is the orientation of the bird on the nest. Birds that are sitting backwards to a person approaching will likely spot them later, therefore having a shorter FID than birds that are sitting sideways. We unfortunately were not able to consistently record this but observed most birds sitting sideways or facing the person(s) approaching the bird. Moreover, birds look around, which makes it hard to investigate this effect. In addition, neighbouring birds may have an effect as well as they display alarm calls (Wilson and Evans 2012; Chabot et al. 2015). We attempted to take this into account by including nest density in our models. Yet a high nest density does not necessarily mean that (many) neighbouring birds display alarm calls. Yet another factor could be the fact that the birds were habituated to human presence, which may occur if there is a lot of human activity in a certain area (Glover et al. 2011). The FID distances for Little Terns may therefore vary not only across time, but also across space.

Conclusion and recommendations

Our results show that the average FID was 45.7 m, with the jogger stimulus causing the largest distance, followed by a single walker and two walkers talking. The FID to a walker (44.7 m ± 9.56 m.) was more than double the average distance found during the non-breeding season (21.5 m ± 7.9 m, Blumstein 2006; Goodship and Furness 2022). Although many factors may explain this difference, it may be partly explained by nest-concealment behaviour, where birds depart earlier to avoid revealing nest locations to predators during the breeding season (Amat et al. 2017). Although regional differences in behavioural responses of species to disturbance may occur, our findings emphasise the importance of doing these types of studies in different seasons.

Whilst FID and FD are frequently used to assess impacts of disturbances on animal populations it is not necessarily true that populations that show larger behavioural response are more affected by disturbances; FIDs and FDs cannot be generalised across bird species, time, space, or disturbance types (Gill et al 2001). Furthermore, factors such as sex or level of egg camouflage, which we were not able to take into account, may also affect behavioural responses and may require further research. For effective species conservation, a varied range of disturbance experiments should therefore be conducted across multiple species and seasons in concert with monitoring reproductive success.

In the Alvor dunes, the distance of the Little Tern nests to the fence (~ 23 m) was substantially shorter than the average FID (~ 46 m). We thus advise the fence to be placed at least 23 m further than its current position in order to reduce stress and nest abandonment. Furthermore, the area is currently only fenced off with a simple rope fence. It may be beneficially for the breeding success of Little Terns, and other species breeding in the area, to place a permanent electric fence to deter humans and terrestrial predators (Wilson et al. 2020).

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Data availability Data from this study are available in the electronic supplementary material.

Declarations

Conflict of interest There are no competing interests to declare. The authors have no relevant financial or non-financial interests to disclose.

Ethical approval This study complied with all current Portuguese laws and regulations. All data collected for this study were obtained using minimally invasive methods. Birds were not handled. They were habituated to the presence of humans, as the colony is situated in a heavily utilised tourist area.

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