


Effects of experimental land management on habitat use by Eurasian Stone-curlews

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Abstract

Effective conservation is often informed by focal species studies to identify beneficial land management interventions. For nocturnal or cryptic species, quantifying habitat use across individually marked animals can allow unbiased assessment of intervention efficacy and identify other important habitats. Here, using a landscape-scale experiment, we examine whether interventions intended to create nesting habitat for the largely nocturnal Eurasian Stone-curlew *Burhinus oedicnemus* within semi-natural grassland also provide foraging habitat. GPS loggers were fitted to five adult Stone-curlews during the breeding season within an extensive area of semi-natural grassland (3850 ha, hereafter 'grassland'), surrounded by a mosaic of arable cropland (total study area 118 600 ha). The largely closed-sward grassland was diversified by experimental ground-disturbance plots (the intervention) prior to this study. We used the GPS fixes to identify 1881 foraging locations (510 during nesting and 1371 post-breeding) across the grassland and surrounding landscape. Most foraging locations were close to the nest-site during the nesting period (90% within 1 km) or day-roost during post-breeding (90% within 5 km), but birds travelled up to 4.1 km from these sites during nesting and 13 km post-breeding. Stone-curlews were two- (by night) or three-times (by day) more likely to select disturbed-grassland over unmodified grassland for foraging during nesting, and *c.* 15 times more likely to do so post-breeding. Spring-sown crops and pig fields or manure heaps were also selected over grassland for nocturnal foraging. Given that central place foraging occurs in this species, conservation efforts that promote breeding attempts through ground-disturbance should ensure suitable foraging habitat is near the nest (<1 km). Creating multiple areas of disturbed-ground close to the edge of large grassland blocks can provide a network of nesting and foraging habitats, while allowing access to foraging habitats on the surrounding arable farmland. Similar interventions may benefit other disturbance associated grassland waders.

Introduction

Effective conservation often depends upon land management interventions. Such management is particularly effective when the design of the interventions is informed by knowledge of the target species' ecology and their efficacy is subsequently tested (Peach *et al.*, 2001; O'Brien, Green & Wilson, 2006; Bretagnolle *et al.*, 2011). While many studies have appraised land management interventions by comparing the abundance of the target species on treated areas to unmodified controls (Bright *et al.*, 2015; Daskalova *et al.*, 2019), the inconspicuous behaviours of certain species are often overlooked. Instead, accurate tracking data combined

with well-replicated land management experiments can provide a more rigorous and unbiased test of intervention efficacy for nocturnal or cryptic species. Tracking can also provide insights into how intervention areas should be distributed to facilitate access to other important habitats.

Land management interventions are critical to the effective conservation of the biparental and largely nocturnal (but also crepuscular) Eurasian Stone-curlew *Burhinus oedicnemus* (hereafter, 'Stone-curlew'), which suffered widespread declines across Europe during the 20th century (Tucker & Heath, 1994). In Western Europe, Stone-curlews occupy sparsely vegetated ground in spring-sown crops and semi-natural dry grassland or dwarf-shrub heathland (hereafter collectively

'semi-natural grassland'), with open and short swards produced by grazing and physical disturbance providing their preferred nesting habitat (Green, Tyler & Bowden, 2000). Earthworms, soil-surface invertebrates and molluscs are the main prey of adults and chicks, which adults hunt by scanning the ground and pecking from the surface. The UK's migratory Stone-curlew population declined for much of the 20th century, but has been subject to an intensive conservation programme – informed by detailed study of the species breeding ecology and habitat use (Green *et al.*, 2000) – and has partly recovered (Evans & Green, 2007). 'Rescue' interventions were used to protect nests and chicks from crop-management operations and thereby counteract the low breeding success of crop-nesting Stone-curlews. To reduce dependence on individual nest-protection, 'safe' suitable (bare-open, cultivated) uncropped 'plots' (1–2 ha) are provided within arable farmland and semi-natural grassland. Although these efforts have led to a partial population recovery (Supporting Information, Figure S1), declines would resume if rescue interventions were to cease (Johnston, 2009).

Reducing the reliance of Stone-curlew conservation on resource-intensive rescue interventions, by increasing the proportion of breeding attempts on semi-natural grassland and nest plots, is considered a high priority in the UK (Johnston, 2009) and a possible conservation measure elsewhere (Gaget *et al.*, 2019). The number of plots on arable farmland is limited by the number of landowners willing to undertake this management, and the availability of agri-environment scheme funding to compensate for the loss of crop production. However, in semi-natural grasslands plot creation does not cause significant loss of revenue because extensive livestock management is primarily for conservation.

