

Preface

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Justification: IBIS publishes articles on ornithological science, with a particular emphasis on the behaviour, ecology, evolution, and conservation of birds, as well as relevant methodological advances. This study contributes to understanding how recreational disturbance affects Common Ringed Plover behaviour on the Isles of Scilly, using camera-traps, which is understudied in this species and study system. It also aims to contribute to Ringed Plover conservation management through its collaboration with the Isles of Scilly Wildlife Trust and is therefore well suited to this journal's aims and audience.

**Using Camera-traps to Monitor Behavioural Responses and Nest
Outcomes of the Common Ringed Plover (*Charadrius hiaticula*) on the
Isles of Scilly**



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Declaration

I certify that this dissertation is entirely my own work and no part of it has been submitted for a degree or other qualification in this or another institution and give permission for a copy to be held by my supervisor and distributed at their discretion.

AI Declaration

Generative AI (Claude, Anthropic) was used during the preparation of this dissertation for:

(a) statistical troubleshooting, RStudio code generation for the basis of the figures and debugging; (b) explanation of statistical concepts; and (c) drafting a suggested structure of the Discussion section. See Appendix 1 for full list of prompts.

Abstract

Accelerating human activities have driven widespread biodiversity loss, with shorebirds inhabiting coastal ecosystems particularly vulnerable, facing both indirect pressures such as climate change and direct pressures from human activities. While previous studies have documented the energetic and reproductive costs of recreational disturbance for shorebirds, no studies have directly monitored behavioural responses at the individual nest level using camera-traps.

This study addresses this gap by annotating 40.3 hours of footage of incubating Common Ringed Plover nests on the Isles of Scilly. The Isles of Scilly provide a unique context: home to the last breeding population in southwest England, where conservation initiatives are balanced with increasing recreational use. The footage captured 704 disturbance events and enabled the investigation of how disturbance type, frequency, proximity, and compounding effects (repeated or clustered disturbances) influenced Ringed Plover behavioural responses (flush probability and latency to return), and of how these responses were linked to nest outcomes and to proximity to footpaths and settlements.

Disturbance type emerged as the strongest predictor overall. Categories containing walkers elicited the highest flush probabilities and the longest latencies, contrary to current disturbance literature, which identifies dogs as the most persistent disturbance. Here, instead, dog presence had an additive effect, with walkers accompanied by dogs producing the highest responses of any category. Nonetheless, these findings remain tentative due to sample-size constraints and, consequently, insufficient statistical power.

Nevertheless, this study was the first of its kind to link nest-level behavioural responses to breeding outcomes, highlighting the complexity of disturbance effects on this species and study system. Additionally, this work marked the start of a collaboration between the

University of Exeter and the Isles of Scilly Wildlife Trust's Ringed Plover Conservation Project, supporting ongoing conservation efforts for this species.

1. Introduction

In the Anthropocene, accelerating human activities are driving widespread biodiversity loss, threatening the integrity of ecosystems worldwide (Ceballos *et al.*, 2015; Johnson *et al.*, 2017; Dirzo *et al.*, 2022; Finn *et al.*, 2023). Birds (*Aves*) are often used as indicators of ecosystem health due to their sensitivity to environmental change (Bryce *et al.*, 2002; Parsons *et al.*, 2008; Maznikova *et al.*, 2024). Notably, the IUCN and BirdLife International recently reported that more than half of global bird species (61%) are in decline (IUCN, 2025; BirdLife, 2025).

In the UK, a similar story unfolds: plant and animal populations have declined by 19% since 1970, with nearly one in six species now threatened with extinction (Burns *et al.*, 2023). This trend has largely been attributed to major changes in land management practices (Fuller *et al.*, 2007), such as agricultural intensification (Donald *et al.*, 2001; Bell & Calladine, 2017). While these drivers harm all UK bird species, anthropogenic pressures vary across ecosystems.

Coastal ecosystems, among the most productive and dynamic on the planet, support a wide range of biological communities (Halpern *et al.*, 2025), including shorebirds (Order *Charadriiformes*). Some shorebirds rely on coastal habitats for feeding, roosting and nesting (Smart & Gill, 2003), making them particularly vulnerable to both broad-scale threats such as climate change and rising sea levels (Clausen & Clausen, 2014), and more immediate pressures from human recreational activity (Rosa *et al.*, 2006; Collop *et al.*, 2016; Tratalos *et al.*, 2021).

Recreational disturbance is an increasingly recognised factor affecting coastal bird populations. In 2024, it was identified as contributing to 14% of the global pressure on bird populations (BirdLife, 2025) and is defined as: “an activity that causes an individual or group of shorebirds to alter their normal behaviour, leading to additional energy expenditure and potential reductions in productivity and survival rates” (Mengak & Dayer, 2020). Recreational disturbances include a range of activities, such as cars, boats, walkers, and domestic dogs (see Cutts *et al.*, 2024 for a more comprehensive summary).

Shorebird breeding strategies, while effective against natural predators, may expose them to new risks from increased coastal recreational activity (Tablado & Jenni, 2015).

Shorebirds likely perceive humans as predators (Frid & Dill, 2002; Beale & Monaghan, 2004b). Thus, even low levels of human presence may trigger trade-offs similar to those caused by natural predation risk, thereby affecting productivity through changes in parental investment (Frid & Dill, 2002; Liley & Sutherland, 2007).

The Common Ringed Plover (*Charadrius hiaticula*; referred to as Ringed Plover hereafter) is a widespread shorebird along the UK’s coasts and serves as an excellent model for studying recreational disturbance. Ringed Plovers breed in open habitats, such as beaches, leaving them vulnerable to disturbances from humans who frequent these areas for recreation (Burger, 1994; Weston & Elgar, 2005; Liley, 2022). Furthermore, they exhibit easily quantifiable behavioural responses to disturbance, including alarm calling, distraction displays and changes in incubation behaviour (Pienkowski, 1984b; Gómez-Serrano, 2020; de Framond *et al.*, 2022).

This study selected two commonly used metrics in the disturbance literature to assess Ringed Plover behavioural responses. The first was flush probability, defined as the likelihood that an incubating bird leaves the nest in response to a disturbance, thereby increasing adult energy expenditure and interrupting incubation (Gómez-Serrano, 2020;

Watson *et al.*, 2021; Ozkan *et al.*, 2024). However, as Gill, Norris & Sutherland noted, flush probability alone may not fully capture the consequences of disturbance. Thus, a second metric, latency to return, was also selected. This measure may better explain the cost to breeding success because it captures the duration of adult absence from the nest, which has been linked to increased nest predation and reduced productivity (Weston, Ehmke & Maguire, 2011; Smith *et al.*, 2010).

While recreational disturbance is recognised as a major threat to Ringed Plover productivity (Liley & Sutherland, 2007) and distribution (Tratalos *et al.*, 2021), no studies have directly linked disturbance frequency and type to breeding success using continuous behavioural monitoring, such as camera traps. This approach may provide more detailed insight into disturbance effects that traditional field studies may miss.

To address this gap, this study analyses camera-trap footage of the Isles of Scilly's breeding Ringed Plover population, examining the direct effects of disturbance type, frequency, and proximity on behaviour and linking these effects to nest outcomes. It also examines how spatial factors, such as nest proximity to footpaths and settlements, influence nest outcomes.

This project is also a result of a collaboration between the University of Exeter and the Isles of Scilly Wildlife Trust (ISWT), aiming to inform targeted conservation measures for breeding shorebirds in high-use recreational coastal ecosystems. With increasing recreational activity, active conservation management, and the last remaining breeding population of Ringed Plovers in south-west England (Isles of Scilly Wildlife Trust, 2024), the Isles of Scilly provide an exceptional context for this study.

Since 2024, the ISWT has undertaken the Ringed Plover Conservation Project. This project uses a mixed approach to Ringed Plover conservation: during the breeding season, it deploys cordons and signage and imposes seasonal on-lead requirements for

dogs, whilst also monitoring nest outcomes via camera traps. This framework provides a valuable opportunity to assess the impacts of recreational disturbance on a population of high regional importance.

2. Methods

2.1. Study site

The Isles of Scilly are a small oceanic archipelago located southwest of the British Isles, approximately 24.5 nautical miles from Land's End (49°56'N, 6°16'W; Figure 1). It comprises more than 300 individual islands, of which only 5 are inhabited (total area approximately 14 km²), and supports a small resident population of ~2100 people (Liley & Saunders, 2024). The islands and surrounding waters support a wide range of habitats, including maritime heathland, grassland, rocky shore, dunes, intertidal flats, reefs, and seagrass beds, which in turn support a range of protected species. Consequently, the Isles contain several nationally protected areas and bird breeding sites, including 27 Sites of Special Scientific Interest (SSSI) and one Special Area of Conservation (SAC) (Natural England, 2015).

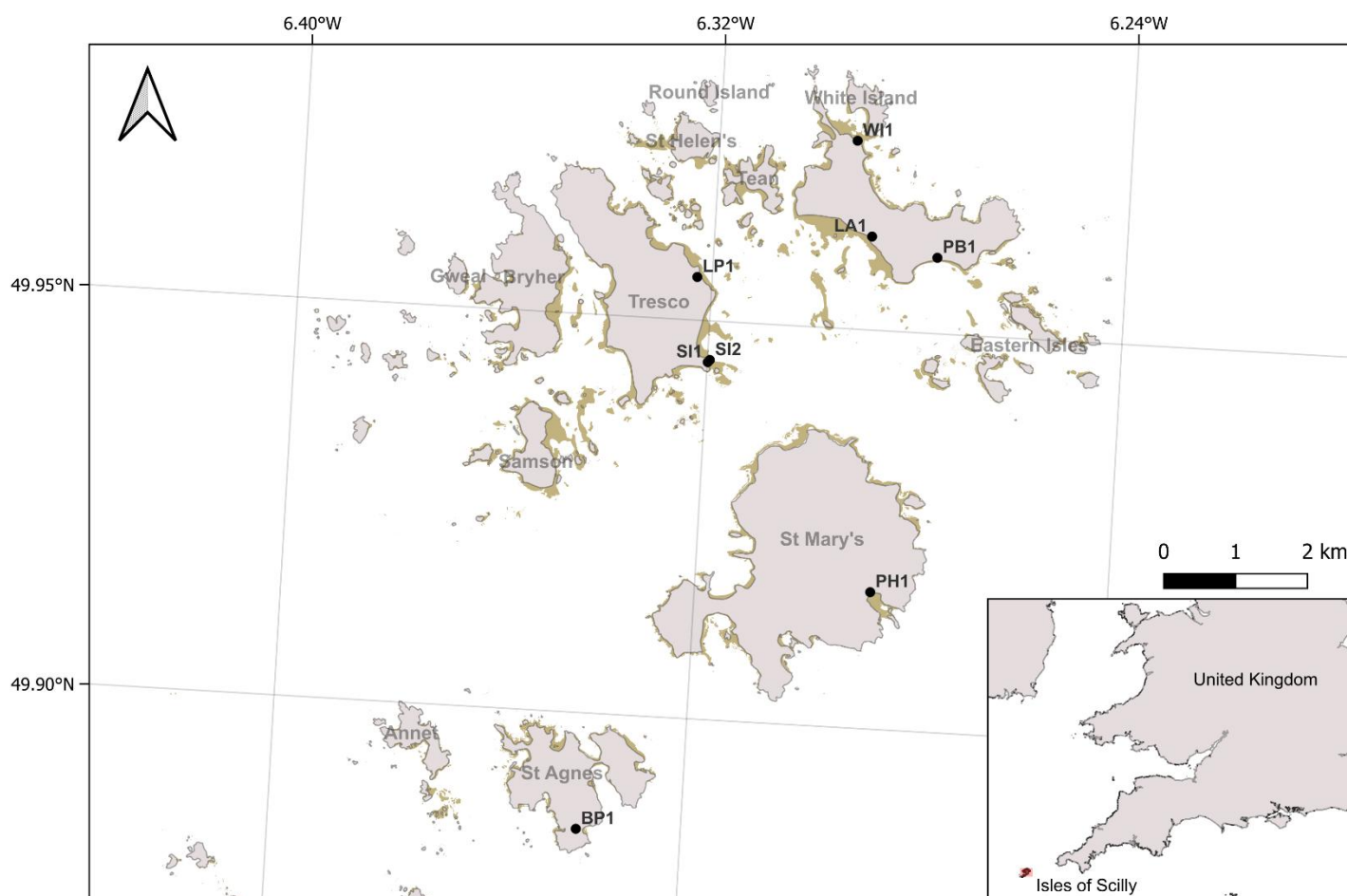


Figure 1 shows a map of the Isles of Scilly and their relative location (49°56'N, 6°16'W) in the United Kingdom (inset, bottom right). Black circles indicate the locations of all 8 camera-monitored nests. WI1 = White Island 1 (2025), SI1 = Skirt Island 1 (2025), LA1 = Lawrence's 1 (2024), SI2 = Skirt Island 2 (2025), BP1 = Beady Pool 1 (2025), LP1 = Lizard Point 1 (2025), PH1 = Porth Hellick 1 (2025), PB1 = Par Beach 1 (2025).

2.2. Field surveys

This project has been undertaken in partnership with the ISWT. Data were shared, and fieldwork was conducted in 2026 to support this year's data collection. Unfortunately, due to time constraints, this footage was unable to be used; instead, footage from 2024 and 2025 was used (see Figure 1 for the relative locations of monitored nest sites). Appendix 2 summarises the ISWT's fieldwork undertaken to collect these data.

2.3. Camera traps

Camera traps were installed at identified nest sites (see Appendix 2 for details on how nests were identified), typically within cordoned-off areas and at a distance of 1-2 metres. However, placement sometimes varied because beach topography could make it difficult

to standardise the distance. Camera installation was also completed promptly to minimise nest disturbance.

The cameras were Brownings Dark Ops Prox X 1080 models, motion-activated, capturing 10- to 30-second clips, depending on the year. They were positioned to capture the nest, incubating adults, and both visible and audible disturbances, such as walkers, dogs, and boats, as well as natural disturbances, such as Eurasian Oystercatchers (*Haematopus ostralegus*), Carrion Crows (*Corvus corone*), and European Herring Gulls (*Larus argentatus*).

2.4. Camera trap annotations

A postdoctoral researcher from the University of Exeter previously analysed footage from one site in 2024. In 2025, a volunteer initially annotated the footage, with further annotation and analysis in 2026 completed by the author of this study. Both the available 2024 and 2025 footage (totalling 8 nests) were reprocessed using TimeLapse ([2.5.0.6](#)) software. This allowed the frequency of disturbance to be determined, i.e. the probability of an incubating adult flushing the nest in response to a visual or audible disturbance, the time taken for the bird to return to the nest after a disturbance event (latency), and the resulting nest outcome.