Mechanical ground disturbance of semi-natural grassland provides suitable Stone-curlew nesting habitat (Johnston, 2009; Hawkes *et al.*, 2019b); however, it remains unclear whether such management also provides suitable foraging habitat and whether other habitats are also utilized. To investigate this, we examined Stone-curlew resource selection (from tracked adults) during the breeding season in a large (3850 ha) block of semi-natural grassland which had been diversified by experimental ground-disturbance treatments (66 plots that were 2–3 ha, providing 172 ha). Given prior knowledge of the species ecological requirements (Green *et al.*, 2000) our expectation was that disturbed-grassland would be selected over undisturbed-grassland for foraging, but other surrounding farmland habitats would also be important. Last, to establish whether ground-disturbance detail matters, we also examined foraging site selection among subplots that differed in disturbance frequency or time since treatment.

Materials and methods

Study area

The study was carried out in 2016 in the Breckland region of Eastern England, which is characterized by sandy soils, a

semi-continental climate and varied landcover including mixed farmland, plantation forestry and semi-natural grassland comprising native plant communities. Breckland held an estimated 207 pairs of breeding Stone-curlews in 2016 (*c.* 58% of the UK population; with the rest in the Wessex region of Southern England and other smaller satellite populations; Supporting Information, Figure S1). This study focused on three semi-natural grassland sites (the Stanford Training Area, STANTA, 52°51'N, 0°76'E, 3500 ha; Bridgham Heath 52°44'N, 0°83'E, 150 ha; and Brettenham Heath, 52°43'N, 0°83'E, 200 ha) (Supporting Information, Appendix S1) but also extended across a wider landscape of grassland and arable cropland encompassing the home ranges of tracked birds (118 600 ha; Supporting Information, Figure S2). Although this study was conducted over a single year the weather was typical of previous years (Supporting Information, Appendix S1).

Ground-disturbance plots

To test whether ground disturbance provides suitable foraging habitat, we implemented 66 replicate 2-ha plots (33 shallow-cultivated, created with a rotary-rotovator; 33 deep-cultivated, created with an agricultural plough) across the three areas of semi-natural grassland (Supporting Information, Figure S2) for the first time in early 2015 (January to early May). Plots were restricted to the outer areas of STANTA, plus Bridgham and Brettenham Heaths, because of the risks imposed by unexploded ordnance in the central area of STANTA. Treatments were repeated in late 2015/early 2016 (November 2015 to February 2016), maintaining 26 as 2-ha 'homogenous' plots (same area disturbed in both years) and diversifying 40 as 3-ha 'complex-mosaic' plots. A complex mosaic plot comprised: half (1 ha) of the initial 2-ha plot left undisturbed in winter 2015/2016 ('fallow'); half of the initial plot on which the ground-disturbance was repeated in winter 2015/2016 ('repeat-cultivated'); and an adjacent 1-ha area of unmodified grassland cultivated for the first time in winter 2015/2016 ('first-time-cultivated').

Stone-curlew capture and monitoring

Between March and July 2016, all ground-disturbance plots were searched for Stone-curlews approximately every 10 days. During each visit, we scanned the plot from a vehicle located over 100 m away. Five pairs were located (one in each of Bridgham and Brettenham Heath, and three in STANTA), and the sex of each bird was resolved by observing their plumage characteristics and social interactions (Green & Bowden, 1986) prior to capture (at least one bird from each pair was marked with darvic colour rings). Following Green *et al.* (2000), one individual from each pair was trapped before dawn with a small elastic-powered clap net baited with a tethered beetle prior to breeding ($n = 3$) or by day with a cage trap on the nest ($n = 2$) between 20 April and 12 June. We fitted solar-powered 'nanoFix Geo' GPS tags (PathTrack Ltd, Otley, UK) measuring 41 × 12 × 10 mm (L × W × H) plus an external whip

antenna and weighing 5.2 g (*c.* 1.5% of the body weight) (see Supporting Information, Appendix S1 for attachment details). Tags were configured to record GPS fixes (accurate to *c.* ± 15 m) once every hour (71% of fixes) when fully charged, or once every 2 or 3 h (25% and 4% of fixes respectively) when battery voltage was low. GPS data were routinely downloaded to a remote base station through a radio connection until the tag either dropped off ($n = 4$) or ceased functioning ($n = 1$).

Tagged birds were visited at least once a week to establish their status as pre-breeding, nesting-phase, chick-phase or post-breeding (after nest/brood loss). Once a nest was located, eggs were weighed and their length and breadth measured to calculate the hatch date (Day, 2003). Three days prior to hatching, and thereafter until brood failure, visits were every 3 days to determine whether the eggs had hatched, and if so, whether the chick(s) were alive.