For each video, the following was recorded: (i) whether a disturbance event occurred; (ii) the disturbance type, e.g. Walker or Walker with dog; (iii) the time of the event; (iv) whether the bird was on the nest at the start of the video; (v) whether the bird left the nest and, if so, the time it did so; and (vi) whether the bird returned to the nest and, if so, the time it did so.

Often, the same disturbance event occurred across several consecutive timestamps (e.g., an aircraft overflight audible in three successive videos). Raw rows that were the same disturbance type at the same nest, on the same date, and no more than 15 minutes apart

were treated as one disturbance event. A 15-minute threshold was chosen as a conservative cut-off that captured the initial disturbance event while avoiding conflation of consecutive events, following a similar approach to threshold-based event discrimination used in other camera-based disturbance studies (e.g., De Pascalis *et al.*, 2018).

Disturbance types were further grouped into broader categories (Walker, Walker with *dog*, Dog-only (unaccompanied), Equestrian, Land vehicle, Aircraft, Watercraft, Livestock, Avian, Mammal and Mixed encounters, which contained more than one concurrent disturbance). Dogs were also further divided into on-lead vs off-lead to allow for further analysis.

The distance at which each disturbance occurred was categorised on an ordinal scale ('Away', 'Close', 'Very close'), as quantitative distances could not be calculated from the footage. This was recorded only for human-related disturbances (Walkers, Walkers with dogs, etc.). Wildlife and vehicles were less reliable and thus excluded from the distance-based analysis.

Latency to return was calculated by subtracting the return time from the leave time for each individual disturbance event. When leave and return times occurred within a short time frame at the same nest, each leave time was paired with the subsequent return time. Events without a corresponding return time (limited by camera trap detection) were excluded from the calculations.

Ringed plovers take flight or walk away in response to disturbance, coded as 0 for no flush and 1 for flush.



Image 1 shows a frame of camera-trap footage from the TimeLapse software, taken at the Lizard Point 1 nest site in 2025. This image shows a flushing event, with the incubating bird leaving the nest in the bottom right; a walker disturbance approached and was classified as 'Away' distance.

2.5. Further analyses

2.5.1. Compounding disturbance

Whilst annotating the camera trap footage, it became apparent that the cameras did not always capture the bird's departure or return times. This was exacerbated at night, with return times rarely captured at all. Thus, comparisons between day and night-time disturbance were limited. Therefore, a new analysis was created, named 'compounding disturbance'.

Compounding disturbance effects were measured by classifying each disturbance event according to its relationship to nearby flush events at the same nest, using a 30-minute cut-off threshold: 'Clustered' (a flush event within 30 minutes of another flush event),

‘Isolated’ (flush events more than 30 minutes apart), or ‘First of day’ (the first flush event of the day associated with a disturbance event).

The 30-minute threshold was chosen because it aligns with previous studies on avian stress physiology (Brunner, Penticoff & Tully, 2026). For example, Romero & Reed showed that corticosterone levels typically peak 15-30 minutes after an acute stressor in wild and captive birds. Thus, a flush event within this window may occur while the bird remains in a physiologically elevated state from the preceding disturbance, thereby affecting subsequent flushing probability.

2.5.2. Proximity to footpaths and settlements

This further analysis tested whether proximity to footpaths or settlements influenced Ringed Plover nest outcomes. It utilised all confirmed success/fail outcomes from 2024 and 2025, not just the 8 camera-monitored nests. ‘Unsure’ outcomes were excluded (see Appendix 3 for the full dataset).

As noted in the field surveys in Appendix 2, the relative locations of nests in 2024 and 2025 were recorded using the QuickCapture app. Subsequently, the ISWT presented these points in maps for each year; see Appendix 4. The locations were georeferenced in QGIS (version 3.44.9), and footpath layers were created manually in OpenStreet Maps by drawing line polygons for the nearest relevant footpaths. Settlements were imported from OpenStreet Digimaps (EDINA Digimap, 2022). Distances to footpaths were calculated using the Distance to Nearest Hub (line to hub) tool, whilst distances to settlements were calculated using the Join Attributes by Nearest tool.

2.6. Statistical analysis

Statistical analyses were structured around three levels: (1) whether disturbance affects behaviour, with disturbance type, distance and latency considered separately; (2) whether recent disturbance history affects behaviour in addition to disturbance type; and (3) whether disturbance translates into population-relevant consequences at the nest outcome level.

Raw disturbance-type variables from the annotated footage originally comprised more categories (e.g. Equestrian, Livestock, Land vehicle, etc.), several of which contained very few recorded events. Preliminary models using these variables returned singular fits, reflecting insufficient data in sparse categories. Thus, these categories were collapsed into five broader groups for the main analyses: Aircraft, Dogs only (unaccompanied), Walkers, Walkers + dog, and Other (containing Equestrian, Land vehicle, Livestock, Avian, Mammal and Watercraft; see Appendix 3 for a full list).

The full disturbance-type-by-distance interaction was not modelled due to sparse cell counts across disturbance and distance categories. Latency by distance was instead assessed using only the two most frequent categories (Walkers & Walkers + dog).

All models were checked using simulated residuals (DHARMA package), assessing overall fit via the Kolmogorov-Smirnov test, dispersion, and singular fits (Appendix 6).

For each model, an omnibus likelihood ratio test was used to assess the overall significance of each predictor, in addition to the pairwise contrasts reported in the default model summaries. For predictors with more than two levels, pairwise comparisons between levels were conducted using the emmeans package, with p-values adjusted for multiple comparisons using the false discovery rate (FDR) method.

All statistical analyses were conducted in RStudio (version 4.5.2), using the packages tidyverse, lme4, glmmTMB, DHARMA, emmeans, car, and performance.

2.6.1. Level 1: How does disturbance affect behaviour?

The 1st model, flush probability by disturbance type, tested how much disturbance type affected the odds of a bird leaving the nest. Flush outcome (0/1) was modelled as a mixed-effects binomial with a logit link. NestID was included as a random effect to account for multiple disturbance events recorded per nest.

This model was further streamlined to test whether flush probability differed between on-lead and off-lead dogs, restricted to dog-present events.

The 2nd model, which investigated flush probability by distance, was restricted to disturbance types for which a meaningful approach distance was recorded (Walkers, Walkers + dog, and Dog only). It was fitted separately from the first model because distance was unrecorded for several categories (e.g. Aircraft), and otherwise the two predictors would have produced an unstable additive combination.

The 3rd model examined latency to return to the nest. The data were a continuous, heavily right-skewed positive variable and were modelled using a lognormal error distribution with a log link. The data were restricted to a subset of events in which a flush occurred (as latency cannot be defined for a bird that never left the nest).

2.6.2. Level 2: Does recent disturbance history matter, on top of type?

The 4th model tested whether a flush event occurring soon after a previous disturbance changed the odds of flushing again, after controlling for disturbance type and distance. Both predictors were included because the raw association between recent disturbance history and flush probability could otherwise simply reflect which disturbance types tend to co-occur in time, rather than a genuine clustering effect. Dog-only events had to be collapsed into the Other category for this model, since splitting them across three levels of cluster status resulted in near-empty cells.

2.6.3. Level 3: Does disturbance translate into nest outcomes?

Model 5 utilised the full nest outcome dataset (not restricted to camera-monitored nests). To test whether proximity to the nearest footpaths and/or settlements influenced nest outcomes, models were fitted with settlement distance alone and with both predictors. A plain generalised linear model was selected because each nest contributed only one row and there were no repeated measures. This was followed by a mixed-effects model, including Beach as a random effect, fitted as a robustness check, as some sites were monitored in both 2024 and 2025.

3. Results

3.1. Monitoring effort

In total, 8 camera-trap footage nests were annotated, covering 5 islands and totalling 704 disturbance events from the 2090 time-stamped raw rows, with over 30 monitoring days (between the 9th of May and 30th of June in 2025, and the 17th of May and 6th of July in 2024) (Table 1).

Table 1. Summary of monitoring effort for each nest, showing the total number of observations, disturbance events, days monitored and the first and last dates for each nest.

Nest ID	Island	Beach	Total Number of Observations	Total Number of Disturbance Events	Days monitored	First date	Last date
BP1	St Agnes	Beady Pool	1,189	126	16	19 May 2025	20 Jun 2025
LA1	St Martin's	Lawrences	669	59	11	17 May 2024	6 July 2024
LP1	Tresco	Lizard Point	1,836	103	8	30 May 2025	6 Jun 2025
PB1	St Martin's	Par Beach	5,652	298	15	9 May 2025	23 May 2025
PH1	St Mary's	Porth Hellick	2,750	58	4	12 May 2025	15 May 2025
SI1	Tresco	Skirt Island 1	244	6	3	28 May 2025	30 May 2025
SI2	Tresco	Skirt Island 2	470	50	8	10 Jun 2025	17 Jun 2025
WI1	St Martin's	White Island	344	4	4	6 Jun 2025	30 Jun 2025

3.2. Disturbance Frequency

Disturbance frequency, normalised by monitoring effort, varied substantially across nests (mean = 8.7 events/day, Figure 2a), ranging from 1.3 events/day (WI1) to 19.9 events/day (PB1). Day-to-day variability within nests was also considerable (Figure 2b).

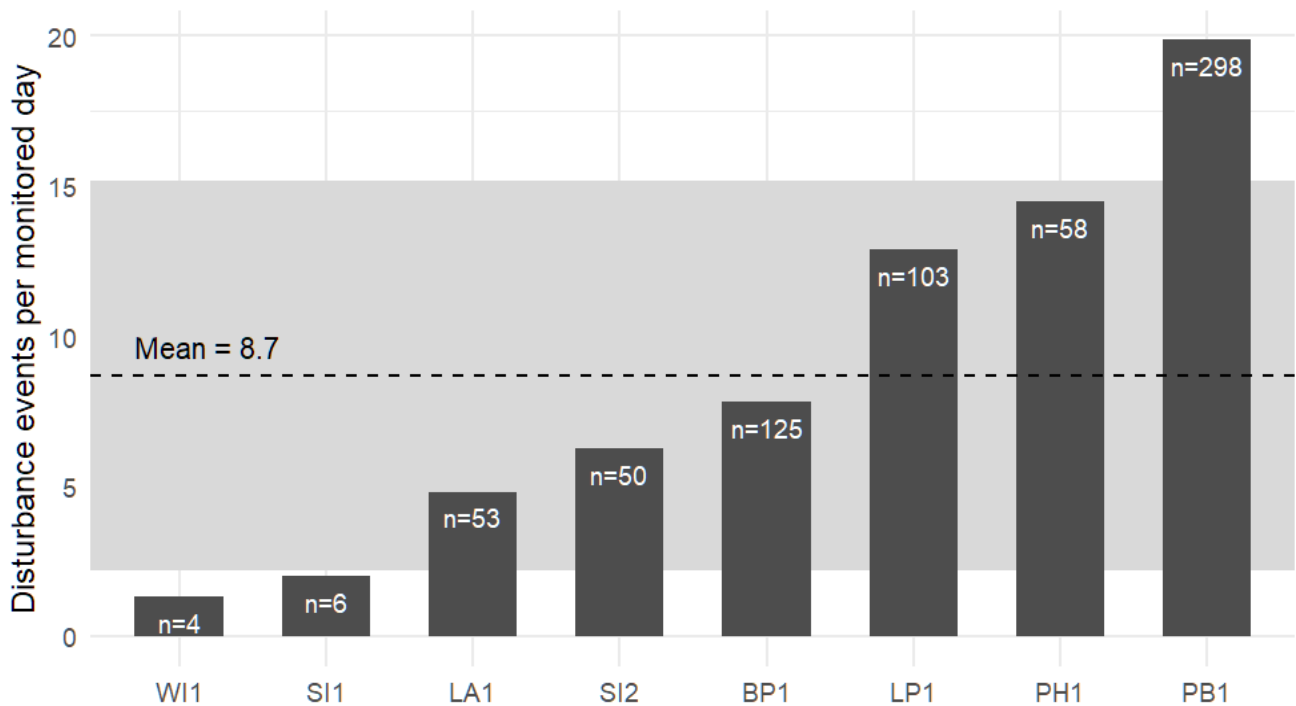


Figure 2a. Disturbance event frequency per monitored day (mean = 8.7 events/day, represented by the dashed line; grey band = ± 1 SD). Labels beneath the dark grey bars indicate the number of days each nest was monitored and its name (see Table 1). White labels on the bars show the number of days each nest was monitored. WI1 = White Island 1 (2025), SI1 = Skirt Island 1 (2025), LA1 = Lawrences 1 (2024), SI2 = Skirt Island 2 (2025), BP1 = Beady Pool 1 (2025), LP1 = Lizard Point 1 (2025), PH1 = Porth Hellick 1 (2025), PB1 = Par Beach 1 (2025). Calculated by dividing the total number of disturbance events recorded at each nest by the number of days that nest was monitored.

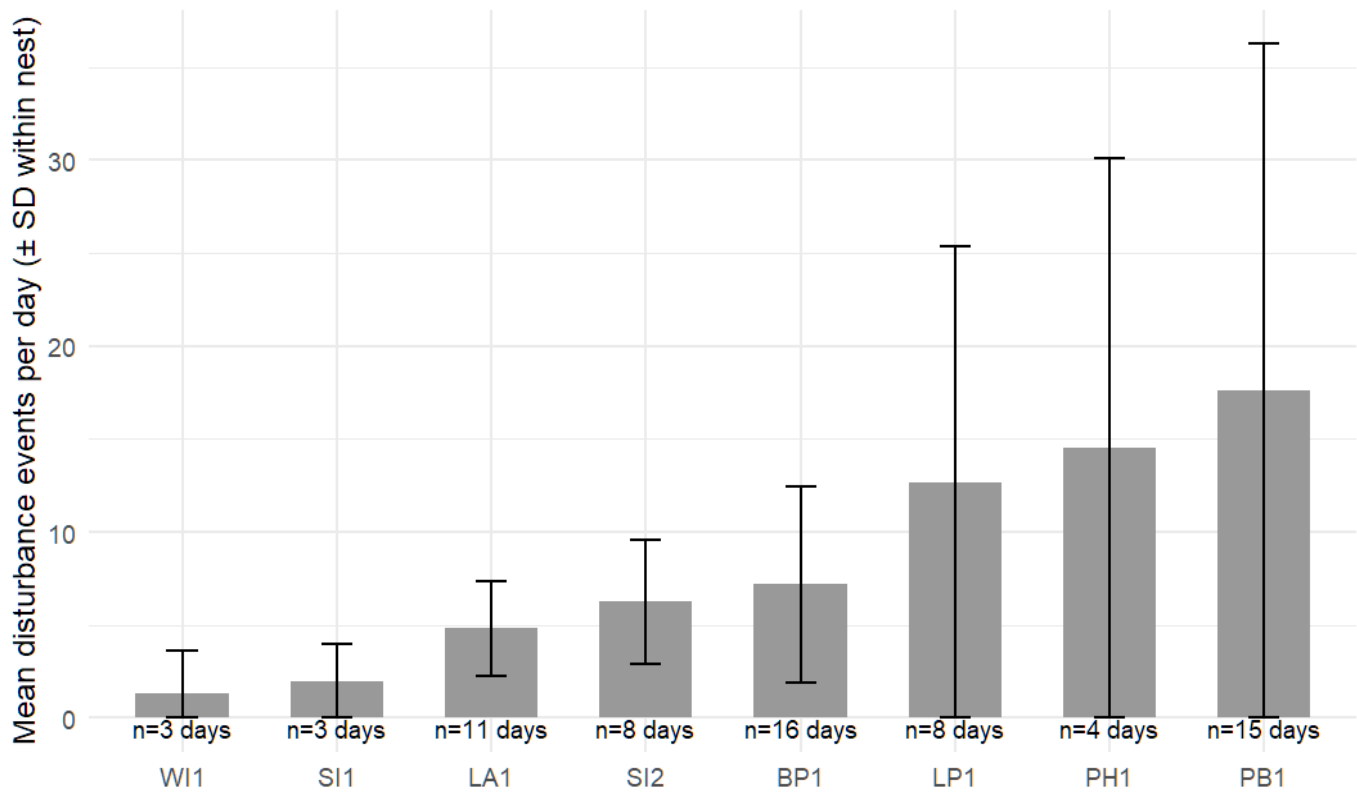


Figure 2b. Mean disturbance events per day within each nest ($\pm$ SD across monitored days). Labels beneath the grey bars indicate the number of days each nest was monitored and its name (see Table 1). WI1 = White Island 1 (2025), SI1 = Skirt Island 1 (2025), LA1 = Lawrences 1 (2024), SI2 = Skirt Island 2 (2025), BP1 = Beady Pool 1 (2025), LP1 = Lizard Point 1 (2025), PH1 = Porth Hellick 1 (2025), PB1 = Par Beach 1 (2025). For each nest, the number of disturbance events was summed per monitored day, and the mean and standard deviation of daily event counts were calculated across that nest's monitored days.

3.3. Flush Probability

3.3.1 Flush Probability by Disturbance Type

A total of 704 nest disturbance events were recorded. Of these, 344 (48.9%) resulted in a flush, with the incubating bird leaving the nest. Disturbance category had a significant overall effect on flush probability ($\chi^2(4)=29.26$, $p<0.001$). Flush probability varied significantly by disturbance type (Figure 3). Aircraft were associated with the lowest flush probability (13.0%), which was significantly lower than for Other (54.2%, $z=3.52$, $p=0.0015$), Walkers (65.8%, $z=4.47$, $p<0.0001$), and Walkers + dog (Walkers

accompanied by a dog) (73.5%, $z=4.52$, $p<0.0001$); the comparison with Dog-only (40.9%) was not significant after FDR correction ($z=1.93$, $p=0.0760$).

Examination of the full set of pairwise contrasts revealed that Dog-only events were significantly lower than those with Walkers accompanied by a dog ($z=2.20$, $p=0.047$), while Walkers, Walkers accompanied by a dog, and Other did not differ significantly from one another, except that Other was significantly lower than both Walkers ($z=2.38$, $p=0.034$) and Walkers accompanied by a dog ($z=2.42$, $p=0.034$).

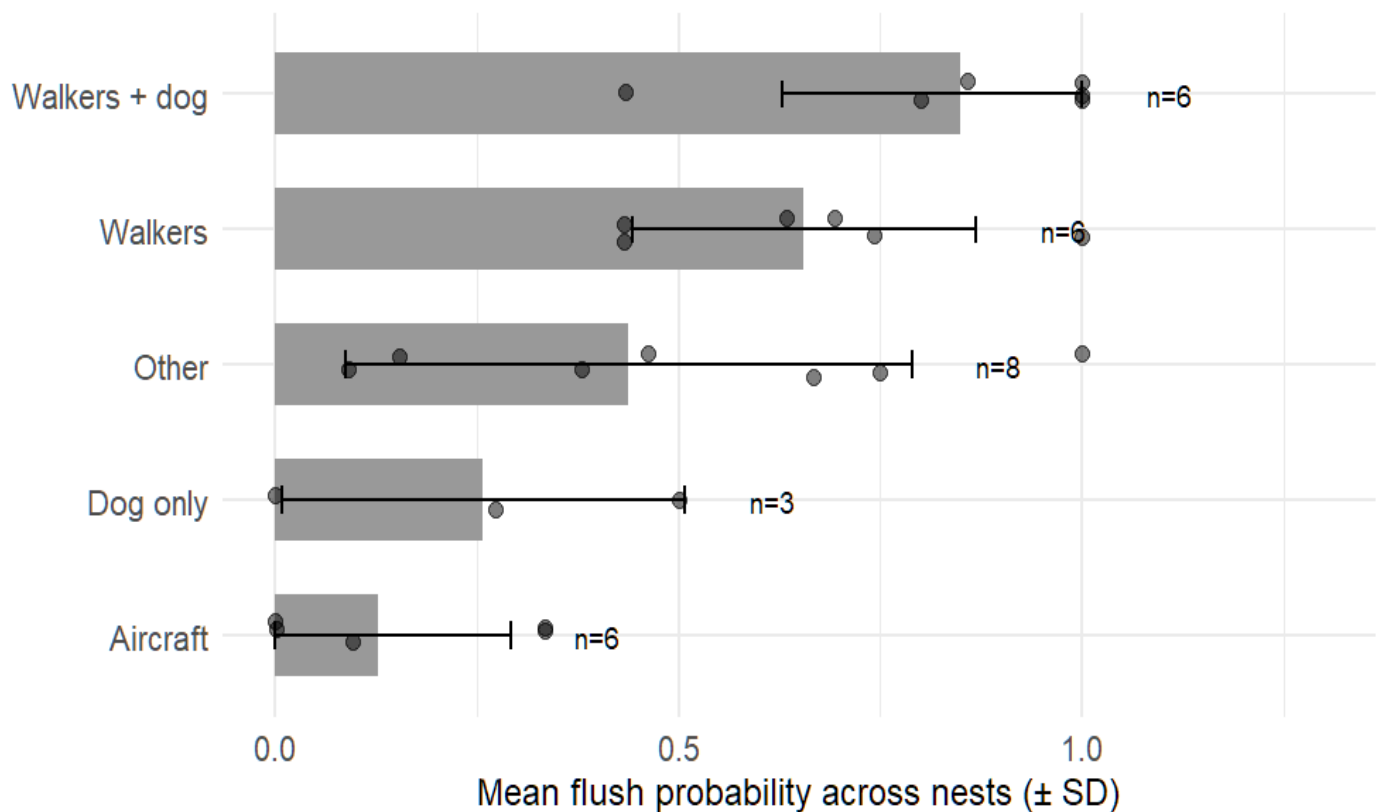


Figure 3. Mean flush probability (0=no flush, 1=flush) by disturbance category, averaged across nests ($\pm$ SD). To the left of the grey bars, disturbance types are labelled, from Walkers + Dog at the top, followed by Walkers, Other, Dog only, and lastly Aircraft. Labels to the right of the bars indicate the number of nests that experienced each disturbance type.

3.3.2 Flush Probability by Distance

Distance was recorded only for disturbance types where a discrete approach could be observed (Walkers, Walkers with dogs, Dogs only) and was categorised as Very close/Close/Away. Among disturbance events with a recorded approach distance (n=471, 6 nests), flush probability increased from Away (52.7%) to Close (72.8%) to Very close (92.9%). However, neither the linear (estimate = 0.92, $p=0.243$) nor the quadratic ($p=0.861$) trends reached significance.

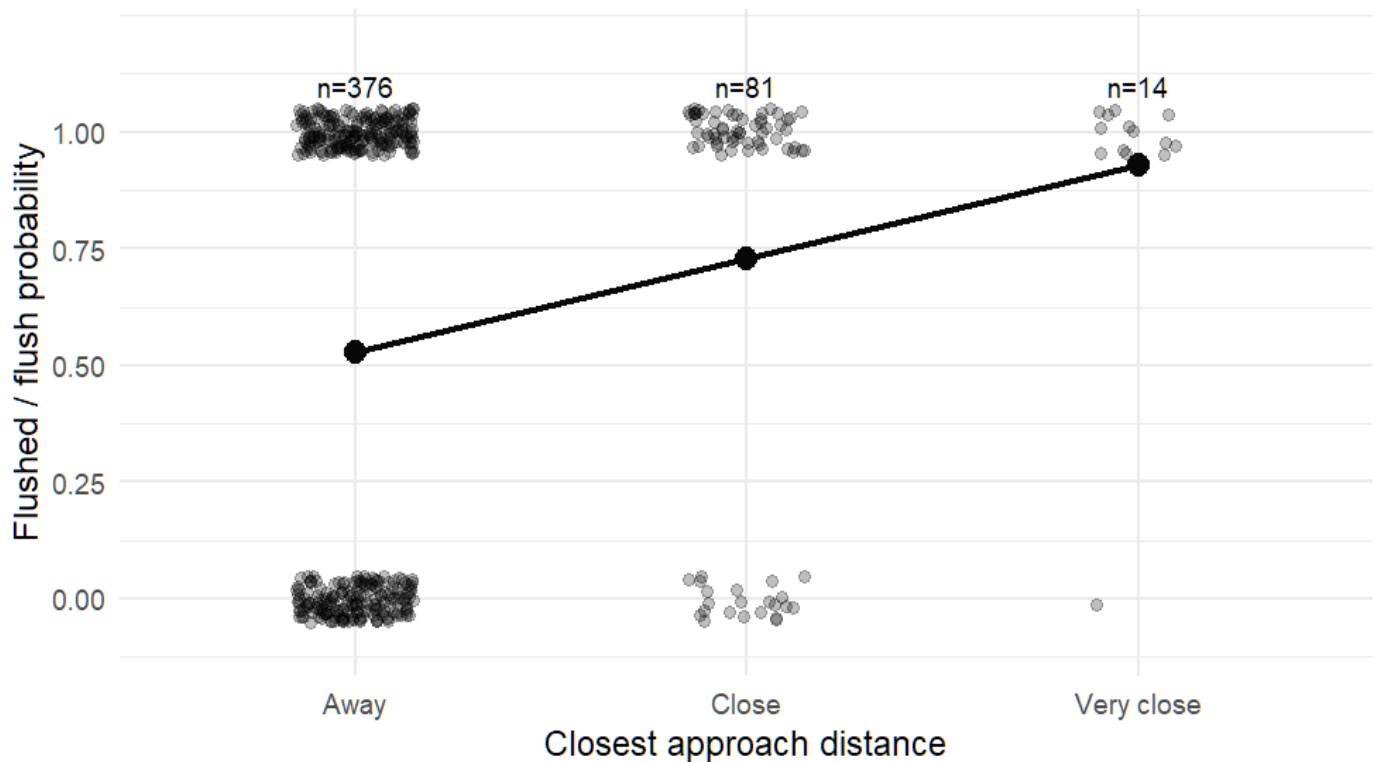


Figure 4. Flush probability (0=no flush, 1=flush) by approach distance, from Away on the left to Close in the middle to Very Close on the right, with raw jittered events clustered at 0 for no flush and 1 for a flush (Away in black, Close in grey, and Very Close in light grey). The bold black line between each category indicates the distance gradient. Sample sizes are shown in the labels above the flush event clusters at the top.

3.3.3 Flush Probability and Dog-lead Status

Among dog-present events with a recorded lead status (n=45, 5 nests), flush probability did not differ significantly by lead status (on-lead: 45.5%, off-lead: 50.0%; estimate=-0.796, SE=0.945, $z=-0.842$, $p=0.400$).

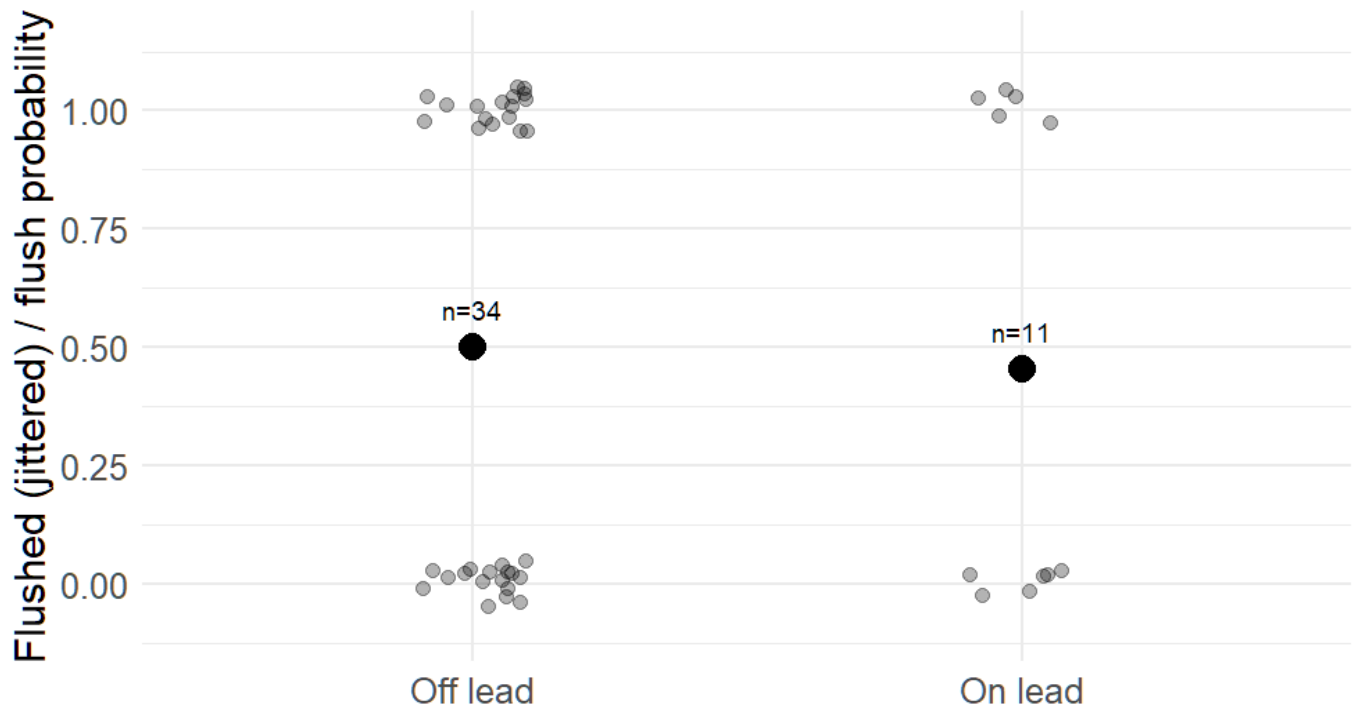


Figure 5. Flush probability (flush=1, no flush=0) by dog-lead status (Off-lead on the left and On-lead on the right), with raw jittered events shown as clusters of grey points and sample sizes indicated by labels above the black circles at the centre of each treatment.

3.4 Disturbance Type x Distance

The majority of disturbance events with a recorded distance occurred at the 'Away' distance (78.8–93.8%), with 'Very close' encounters rare throughout (0–3.3%). Walkers had the highest proportion of close-range events (17.3% Close, 3.3% Very close).

3.5 Latency to Return to the Nest

329 flush events had recorded return latencies. Birds returned to the nest after a median of 3 minutes (mean 20.2 ± 50.5 min; range 0–512 min). Disturbance category had a significant overall effect on return latency ($\chi^2(4)=12.19$, $p=0.016$). Dog presence showed a borderline overall effect, independent of category ($\chi^2(1)=3.48$, $p=0.062$).

Walkers accompanied by a dog had significantly longer latency than both Other ($z=3.36$, $p=0.0079$) and Walkers ($z=2.70$, $p=0.0349$). No other pairwise comparisons were significant. Dog presence (regardless of category) was associated with a 37% reduction in latency (estimate=-0.459, SE=0.246, $z=-1.866$, $p=0.062$).

Latency showed a borderline positive association with proximity (estimate=0.26, $p=0.0999$) among close-encounter disturbance types with a recorded distance (restricted to Walkers and Walkers accompanied by a dog).

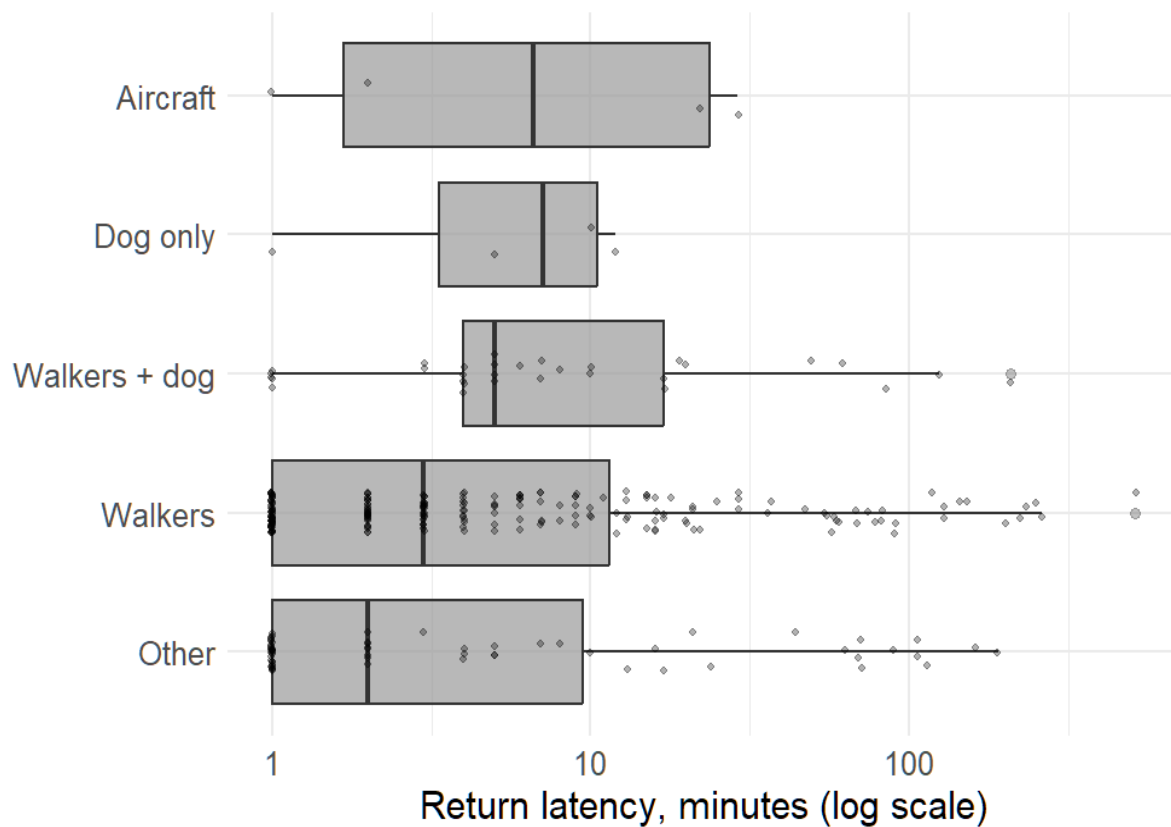


Figure 6a. Return latency (minutes, log scale, range 0–512 min) by disturbance type. To the left of the grey bars, the disturbance types are listed, from Walkers + Dog at the top, followed by Walkers, Other, Dog only, and lastly Aircraft.

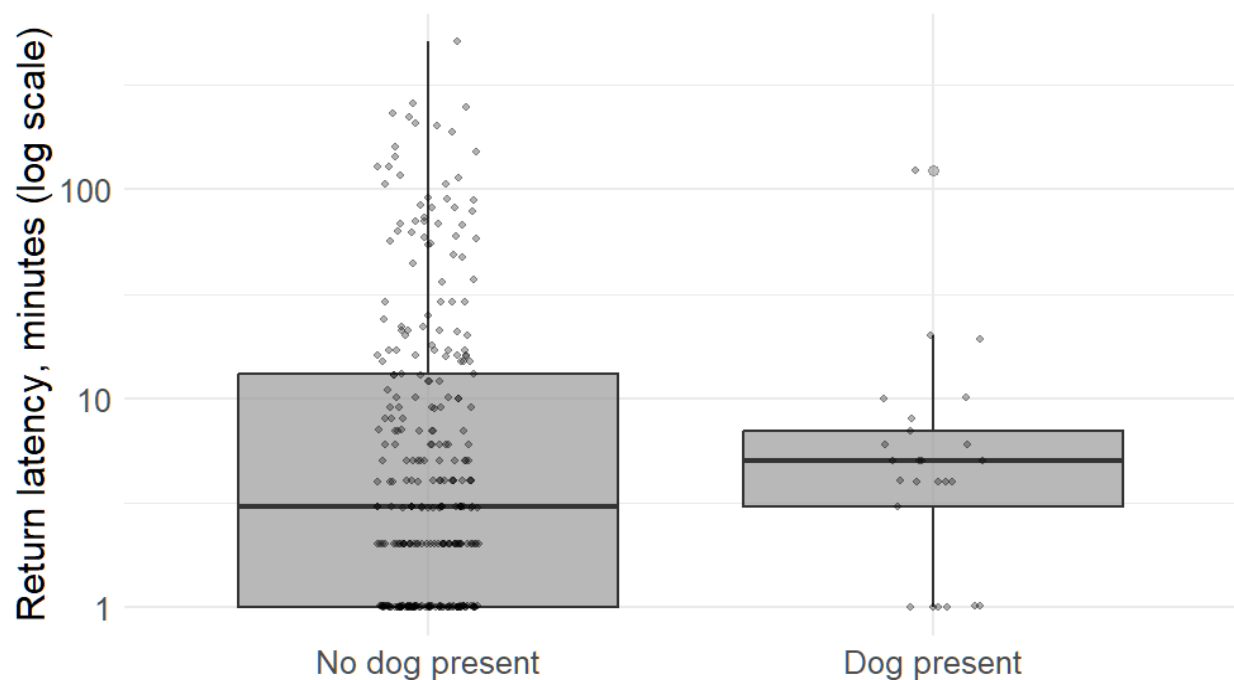


Figure 6b. This figure provides further insight into return latency (minutes, log scale) by dog presence. The grey bar on the left shows the range of return latency when no dog was present, and the grey bar on the right shows the range when dogs were present.

3.6. Compounding Disturbance (Short-term Clustering Effects)

Unadjusted flush probability was highest for first-of-day disturbance events (61.9%) compared with isolated (52.2%) or clustered (47.7%) events (Figure 7). However, once disturbance category was included in the model, cluster status had no significant overall effect on flush probability ($\chi^2(2)=0.91$, $p=0.633$), whereas disturbance category remained highly significant ($\chi^2(3)=28.83$, $p<0.001$). None of the pairwise contrasts between First of day, Isolated and Clustered neared significance (all $p\geq 0.68$, FDR-adjusted).

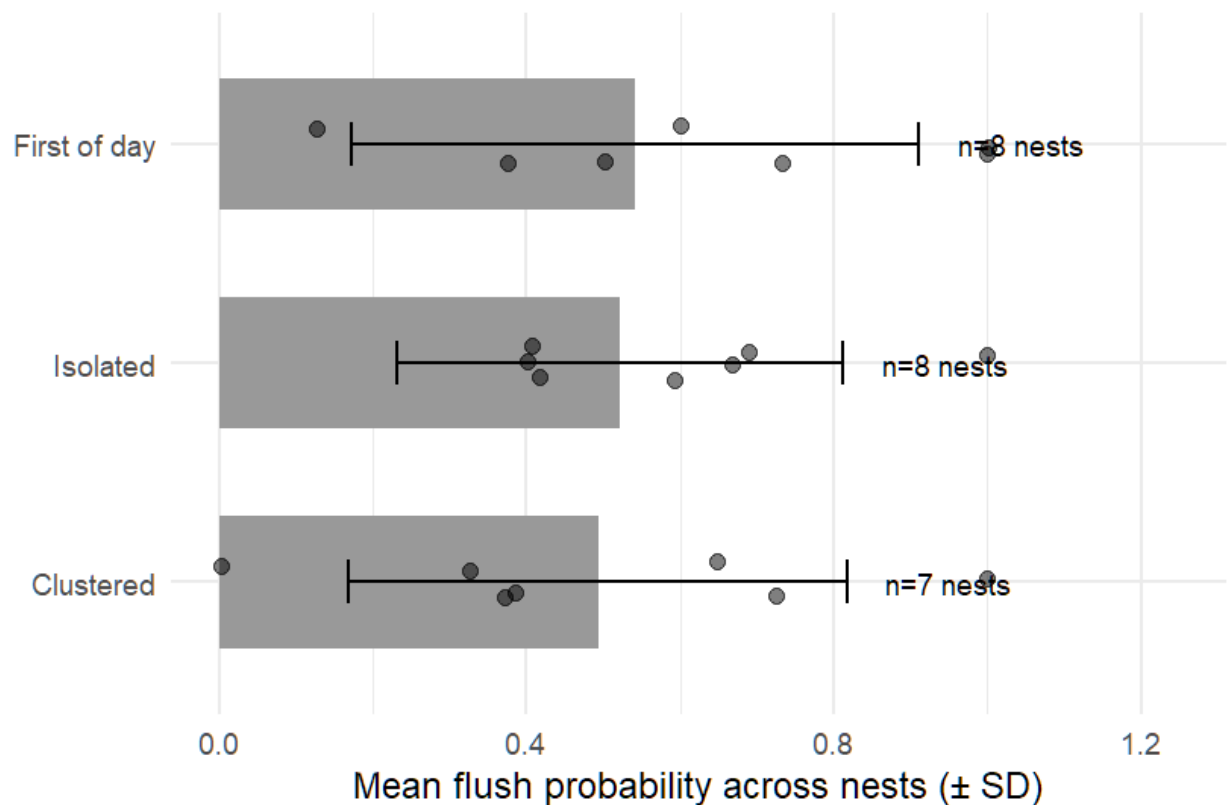


Figure 7. Unadjusted mean flush probability by recent disturbance history, averaged across nests ($\pm$ SD), to investigate potential compounding (cluster) effects. On the left, the dark grey bars are labelled with cluster status (First of day at the top, followed by Isolated in the middle and Clustered at the bottom). Labels to the right of the bars indicate the number of nests for each cluster status.

3.7 Disturbance, Frequency, Flushing and Nest Outcome

Table 2. Nest-level disturbance frequency, flush rate, latency and outcome. *LA1 is from 2024 and was monitored using 30-second clips, rather than 10-second clips for 2025 sites. ‡SI1 has very limited monitoring effort (3 days, 6 events) and should be interpreted with caution.

Nest	Total events	Flush rate	Median latency (min)	Events/day	Outcome
LA1*	53	100%	16	26.5	Fail
PB1	298	40.9%	3	19.9	Success
PH1	58	41.4%	5	14.5	Unsure
LP1	103	37.9%	2	12.9	Fail
BP1	125	69.6%	2.5	7.81	Fail
SI2	50	54.0%	6	5.56	Fail
SI1‡	6	50.0%	50	2.0	Fail
WI1	4	0%	—	1.33	Success

Disturbance frequency alone showed no consistent relationship with nest outcome: LA1 (highest disturbance frequency, 26.5 events/day) failed, but PB1 (second-highest, 19.9 events/day) succeeded, and WI1 (lowest, 1.33 events/day) also succeeded. Flush rate showed a more suggestive, though still non-definitive, pattern: the two nests with the hierarchy flush rates (LA1, BP1) both failed, while the nest with no recorded flushes (WI1) succeeded.

3.8 Nest Outcome and Proximity to Footpaths and Settlements

Across all nests with a confirmed outcome ($n=30$), neither proximity to the nearest footpath (estimate=0.0023, SE=0.0046, $z=0.511$, $p=0.609$) nor proximity to the nearest settlement (estimate=-0.0004, SE=0.0014, $z=-0.305$, $p=0.760$) significantly predicted nest success or failure, either individually or in combination (Figure 8). Combining both predictors did not improve overall model fit (AIC=46.0 vs. 44.1–44.3 for single-predictor models).

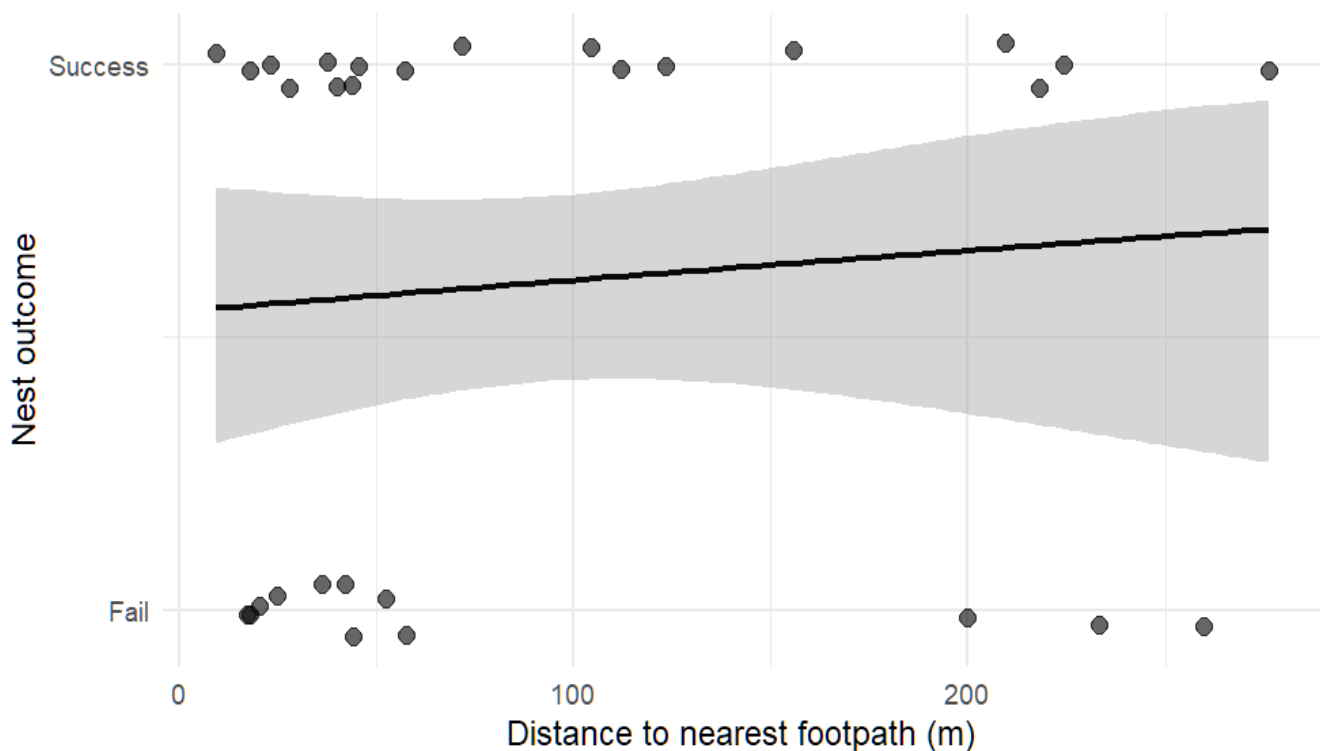


Figure 8. Nest outcome (Fail at the bottom vs Success at the top) against distance to the nearest footpath (metres). The black line represents the fitted logistic curve, and the grey band represents the 95% CI ribbon.

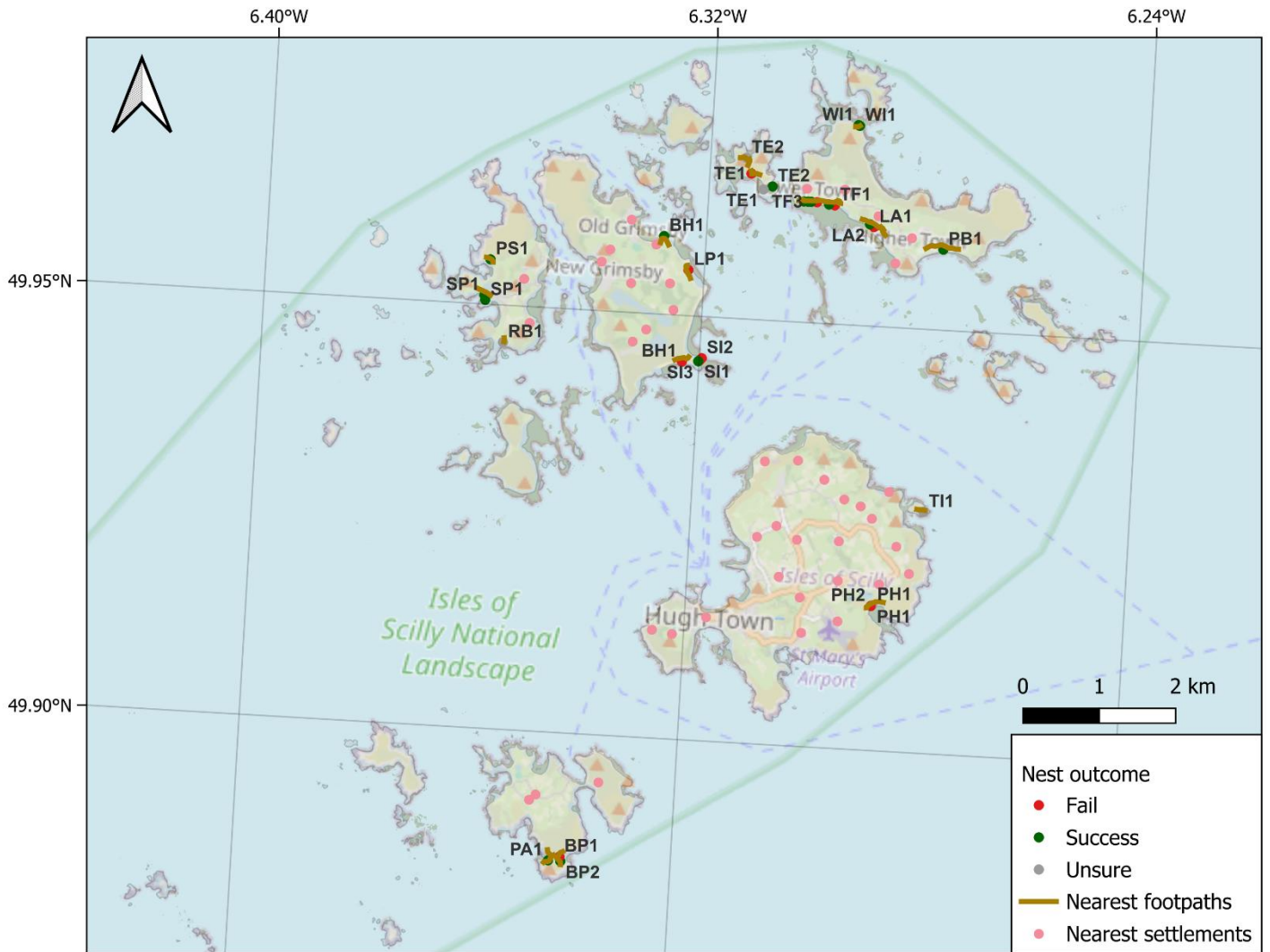


Figure 9 shows the locations of all nests monitored by the Isles of Scilly Wildlife from 2024 to 2025. Nest outcomes are represented by red circles for Fail, green circles for Success, and grey circles for unsure. The generated line polygons of the footpaths are shown as brown lines, and the points of the nearest settlements used in the Join Attributes by Nearest spatial analysis are shown in pink. The OpenStreetMap overlay used to create the nearest footpaths is also included. A full list of the labels for each site is provided in Appendix 3.

4. Discussion

As anthropogenic pressures intensify, shorebirds in coastal ecosystems are particularly at risk, facing both indirect threats, and direct ones, such as recreational disturbance.

Recreational disturbance has been shown to increase energy expenditure (Burger, 1994;

Weston & Elgar, 2005), reduce shorebird productivity (Frid & Dill, 2002; Liley & Sutherland, 2007), and lower survival rates (Mengak & Dayer, 2020).

By annotating 40.3 hours of camera-trap footage, this study combined disturbance frequencies, proximity, and bird nest return times from 704 disturbance events to investigate the effects of recreational disturbance on the Common Ringed Plover's nest outcomes on the Isles of Scilly. This study was the first of its kind to use camera-trap footage to simultaneously examine disturbance type, proximity, latency, and short-term compounding effects within a single study system, and to relate these findings to the population level.

Overall, disturbance type was the strongest predictor of Ringed Plover flush probability and latency to return to the nest across all variables. In addition, disturbance frequency, normalised across nests and monitoring days, varied widely, indicating substantial spatial and temporal heterogeneity in disturbance exposure across nest sites and islands.

4.1 Effects of Disturbance Type

Disturbance type, regardless of proximity or timing, was the strongest predictor. Aircraft disturbances were associated with the lowest flush probability, whereas dog-only events (unaccompanied by a walker) had significantly lower flush probability than events with a dog and a walker. This pattern was mirrored in the latency times (Section 3.5), where walkers with a dog had the longest return times of any category. Dog presence, independent of category, was associated with faster nest return times, contrary to expectations. A loose dog with no visible handler also produced a substantially weaker and less certain effect than any disturbance involving humans. Together, these findings suggest that the presence of a person, regardless of category, primarily drives Ringed Plover disturbance behaviour on the Isles of Scilly.

Comparing this result with established predation risk theory, it is well established that prey animals, including shorebirds, perceive human disturbance as predation risk (Frid & Dill, 2002; Beale & Monaghan, 2004b). Throughout evolutionary history, prey species have evolved antipredator responses to generalised threatening stimuli rather than to specific predators (Frid & Dill, 2002), such as those adopted by Ringed Plovers (see Appendix 2 for further detail), including fleeing (flushing the nest in this context). Furthermore, prey respond when a disturbance crosses a threshold, regardless of whether it is new to their evolutionary history (e.g., loud noises or rapidly approaching objects; see Dill 1974a). This may explain why Ringed Plovers' flush probability differed significantly across disturbance types, as they perceive these disturbances as varying levels of risk and respond accordingly.

The low overall response to aircraft disturbances has been observed in other shorebird studies. For example, in 2019, van der Kolk *et al.* found that in military areas, infrequent transport aeroplanes and bombing jets elicited the strongest responses, whereas regular, predictable activities of jet fighters and small civil aeroplanes elicited far smaller responses.

On the Isles of Scilly, air traffic is limited to scheduled commercial flights operated by Isles of Scilly Skybus or to helicopter services (Isles of Scilly Steamship Group, 2024). Thus, the relatively low flush probability associated with this disturbance type may reflect partial habituation of Ringed Plovers to this stimulus. However, because military aircraft occasionally fly through and operate in Scillies airspace (Council of the Isles of Scilly [accessed 08/09/2026]), Ringed Plovers may respond more strongly to these less frequent disturbances. This study did not consider this, as aircraft observations were limited to audio-only due to the camera traps' scope limitations, but it may be an avenue for future research. Furthermore, other factors may have influenced Ringed Plover responses to aircraft, including the typically greater distance of aircraft compared with other disturbance

types, differences in noise characteristics, and the general predictability of these disturbances compared with those caused by approaching people or dogs.

While these factors may partly explain the low response rates observed here, they do not account for the differences in terrestrial stimuli. This study's findings showed that the presence of people, rather than dogs, most strongly affected Ringed Plover behaviour, diverging from most shorebird disturbance literature. Dogs are usually identified as the most distinct and persistent disturbance source. For example, Gómez-Serrano's study on Kentish Plovers (*Anarhynchus alexandrinus*) found that lone dogs triggered a flushing response 100% of the time in dunes and 50% on the shore. Lafferty found that shorebirds were more reactive to dogs, even when overall beach activity was low, again supporting the idea that dogs elicit the strongest behavioural responses in shorebirds.

So why was this finding not observed here? In this study, Walkers accounted for the highest number of disturbance events overall (n=389), compared with other categories such as Aircraft (n=42), Walkers with dogs (n=46), and Dog-only events (n=17). This suggests that the study did not collect sufficient observations to fairly compare dog and human events, and therefore requires further testing to confirm the significance of disturbance-type comparisons.

Furthermore, this study did not investigate the effects of group size due to methodological limitations, which may have explained the divergence observed here. However, Gómez-Serrano found that group size did not significantly affect Kentish Plover flush probability. Since Kentish Plovers are in the same family as Ringed Plovers, group size may likewise have little effect on Ringed Plover behaviour. Nevertheless, Gómez-Serrano's study used a different study system and disturbance types. Thus, whether this holds true for Ringed Plovers in a system like Scilly's remains an open question.

In addition, this study examined the influence of unleashed and leashed dogs on Ringed Plover behaviour, a topic few studies have investigated to date. The results indicated no significant difference in flush probability between these two conditions (Figure 5 and Section 3.3.3). Interestingly, despite seasonal off-lead restrictions, there were more off-lead observations than on-lead ($n=34$ vs $n=11$), which may also explain the absence of a significant difference. However, a study by Barnett *et al.* on urban magpie-larks (*Grallina cyanoleuca*) found that unleashed dogs elicited stronger escape responses (predominantly flying rather than walking away) than leashed dogs. This finding may indicate that Ringed Plover behaviour towards dogs is more complex than the flush metric captured in this study and may warrant further research.

Differences in behavioural responses observed here, compared with established literature, may be attributed to a factor highlighted in other studies. Habituation, whilst generally thought to occur to some extent, can often be partial (Burger & Gochfeld, 1981; Steidl & Anthony, 2000) or negligible (Berger *et al.*, 1983; Bleich *et al.*, 1994), since animals are expected to overestimate rather than underestimate risk given the cost of error (Frid & Dill, 2002). Habituation results from slow, predictable, relatively benign stimuli (e.g., walkers), while sensitisation results from more erratic or higher-risk stimuli (e.g., dogs, unfamiliar vehicles) (Weston *et al.*, 2012). These concepts may explain the low responses that Ringed Plovers elicited towards Aircraft (partial habituation), and the faster return times for dog-only categories may be attributed to sensitisation; however, because these results are constrained by sample size and other factors may be at play, caution is warranted. This is because, as Frid & Dill established, behavioural responses are complex and should not be used as a default explanation whenever responses appear muted or different.

4.2 Effects of Approach Distance

Flush probability increased from 52.7% at 'Away' distance to 92.9% at 'Very close' distance, yet this trend was not statistically significant. A similar pattern emerged in the latency results (restricted to Walkers and Walkers + dog, given the limited sample size in other categories), with latency showing a borderline positive trend with distance ($p = 0.0999$, Section 3.5).

Relating these results to Frid & Dill's predation-risk theory, they state that the probability of fleeing increases as an approaching disturbance draws nearer, because a closer, more direct approach signals predatory intent more than a distant one. This broadly explains the positive trends observed in the raw data, where flush probability increased as distance decreased. However, because latency showed only borderline significance with distance and none with flush probability, this data may not be sufficient to explain these interactions and may also reflect both the rarity of very close encounters ($n=14$) and the limitations of the categorical distance measure.

As this study relied on camera-trap footage, a categorical distance metric had to be used because a quantitative measure was not feasible. In contrast, most shorebird disturbance studies measure disturbance distance as Flight Initiation Distance (FID). Whilst this limits direct comparison with the literature, where mean FIDs for Ringed Plovers ranged from 9-100 m depending on the context (Liley & Sutherland, 2007; NatureScot, 2023), most FID studies do not consider nest-based approaches to the effects of repeated disturbance events (Section 4.3).

Moreover, this study did not include other factors theorised to influence flush probability, such as disturbance size or speed, due to methodological limitations. Additionally, abiotic factors such as habitat type, weather and tidal state may further mediate Ringed Plover responses (Mayer, Natusch & Frank, 2019; Gutiérrez *et al.*, 2023). Anecdotal observations

from the footage, which were not included in the analysis, suggested that closer encounters occurred more frequently around high tide. This is unsurprising given the lack of beach space, but it may have significant consequences for Ringed Plover productivity. Linssen *et al.* observed that tidal disturbances carry a measurable energetic cost to shorebirds, suggesting that more frequent events (attributed to climate change) could further reduce breeding success in the future. Thus, this presents plausible avenues for exploring the combined influence of abiotic and anthropogenic disturbance on Ringed Plover behaviour and productivity.

4.3 Effects of Compounding Disturbance

Raw patterns in the data indicated a higher flush probability for the first disturbance events of the day (categorised as 'First of day'). However, when data were averaged at the nest level, differences between the categorised groups narrowed (First of day: 0.542; Isolated: 0.522; Clustered: 0.493), consistent with the non-significant result after adjustment. These null findings may reflect differences in which disturbance types occur within the daily disturbance cycle, rather than a genuine short-term sensitisation or habituation effect (Section 3.6).

This exploratory analysis was developed as an alternative to comparing night and day flush events and return latency, which was not feasible given camera-trap limitations. Difficulty measuring night vs day events is a well-known limitation in other studies (and has been addressed in recent studies, e.g. Rendall *et al.*, 2024), so these null results likely reflect that ongoing challenge.

Nevertheless, this limitation also enabled testing a new hypothesis: that a flush event occurring within a defined window after a previous event is likely to occur while the bird remains in a physiologically elevated state, potentially influencing flush probability (see Section 2.5.1 for justification). The lack of significance indicates that distinguishing

between individual learning and population-level habituation remains challenging. However, this analysis offers a direct, if preliminary, contribution towards addressing the gap in individual learning.

Additionally, Blumstein noted that time-latent responses are particularly complex and driven by interactions among multiple factors (e.g., FID and encounter rate). This complexity may explain why a simple time-since-last-disturbance measure here did not show a clear pattern. Moreover, the 30-minute threshold, while balanced against category and previous studies, remained, for the most part, a judgement call.

4.4 Nest Outcomes

Given the small number of monitored nests ($n=8$) and the likelihood that factors beyond recreational disturbance determine nest outcomes, the relationship between disturbance and nest fate is presented descriptively rather than as a tested effect. For example, at Par Beach, the nest site with the highest disturbance frequency succeeded, whereas at Beady Pool, a lower-frequency site failed due to predation (Figures 2a, 2b; Table 1; Appendix 3).

Across the wider dataset of 30 nests, neither proximity to the nearest footpath nor to the nearest settlement significantly predicted nest success or failure, either individually or in combination. This contrast shows that neither disturbance frequency nor static spatial proximity fully captures nest fate, and that other factors (e.g. predation, habitat quality, previous nesting experience) act as confounding or competing pressures outside the scope of this study's metrics.

Tablado and Jenni's review offers potential insight into why the picture presented here is not entirely clear. They argue that disturbance studies yielding seemingly contradictory or inconclusive results often stem from the many interacting factors that modulate animal responses. Species characteristics, individual state, and contextual variables all play a role, and uncertainty accumulates as effects move from behavioural responses to

reproductive and population-level outcomes. Thus, a clear behavioural effect does not necessarily translate into a straightforward outcome in nest-level success.

This is directly relevant to the contrast between this study's significant behavioural findings (Sections 3.3 & 3.5) and its null outcome-level result. Even if disturbance genuinely affects Ringed Plovers at the behavioural level, other factors may confound any simple relationship between disturbance and reproductive outcomes. For instance, previous studies have found a bell-shaped relationship between body condition and flushing distance, indicating that behavioural and physiological responses do not always align (Ydenberg & Dill, 1986; Beale & Monaghan, 2004a).

Nevertheless, more recent studies support the idea that human activity significantly affects nest success. For example, Chabani *et al.* found that Kentish Plover and Little Ringed Plover (*Anarhynchus alexandrinus*; *Charadrius dubius*) nests successfully produced chicks when few visitors were present during the COVID-19 closures. However, once visitors returned over the next two years, no nests succeeded, suggesting that recreational disturbance may be a major limiting factor for shorebird breeding success. The study also found that after visitors returned, 80% of available habitat became unsuitable due to disturbance and habitat degradation.

Degradation of coastal habitats, driven by increased human activity, can further reduce the availability and quality of nesting areas for shorebirds (Battisti, 2023). Vegetation loss, nest trampling, and increased erosion from footfall can compound the negative effects of direct human disturbance (Farris, Ceccherelli & Filigheddu, 2013; Battisti *et al.*, 2023).

Therefore, although this study's findings were limited, this evidence clearly underscores the need for further research into the behavioural effects of recreational disturbance and habitat degradation, which may be exacerbated by climate change (Galbraith *et al.*, 2002).

Such research is vital for informing future conservation strategies and management interventions on nest outcomes in Ringed Plovers.

4.5 Limitations

The overall nest sample size ($n=8$ camera-monitored nests) limited statistical power and generalisability. There was also no established control site (free from recreational disturbance) to serve as a baseline for Ringed Plover behaviour when undisturbed. Monitoring duration varied widely between sites, limiting the precision of disturbance-frequency comparisons. Approach distance was recorded only when an approach could be observed, and the camera-trap footage did not allow distances to be quantified. This limited the overall precision of both the distance and distance-latency analyses, making it difficult to compare these findings with other studies using metrics such as FID.

Camera trap detectability was also limited at night and did not reliably trigger in most instances of a bird leaving or returning to the nest. Several camera traps also experienced faults, leaving days when footage was unusable.

This study also drew on one full season of data plus a smaller 2024 subset (Lawrences), rather than multiple full seasons. Moreover, the Lawrences site was recorded using a different camera setting (30-second clips vs 10-second clips at 2025 sites). This site reported the highest disturbance rates, so it remains unclear whether it was truly more disturbed or simply measured differently.

Several additional variables were identified during the literature review but not recorded in this study and likely contribute to disturbance response: the number of people involved in a disturbance event (rather than event frequency alone), weather and tide state, which plausibly affect both visitor numbers and bird vigilance independently; incubation stage, known to affect flush probability and attachment to a nest; and habitat quality/degradation (which may confound disturbance-outcome relationships).

Return latency was modelled using a lognormal GLM rather than a Cox proportional-hazards approach, as suggested by a recent study by Liker *et al.* Behavioural coding also did not distinguish between the bird flying or walking away when leaving the nest; both were recorded as a flush event, even though these behaviours likely reflect different underlying levels of alarm or urgency.

5. Conclusion

This study investigated the effects of recreational disturbance on breeding Common Ringed Plovers in the Isles of Scilly. It was the first of its kind, utilising camera-trap footage to make nest-level observations of this species and study system. Disturbance type emerged as the strongest predictor of behavioural responses, with walkers eliciting the highest flushing probabilities and the longest latency times. These findings contrast with much of the current disturbance literature, which identifies dogs as the most persistent disturbance stimulus. Instead, dog accompaniment showed an additive effect, with walkers with dogs producing the highest responses overall. Nonetheless, due to overall sample size limitations, these findings remain tentative, and most models likely lacked sufficient statistical power to detect significant differences.

Despite these constraints, this study addressed remaining gaps in the literature by attempting to link Ringed Plover behavioural responses at the nest level to nest outcomes. Additionally, this work marked the start of a collaboration between the University of Exeter and the Isles of Scilly Wildlife Trust's Ringed Plover Conservation Project, identifying further avenues for future research on this species and within this study system.

6. Management and Conservation Implications

The findings directly support the Isles of Scilly Wildlife Trust's existing management approach: no-dog areas, seasonal lead requirements, and designated dog-friendly

beaches. Given the clear role of accompanying dogs (rather than dogs on their own) in driving the highest flush probabilities and longest latencies recorded here, there may be a case for evaluating whether seasonal lead requirements could be tightened at the highest disturbance-frequency sites as discussed in 4.4, although this should be considered carefully given the limited nest sample size underlying these results.

Cordon and signage have been used effectively to protect Ringed Plover nesting areas since the project began in 2024. Observations from this study suggest that these interventions may already be having a positive effect, as only 14 very close encounters were recorded. However, this should be weighed against a contrasting observation from the footage: the camera and cordons appeared to attract curiosity at some sites, with visitors approaching to investigate or, in a few cases, handling the camera without realising what it was and almost stepping on the nest in the process.

This management approach aligns with wider guidance from Cutts *et al.*, who found that signs are more effective near exclusion zones than at beach entrances. Moreover, personalised, positively framed messaging has been shown to outperform statistics-heavy or negatively framed messaging, as the ISWT have already implemented. Combining physical barriers with signage has also been shown to be more effective than either approach alone. Furthermore, Burger and Niles found that beach users are generally more supportive of beach closures when engaged early in decision-making and as stakeholders. This is especially relevant for the Isles of Scilly, where local engagement is vital for conservation management.

Finally, this study addresses important gaps in the current literature on recreational disturbance. Historically, studies have focused on single-stimulus, non-breeding contexts, with comparatively little attention to nest-based or breeding responses and to compounding or repeated disturbance. Although the findings from this study are currently

inconclusive, its nest-camera approach directly addresses an under-studied area in the literature, highlighting the importance of continuing this work and collaborating with the ISWT.

7. Recommendations

Building on the suggestions addressed above, the following recommendations for future research are outlined below.

First, incorporating the 2026 camera footage and habitat survey data will substantially increase statistical power and enable habitat quality and degradation to be included in future analyses. Dedicated footfall surveys, potentially using automated trail counters near beach entrances (as suggested in Chabani *et al.*), would allow disturbance frequency to be tested against direct visitor counts (not recorded in this study).

Although this study found that flush probability varied by disturbance type and that distance had an almost significant effect independently, it was not possible to test whether the distance effect differed between disturbance types. This was because sample sizes were too small in some category-distance combinations. Given that disturbance type was the strongest overall predictor of flush probability, and there was a borderline positive result for distance, such an interaction is plausible and, with a larger dataset (where more disturbance types had recorded distances) and an additional year of camera trap data, could be a target for further research.

Moreover, the project introduced nest cages in the 2026 season, providing an opportunity to directly test the effectiveness of predator exclusion in future. An article by Liley *et al.* found that nest predation in Ringed Plovers in Dorset was patchy across nest sites, but it was the largest contributor to nest failure, with breeding pairs tending to avoid re-nesting in areas with high predation rates. Thus, extending monitoring to include chick-fledging success would allow further comparisons with studies focusing on demography. They also

suggest a colour-ringing programme to track individual outcomes across sites and seasons, which would provide further insights into the factors driving nest outcomes.

During the 2026 breeding season, a camera trap was set up on Teän for the first time. This uninhabited island offers a clear opportunity to serve as a control site in future. Moreover, greater standardisation of monitoring duration across nests would strengthen future disturbance-frequency comparisons.

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8. References

1. Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, 1(5), e1400253.
<https://doi.org/10.1126/sciadv.1400253>
2. Johnson, C. N., Balmford, A., Brook, B. W., Buettel, J. C., Galetti, M., Guangchun, L., & Wilmschurst, J. M. (2017). Biodiversity losses and conservation responses in the Anthropocene. *Science*, 356(6335), 270–275.
<https://doi.org/10.1126/science.aam9317>

3. Dirzo, R., Ceballos, G., & Ehrlich, P. R. (n.d.). Circling the drain: The extinction crisis and the future of humanity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 377(1857), 20210378. <https://doi.org/10.1098/rstb.2021.0378>
4. Finn, C., Grattarola, F., & Pincheira-Donoso, D. (2023). More losers than winners: Investigating Anthropocene defaunaation through the diversity of population trends. *Biological Reviews*, 98(5), 1732–1748. <https://doi.org/10.1111/brv.12974>
5. Bryce, S. A., Hughes, R. M., & Kaufmann, P. R. (2002). Development of a Bird Integrity Index: Using Bird Assemblages as Indicators of Riparian Condition. *Environmental Management*, 30(2), 294–310. <https://doi.org/10.1007/s00267-002-2702-y>
6. Parsons, M., Mitchell, I., Butler, A., Ratcliffe, N., Frederiksen, M., Foster, S., and Reid, J. B. 2008. Seabirds as indicators of the marine environment. – *ICES Journal of Marine Science*, 65: 1520–1526. <https://doi.org/10.1093/icesjms/fsn155>
7. Maznikova, V. N., Ormerod, S. J., & Gómez-Serrano, M. Á. (2024). Birds as bioindicators of river pollution and beyond: Specific and general lessons from an apex predator. *Ecological Indicators*, 158, 111366. <https://doi.org/10.1016/j.ecolind.2023.111366>
8. *Arctic seals threatened by climate change, birds decline globally – IUCN Red List—Press release | IUCN*. (2025). Retrieved 26 June 2026, from <https://iucn.org/press-release/202510/arctic-seals-threatened-climate-change-birds-decline-globally-iucn-red-list>
9. *State of the World's Birds 2025 Update*. (2025). BirdLife DataZone. Retrieved 22 June 2026, from <https://datazone.birdlife.org/articles/state-of-the-worlds-birds-2025-annual-update>
10. Burns, F, Mordue, S, al Fulaij, N, Boersch-Supan, PH, Boswell, J, Boyd, RJ, Bradfer-Lawrence, T, de Ornellas, P, de Palma, A, de Zylva, P, Dennis, EB, Foster,

- S, Gilbert, G, Halliwell, L, Hawkins, K, Haysom, KA, Holland, MM, Hughes, J, Jackson, AC, Mancini, F, Mathews, F, McQuatters-Gollop, A, Noble, DG, O'Brien, D, Pescott, OL, Purvis, A, Simkin, J, Smith, A, Stanbury, AJ, Villemot, J, Walker, KJ, Walton, P, Webb, TJ, Williams, J, Wilson, R, Gregory, RD, 2023. State of Nature 2023, the State of Nature partnership, Available at: www.stateofnature.org.uk
11. Fuller, R. J., Smith, K. W., Grice, P. V., Currie, F. A., & Quine, C. P. (2007). Habitat change and woodland birds in Britain: Implications for management and future research. *Ibis*, 149(s2), 261–268. <https://doi.org/10.1111/j.1474-919X.2007.00775.x>
 12. Donald, P. F., Green, R. E., & Heath, M. F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society B: Biological Sciences*, 268(1462), 25–29. <https://doi.org/10.1098/rspb.2000.1325>
 13. Bell, M. V., & Calladine, J. (2017). The decline of a population of farmland breeding waders: A twenty-five-year case study. *Bird Study*, 64(2), 264–273. <https://doi.org/10.1080/00063657.2017.1319903>
 14. Halpern, B. S., Frazier, M., O'Hara, C. C., Vargas-Fonseca, O. A., & Lombard, A. T. (2025). Cumulative impacts to global marine ecosystems projected to more than double by mid-century. *Science*, 389(6766), 1216–1219. <https://doi.org/10.1126/science.adv2906>
 15. Smart, J., & Gill, J. A. (2003). *Climate Change and the Potential Impact on Breeding Waders in the UK*. 100(1).
 16. Clausen, K. K., & Clausen, P. (2014). Forecasting future drowning of coastal waterbird habitats reveals a major conservation concern. *Biological Conservation*, 171, 177–185. <https://doi.org/10.1016/j.biocon.2014.01.033>

17. Rosa, S., Encarnação, A. L., Granadeiro, J. P., & Palmeirim, J. M. (2006). High water roost selection by waders: Maximizing feeding opportunities or avoiding predation? *Ibis*, 148(1), 88–97. <https://doi.org/10.1111/j.1474-919X.2006.00497.x>
18. Collop, C., Stillman, R. A., Garbutt, A., Yates, M. G., Rispin, E., & Yates, T. (2016). *Variability in the area, energy and time costs of wintering waders responding to disturbance*. <https://doi.org/10.1111/ibi.12399>
19. Mengak, L., & Dayer, A. A. (2020). Defining Human Disturbance to Shorebirds Using Manager and Scientist Input. *Environmental Management*, 65(1), 62–73. <https://doi.org/10.1007/s00267-019-01230-2>
20. Cutts, V., Jackson, M. V., Taylor, N. G., Gaffi, L., Hagemeijer, W., & Sutherland, W. J. (2024). *Guidance on reducing disturbance for shorebirds*. (v1.0). Conservation Evidence. <https://doi.org/10.52201/CGS/JPZI7218>
21. Tablado, Z., & Jenni, L. (2015). Determinants of uncertainty in wildlife responses to human disturbance. *Biological Reviews*, 92(1), 216–233. <https://doi.org/10.1111/brv.12224>
22. Frid, A., & Dill, L. (2002). Human-caused Disturbance Stimuli as a Form of Predation Risk. *Conservation Ecology* (11955449), 6(1), 94–109. <https://doi.org/10.5751/ES-00404-060111>
23. Beale, C. M., & Monaghan, P. (2004b). Human disturbance: People as predation-free predators? *Journal of Applied Ecology*, 41(2), 335–343. <https://doi.org/10.1111/j.0021-8901.2004.00900.x>
24. Liley, D., & Sutherland, W. J. (2007). Predicting the population consequences of human disturbance for Ringed Plovers *Charadrius hiaticula*: A game theory approach. *Ibis*, 149(s1), 82–94. <https://doi.org/10.1111/j.1474-919X.2007.00664.x>

25. Burger, J. (1994). The Effect of Human Disturbance on Foraging Behavior and Habitat Use in Piping Plover (*Charadrius melodus*). *Estuaries*, 17(3), 695–701.
<https://doi.org/10.2307/1352418>
26. Weston, M. A., & Elgar, M. A. (2005). Disturbance to brood-rearing Hooded Plover *Thinornis rubricollis*: Responses and consequences. *Bird Conservation International*, 15(2), 193–209. <https://doi.org/10.1017/S0959270905000158>
27. Liley, D., Lock, L., Brown, A., Scott, J., Legg, W. (2021). Beach-nesting Ringed Plovers and their conservation in England. *British Wildlife*, 37(7), pp. 157-165.
28. Pienkowski, M. W. (1984b). Breeding biology and population dynamics of Ringed plovers *Charadrius hiaticula* in Britain and Greenland: Nest-predation as a possible factor limiting distribution and timing of breeding. *Journal of Zoology*, 202(1), 83–114. <https://doi.org/10.1111/j.1469-7998.1984.tb04289.x>
29. Gómez-Serrano, M. Á. (2020). Four-legged foes: Dogs disturb nesting plovers more than people do on tourist beaches. *Ibis*, 163(2), 338–352.
<https://doi.org/10.1111/ibi.12879>
30. de Framond, L., Brumm, H., Thompson, W. I., Drabing, S. M., & Francis, C. D. (2022). The broken-wing display across birds and the conditions for its evolution. *Proceedings of the Royal Society B: Biological Sciences*, 289(1971), 20220058.
<https://doi.org/10.1098/rspb.2022.0058>
31. Watson, H., Monaghan, P., Heidinger, B. J., & Bolton, M. (2021). Effects of human disturbance on postnatal growth and baseline corticosterone in a long-lived bird. *Conservation Physiology*, 9(1), coab052. <https://doi.org/10.1093/conphys/coab052>
32. Ozkan, K., Langley, J. M., Talbott, J. W., Kleist, N. J., & Francis, C. D. (2024). Divergent effects of short-term and continuous anthropogenic noise exposure on Western Bluebird parental care behavior. *PeerJ*, 12, e18558.
<https://doi.org/10.7717/peerj.18558>

33. Gill, J. A., Norris, K., & Sutherland, W. J. (2001). Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation*, 97, 265–268. [https://doi.org/10.1016/S0006-3207\(00\)00002-1](https://doi.org/10.1016/S0006-3207(00)00002-1)
34. Weston, M. A., Ehmke, G. C., & Maguire, G. S. (2011). Nest return times in response to static versus mobile human disturbance. *The Journal of Wildlife Management*, 75(1), 252–255. <https://doi.org/10.1002/jwmg.7>
35. Smith, R. K., Pullin, A. S., Stewart, G. B., & Sutherland, W. J. (2010). Effectiveness of Predator Removal for Enhancing Bird Populations. *Conservation Biology*, 24(3), 820–829. <https://doi.org/10.1111/j.1523-1739.2009.01421.x>
36. Tratalos, J. A., Jones, A. P., Showler, D. A., Gill, J. A., Bateman, I. J., Sugden, R., Watkinson, A. R., & Sutherland, W. J. (2021). Regional models of the influence of human disturbance and habitat quality on the distribution of breeding territories of common ringed plover *Charadrius hiaticula* and Eurasian oystercatcher *Haematopus ostralegus*. *Global Ecology and Conservation*, 28, e01640. <https://doi.org/10.1016/j.gecco.2021.e01640>
37. *Ringed Plover Project Reports | Isles of Scilly Wildlife Trust*. (2024). Retrieved 18 July 2026, from <https://www.ios-wildlifetrust.org.uk/ringed-plover-project-reports>
38. Liley, D. & Saunders, P. (2024). Recreation and the environment on the Isles of Scilly. Report by Footprint Ecology.
39. Natural England (2015). *NCA Profile:158 Isles of Scilly—NE507*. Natural England - Access to Evidence. Retrieved 18 July 2026, from <https://publications.naturalengland.org.uk/publication/6566056445345792>
40. De Pascalis, F., Collins, P. M., & Green, J. A. (2018). Utility of time-lapse photography in studies of seabird ecology. *PLOS ONE*, 13(12), e0208995. <https://doi.org/10.1371/journal.pone.0208995>

41. Brunner, T.J.; Penticoff, H.B.; Tully, Jr., T.N. Continued Advancement in Understanding of Corticosterone in Psittacines. *Animals* **2026**, *16*, 2160. <https://doi.org/10.3390/ani16142160>
42. Romero, L. M., & Reed, J. M. (2005). Collecting baseline corticosterone samples in the field: Is under 3 min good enough? *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *140*(1), 73–79. <https://doi.org/10.1016/j.cbpb.2004.11.004>
43. Dill, L. M. (1974). The escape response of the zebra danio (*Brachydanio rerio*) I. The stimulus for escape. *Animal Behaviour*, *22*(3), 711–722. [https://doi.org/10.1016/S0003-3472\(74\)80022-9](https://doi.org/10.1016/S0003-3472(74)80022-9)
44. van der Kolk, H., Krijgsveld, K. L., Linssen, H., Diertens, R., Dolman, D., Jans, M., Frauendorf, M., Ens, B. J., & van de Pol, M. (2019). Cumulative energetic costs of military aircraft, recreational and natural disturbance in roosting shorebirds. *Animal Conservation*, *23*(4), 359–372. <https://doi.org/10.1111/acv.12546>
45. *Fly and Sail to the Isles of Scilly | Isles of Scilly Travel*. (n.d.). Retrieved 8 September 2026, from <https://www.islesofscilly-travel.co.uk/>
46. *Air Traffic Control | Council of the ISLES OF SCILLY*. (n.d.). Retrieved 8 September 2026, from <https://www.scilly.gov.uk/environment-transport/airport/air-traffic-control>
47. Lafferty, K. D. (2001). Birds at a Southern California beach: Seasonality, habitat use and disturbance by human activity. *Biodiversity & Conservation*, *10*(11), 1949–1962. <https://doi.org/10.1023/A:1013195504810>
48. Barnett, S. C., van Dongen, W. F. D., Plotz, R. D., & Weston, M. A. (2023). Leash Status of Approaching Dogs Mediates Escape Modality but Not Flight-Initiation Distance in a Common Urban Bird. *Birds*, *4*(3), 277–283. <https://doi.org/10.3390/birds4030023>

49. Burger, J., & Gochfeld, M. (1981). Discrimination of the threat of direct versus tangential approach to the nest by incubating herring and great black-backed gulls. *Journal of Comparative and Physiological Psychology*, 95(5), 676–684.
<https://doi.org/10.1037/h0077811>
50. Steidl, R. J., & Anthony, R. G. (2000). Experimental Effects of Human Activity on Breeding Bald Eagles. *Ecological Applications*, 10(1), 258–268.
[https://doi.org/10.1890/1051-0761\(2000\)010%255B0258:EEOHAB%255D2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010%255B0258:EEOHAB%255D2.0.CO;2)
51. Berger, J., Daneke, D., Johnson, J., & Berwick, S. H. (1983). Pronghorn foraging economy and predator avoidance in a desert ecosystem: Implications for the conversion of large mammalian herbivores. *Biological Conservation*, 25(3), 193–208. [https://doi.org/10.1016/0006-3207\(83\)90036-8](https://doi.org/10.1016/0006-3207(83)90036-8)
52. Bleich, V. C., Bowyer, R. T., Pauli, A. M., Nicholson, M. C., & Anthes, R. W. (1994). Mountain sheep *Ovis canadensis* and helicopter surveys: Ramifications for the conservation of large mammals. *Biological Conservation*, 70(1), 1–7.
[https://doi.org/10.1016/0006-3207\(94\)90292-5](https://doi.org/10.1016/0006-3207(94)90292-5)
53. Weston, M. A., McLeod, E. M., Blumstein, D. T., & Guay, P.-J. (2012). A review of flight-initiation distances and their application to managing disturbance to Australian birds. *Emu - Austral Ornithology*, 112(4), 269–286.
<https://doi.org/10.1071/MU12026>
54. NatureScot Research Report 1283 - *Disturbance Distances Review: An updated literature review of disturbance distances of selected bird species* | NatureScot. (2023). Retrieved 24 June 2026, from <https://www.nature.scot/doc/naturescot-research-report-1283-disturbance-distances-review-updated-literature-review-disturbance>

55. Mayer, M., Natusch, D., Frank, S. (2019). Water body type and group size affect flight initiation distance of European waterbirds. *PLOS ONE*, 14(7).
<https://doi.org/10.1371/journal.pone.0219845>
56. Gutiérrez, J. S., Catry, T., Espinosa-Colín, M., Masero, J. A., & Granadeiro, J. P. (2023). Heat stress increases risk taking in foraging shorebirds. *Functional Ecology*, 37(4), 1005–1019. <https://doi.org/10.1111/1365-2435.14288>
57. Linssen, H., van de Pol, M., Allen, A. M., Jans, M., Ens, B. J., Krijgsveld, K. L., Frauendorf, M., & van der Kolk, H.-J. (2019). Disturbance increases high tide travel distance of a roosting shorebird but only marginally affects daily energy expenditure. *Avian Research*, 10(1), 31. <https://doi.org/10.1186/s40657-019-0171-8>
58. Rendall, A. R., Plotz, R. D., Yokochi, K., Krauss, J., Pengelly, A., Di Stefano, S. A., Swindell, S., Ranawana, K., Vidanapathirana, D. R., & Weston, M. A. (2024). Lifting the Veil of Darkness: Thermal Technology Facilitates Collection of Flight-Initiation Distances by Night. *Ecology and Evolution*, 14(11), e70450.
<https://doi.org/10.1002/ece3.70450>
59. Blumstein, D. T., Fernández-Juricic, E., Zollner, P. A., & Garity, S. C. (2005). Inter-specific variation in avian responses to human disturbance. *Journal of Applied Ecology*, 42(5), 943–953. <https://doi.org/10.1111/j.1365-2664.2005.01071.x>
60. Tablado, Z., & Jenni, L. (2017). Determinants of uncertainty in wildlife responses to human disturbance. *Biological Reviews*, 92(1), 216–233.
<https://doi.org/10.1111/brv.12224>
61. Ydenberg, R. C., & Dill, L. M. (1986). The Economics of Fleeing from Predators. In J. S. Rosenblatt, C. Beer, M.-C. Busnel, & P. J. B. Slater (Eds), *Advances in the Study of Behavior* (Vol. 16, pp. 229–249). Academic Press.
[https://doi.org/10.1016/S0065-3454\(08\)60192-8](https://doi.org/10.1016/S0065-3454(08)60192-8)

62. Beale, C. M., & Monaghan, P. (2004a). Behavioural responses to human disturbance: A matter of choice? *Animal Behaviour*, 68(5), 1065–1069.
<https://doi.org/10.1016/j.anbehav.2004.07.002>
63. Chabani, S., Khames, G. E. Y., Djemadi, I., Draidi, K., Rezouani, I. E., Mezhoud, B., Moussouni, A., Mederbal, K. E., Telailia, S., & Bakhouch, B. (2026). Breeding Under Pressure: Shorebird Reproductive Success Amid Urban Disturbance Along a Mediterranean Urban Waterfront. *Birds*, 7(1), 13.
<https://doi.org/10.3390/birds7010013>
64. Liker, A., Sinkovics, C., Sándor, K., Bukor, B., Nagy, N., Ódor, L., Klucsik, K. P., & Ágh, N. (2026). Behavioural Effects of Persistent Human Disturbance: A Playback Experiment in a Forest Bird. *Ecology Letters*, 29(2), e70316.
<https://doi.org/10.1111/ele.70316>
65. Battisti, C. (2023). Rock and Plovers—A Drama in Three Acts Involving a Big Musical Event Planned on a Coastal Beach Hosting Threatened Birds of Conservation Concern. *Conservation*, 3(1), 87-95.
<https://doi.org/10.3390/conservation3010008>
66. Farris, E., Pisanu, S., Ceccherelli, G., & Filigheddu, R. (2013). Human trampling effects on Mediterranean coastal dune plants. *Plant Biosystems - An International Journal Dealing with All Aspects of Plant Biology*, 147(4), 1043–1051.
<https://doi.org/10.1080/11263504.2013.861540>
67. Battisti, C., Perchinelli, M., Vanadia, S., Giovacchini, P., & Marsili, L. (2023). Monitoring Effectiveness of an Operational Project on Two Threatened Landbirds: Applying a Before–After Threat Analysis and Threat Reduction Assessment. *Land*, 12(2), 464. <https://doi.org/10.3390/land12020464>

68. Burger, J., & Niles, L. (2013). Shorebirds and stakeholders: Effects of beach closure and human activities on shorebirds at a New Jersey coastal beach. *Urban Ecosystems*, 16(3), 657–673. <https://doi.org/10.1007/s11252-012-0269-9>

8.1. RStudio & Packages Citations

- R Core Team (2025). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria <<https://www.R-project.org/>>.
- Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Golemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Bache SM, Müller K, Ooms J, Robinson D, Seidel DP, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019). “Welcome to the tidyverse.” *Journal of Open Source Software*, 4(43), 1686. <https://doi.org/10.21105/joss.01686>
- Douglas Bates, Martin Maechler, Ben Bolker, Steve Walker (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1-48. <https://doi:10.18637/jss.v067.i01>
- McGillicuddy M, Warton DI, Popovic G, Bolker BM (2025). “Parsimoniously Fitting Large Multivariate Random Effects in glmmTMB.” *Journal of Statistical Software*, 112(1), 1-19. <https://doi.org/10.18637/jss.v112.i01>
- Hartig F (2026). DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. <https://doi.org/10.32614/CRAN.package.DHARMA> R package version 0.5.0, <https://CRAN.R-project.org/package=DHARMA>
- Lenth R, Piaskowski J (2026). emmeans: Estimated Marginal Means, aka Least-Squares Means. <https://doi.org/10.32614/CRAN.package.emmeans> R package version 2.0.4, <https://CRAN.R-project.org/package=emmeans>
- Fox J, Weisberg S (2019). *An R Companion to Applied Regression*, Third edition. Sage, Thousand Oaks CA. <https://www.john-fox.ca/Companion/>

- Lüdecke et al., (2021). performance: An R Package for Assessment, Comparison and Testing of Statistical Models. Journal of Open Source Software, 6(60), 3139.
<https://doi.org/10.21105/joss.03139>

8.2. EDINA Digimap Citation

- OS Open Built Up Areas [GeoPackage geospatial data], Scale 1:25000, Tiles: GB, Updated: 4 November 2022, Ordnance Survey (GB), Using: EDINA Digimap Ordnance Survey Service, <<https://digimap.edina.ac.uk>>, Downloaded: 2026-07-14 15:12:54.175.

Appendix

Appendix 1: Generative AI prompts table

Date	AI tool used	Purpose	Prompt	Hyperlink to output (where possible)	Section of work used for
15/07/2026	Claude	To generate summaries of data to aid in writing of results	'Hi, I'm working on my msc project on the recreational disturbance and population viability of ringed plovers on the isles of scilly. I have annotated 1 year of camera trap footage so far (hoping to add another soon) and would like some summaries of the data to include in the start of my results. my aims are to quantify if disturbance type affects the probability of flushing (the bird leaving the nest), distance, disturbance type and distance, and frequency and anything else interesting you think I could add'	https://claude.ai/share/283b42f2-860d-4ea3-918c-9ce0a299d7f8	Results

16/07/2026	Claude	To develop ideas	these questions are based off literature but would you suggest anything else I could do with it? also thanks for the advice on my data, I'm planning on adding the sites from 2024 and more sites to make the stats more robust if you think that's a good idea and then fixing year as a random effect?	https://claude.ai/share/283b42f2-860d-4ea3-918c-9ce0a299d7f8	Results
16/07/2026	Claude	Help with proofreading data (Disturbance events and nest effort spreadsheets) and generate RStudio code for the basis of the figures in the Results	Would you be able to proofread the spreadsheets? Then, I'd like to make some figures in RStudio to show my results. Could you help with that?	https://claude.ai/share/283b42f2-860d-4ea3-918c-9ce0a299d7f8	Results
16/07/2026	Claude	To help understand key concepts and theories. Explanations of statistical concepts	What statistical models would you recommend using?	https://claude.ai/share/283b42f2-860d-4ea3-918c-9ce0a299d7f8	Results
16/07/2026	Claude	To proofread and correct R code	Error in `mutate()`: ! In argument: `Date = as.Date(Date)`. Caused by error in `charToDate()`:	https://claude.ai/share/283b42f2-860d-4ea3-918c-9ce0a299d7f8	Results

			! character string is not in a standard unambiguous format Run `rlang::last_trace()` to see where the error occurred.		
17/07/2026	Claude	To help understand key concepts and theories Explanations of statistical concepts	Based on these [data], what models would you recommend? I will be adding another year in a few weeks, so what can I do for now as well?	https://claude.ai/share/283b42f2-860d-4ea3-918c-9ce0a299d7f8	Results
17/07/2026	Claude	To improve the plan or structure of my assessment	I'm starting to think about planning out my discussion for when I have my modelling and figures finished. Would you be able to give me some heading suggestions?	https://claude.ai/share/283b42f2-860d-4ea3-918c-9ce0a299d7f8	Discussion

Appendix 2: Field Survey full methods

Field surveys were conducted across all inhabited islands (Bryher, Tresco, St Martin's, St Mary's, and St Agnes) and one uninhabited island (Teãñ), focusing on habitats suitable for Ringed Plover territory establishment; primarily sand and shingle beaches. Each day, a different island was surveyed.

Surveys were carried out from mid-April to the end of July, coinciding with the Ringed Plover breeding season, as established by the ISWT's monitoring programme since 2024. This period was selected to maximise the probability of detecting both nesting and territorial behaviour.

Surveys followed protocols developed by the ISWT:

1. Nest site identification
 - a. Systematic beach walks: when in teams, one surveyor walked along the high-tide mark while another surveyed the upper beach; when alone, a zig-zag pattern was adopted as this has been shown to reduce missing nests.
 - b. Behavioural observation: surveyors observed adult behaviour (alarm calling, circling, running to and from a particular area) and waited 5-10 minutes for adults to return to the nest to locate eggs accurately.

All previously known nesting locations from the past two years were checked, as Ringed Plovers tend to return to the same nesting locations annually. Nevertheless, all areas with suitable habitat were surveyed also. Nests were identified based on indications of their presence. First, adults' territorial behaviour, including slow wingbeat "butterfly" song flights, confrontations with neighbouring and intruding birds of the same or different species (e.g. oystercatchers, which often share territories), alarm calling, mobbing, and agitated behaviour such as head bobbing (Pienkowski, 1984; Tratalos *et al.*, 2021). Evidence also

included a scrape with eggs, an adult distraction display (i.e. broken wing or injury) (de Framond *et al.*, 2022), or the presence of chicks (see Images below).



Image 2. An image showing a Common Ringed Plover nest with a clutch of 4 eggs, laid in a nest scrape.



Image 3 depicts a Common Ringed Plover chick on the left and an unhatched egg on the right for reference.

The locations of nests were recorded using the QuickCapture app, which records Global Positioning System (GPS) coordinates, and the user can also record the number of eggs, adults and chicks (if hatched).

No surveys were undertaken during winds exceeding a moderate breeze or during periods of prolonged rain, due to poor visibility, challenges with boat travel, and to reduce the risk of chilling eggs or young if incubating or brooding adults were disturbed.

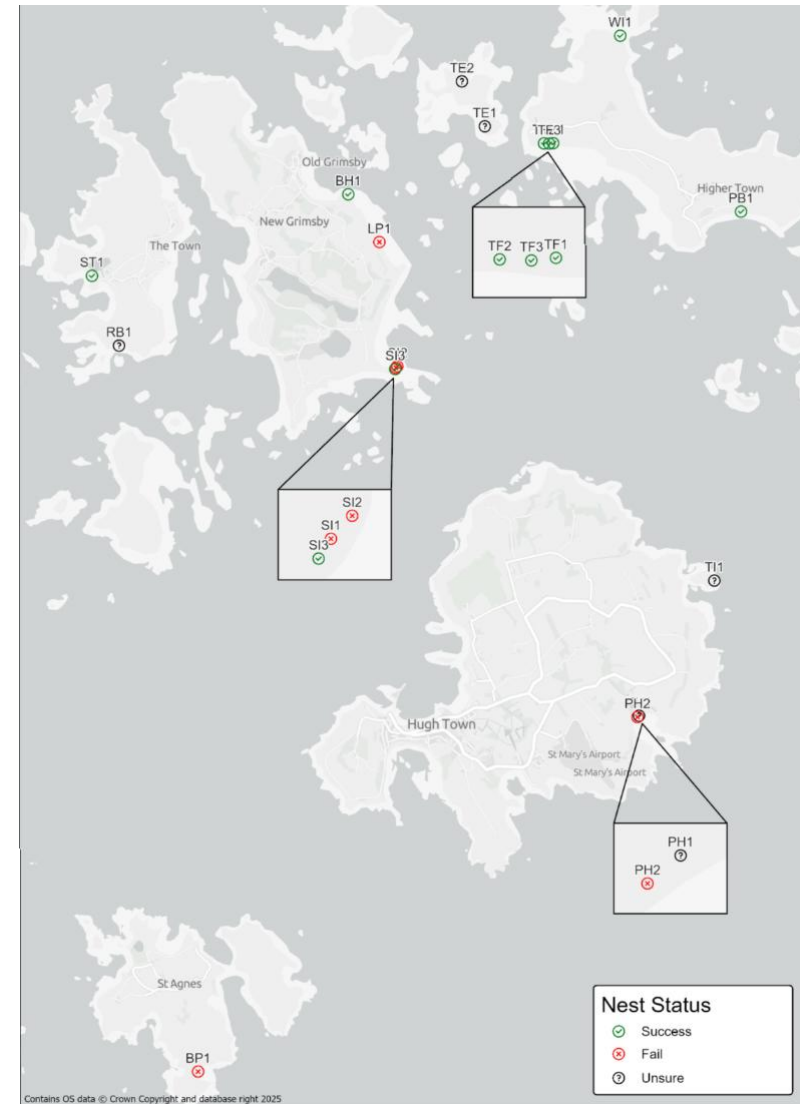
Appendix 3: Isles of Scilly Wildlife Trust full nest outcomes dataset

Year	Island	Beach	NestID	Outcome
2024	StAgnes	Porth Askin	PA1	Success
2024	StAgnes	Beady Pool	BP1	Fail
2024	StAgnes	Beady Pool	BP2	Success
2024	StMarys	Porth Hellick	PH1	Success
2024	StMartins	Lawrences	LA1	Fail
2024	StMartins	Lawrences	LA2	Success
2024	StMartins	The Flats	TH1	Fail
2024	StMartins	The Flats	TH2	Success
2024	StMartins	The Flats	TH2b	Fail
2024	StMartins	White Island	WI1	Success
2024	Teian	Teian	TE1	Fail
2024	Teian	Teian	TE2	Success
2024	Tresco	Skirt Island	SI1	Success
2024	Tresco	Bathing House	BA1	Fail
2024	Bryher	Stinking Par	ST1	Success
2024	Bryher	Popplestones	PS1	Success
2025	StAgnes	Beady Pool	BP1	Fail
2025	StMarys	Porth Hellick	PH1	Unsure
2025	StMarys	Porth Hellick	PH2	Fail
2025	StMarys	Tolls Island	TI1	Fail
2025	StMartins	Par Beach	PB1	Success
2025	StMartins	The Flats	TF1	Success
2025	StMartins	The Flats	TF2	Success
2025	StMartins	The Flats	TF3	Success
2025	StMartins	White Island	WI1	Success
2025	Teian	Teian	TE1	Unsure
2025	Teian	Teian	TE2	Unsure
2025	Tresco	Lizard Point	LP1	Fail
2025	Tresco	Skirt Island	SI1	Fail
2025	Tresco	Skirt Island	SI2	Fail
2025	Tresco	Skirt Island	SI3	Success

2025	Tresco	Block House	BH1	Success
2025	Bryher	Stinking Par	ST1	Success
2025	Bryher	Rushy Bay	RB1	Unsure

Appendix 4: Maps of relative Ringed Plover nest locations from 2024 and 2024

Two maps of the relative Ringed Plover nest locations from 2024 (on the left) and 2025 (on the right). Credits: Isles of Scilly Wildlife Trust



Appendix 5: Table of Raw Disturbance Categories

Raw disturbance types recorded during camera-trap annotation were collapsed into broader categories for analysis, as show in table below. Note: For the compounding disturbance model, “Dog only” events were further collapsed into the “Other” category due to sparse cell counts when cross-tabulated with cluster status (see Methods).

Raw disturbance category	Grouped category
Human (on foot)	Walkers
Human + dog	Walkers + dog
Dog (unaccompanied/loose)	Dog only
Aircraft	Aircraft
Equestrian	Other
Land vehicle	Other
Livestock	Other
Mixed (human+natural)	Other
Mixed (human+recreational)	Other
Natural - avian	Other
Natural - mammal	Other
Watercraft	Other

Appendix 6: Diagnostic tests in full

Flush Probability by Disturbance Type

Model diagnostics indicated an adequate fit (DHARMA dispersion test $p=0.864$; KS test $p=0.906$; not singular; NestID random effect SD=1.56 on the log-odds scale).

Flush Probability by Distance

Model diagnostics indicated an adequate fit (dispersion $p=0.976$; KS test $p\approx 0.75$; not singular)

Return Latency by Disturbance Type

DHARMA diagnostics indicated a significant deviation from the expected distribution for the category model (KS test, $p<0.001$), likely reflecting the extremely heavy-tailed nature of return latency; dispersion was not a concern ($p=0.36$) and no single category was disproportionately responsible for the deviation (mean scaled residuals ranged 0.42–0.50 across categories). A sensitivity analysis excluding the ten most extreme latency values (≥ 151 min) reproduced essentially identical coefficients and p-values (e.g. dog effect: -0.459 $\rightarrow$ -0.463, $p=0.062 \rightarrow 0.057$), confirming the distributional deviation does not undermine the reported effect directions.

Compounding effects

Model diagnostics indicated an excellent fit dispersion $p=0.952$; KS test $p=0.987$; residuals-vs-predicted plot showed no significant problems; not singular).

Nest outcome and proximity

The two distance measures were uncorrelated ($r=-0.068$), and a mixed-effects check accounting for repeated use of the same beach across years (7 of 15 sites monitored in

both 2024 and 2025) found no meaningful site-level clustering (singular fit, variance=0), thus supporting the simpler generalised mixed model as the primary model. Diagnostics indicated an adequate fit (dispersion $p=0.76$; KS test $p=0.594$).