Landcover categorization

We used the Centre of Ecology and Hydrology *Land Cover Map 2015* (LCM2015) (Rowland *et al.*, 2017) to map semi-natural grassland, improved grassland and arable fields across the study area in ArcGIS V.10 (ESRI, 2011), and to identify landcovers known to be unsuitable for Stone-curlews (woodland, freshwater, wet or seasonally-wet habitat and urban). Informed by prior information about Stone-curlew foraging habitat preferences (Green *et al.*, 2000), we combined semi-natural grassland with improved grassland (hereafter collectively 'grassland'). Next, based on field-based surveys carried out across part of the study area (13 480 ha; Supporting Information, Figure S2) and satellite images obtained from the European Space Agency Copernicus Sentinel-2 satellite (available at: <https://scihub.copernicus.eu/dhus/#/home>), we mapped: (1) experimental ground-disturbance plots and other areas of physically disturbed grassland (hereafter collectively 'disturbed-grassland'); (2) outdoor pig fields and (3) cultivated Stone-curlew nest plots within arable crops. Lastly, we mapped manure heaps, which are typically left alongside fields, by field-based surveys. We buffered each heap by 30 m and combined them with pig fields to give 'pig fields or manure heaps'.

To determine the crop identity within each arable field, we used the 2016 Crop Map for England (CROME; Rural Payments Agency, 2019), a dataset comprised of 0.41 ha cells classified by remote sensing as a crop type or a non-crop landcover category. The most frequent category within each field determined its identity, resulting in 14 initial crop categories (Table 1), four non-crop categories (grassland and fallow fields; and two categories excluded from analysis: woodland and freshwater) plus cases where identity was not resolved (classified as 'unidentified field'). Next, supported by prior information on Stone-curlew habitat preferences (Green *et al.*, 2000), crop types with similar sowing dates, vegetation structure and profile (*i.e.* raised- vs. flat-beds) were merged, producing eight habitat categories (Table 1). Remotely sensed uncropped fallow fields were combined with Stone-curlew nest plots within arable crops to give an

'arable fallow' category, as both were typically cultivated (but left fallow) in winter 2015/2016 and characteristically bare throughout the year.

To examine the accuracy of this simplified crop classification, we undertook cross-validation for 561 arable fields (Supporting Information, Figure S2) against their ground-truthed identity established from a field-based survey conducted between April and July, which led us to combine autumn cereals with spring cereals (now 'cereals'), and omit field beans, peas and linseed entirely from further analysis owing to high misclassification (Supporting Information, Table S1; field beans, peas and linseed were scarce, comprising just 16 of the ground-truthed fields). Last, to improve the classification accuracy of remotely sensed arable fallows, which field-based surveys showed were frequently 'vegetable or root crops' (Supporting Information, Table S1), and to determine the identity of remotely sensed unidentified fields, which were mostly arable fallows or 'vegetable or root crops', we visually inspected each of these fields using Sentinel-2 imagery; classifying as 'vegetable or root crops' where a crop was present in June or August (this was unlikely to be any other crop; Supporting Information, Table S1), and otherwise as arable fallow.

Classifying locations

GPS fixes (hereafter, 'locations') were classified by breeding stage as: pre-breeding, nesting, chick-phase or post-breeding (pre-migratory staging period), and as diurnal (after sunrise, before sunset) or nocturnal (after sunset, before sunrise). Pre-breeding and chick-phase locations were not considered subsequently because tracking was over a short period (pre-breeding, 34 days across three individuals [211–326 locations per individual]; chick-phase, 23 days across two individuals that lost their broods shortly after hatching [96–169]) compared to the nesting and post-breeding phases (nesting, 106 days across four individuals [379–672]; post-breeding, 260 days across five individuals [315–1594]).

For locations identified during the nesting period, we excluded those within 50 m of the nest (where individuals mostly incubated or loafed), whereas those >50 m from the nest were classified as foraging trips. For locations identified during the post-breeding period, when foraging is almost entirely conducted at night, the fix closest in time to 16:00 (per bird, per day) was classified as the day-roost; definition of the day-roost location by this fix is justified as a movement during the day was minimal [median displacement between fixes closest in time to 12:00 vs. 16:00 h = 32 m, interquartile range (IQR) 16–92 m]. All retained nesting (diurnal and nocturnal) and nocturnal post-breeding period locations were assumed to represent foraging locations. Post-breeding foraging locations were paired with the day-roost from that day (locations before midnight) or the previous day (after midnight). Last, we omitted foraging locations from landcover categories that were: (1) known to be unsuitable for Stone-curlews (Supporting Information, Table S2), (2) frequently misclassified by remote sensing (Supporting Information, Table S1), or (3) used too infrequently to

Table 1. Landcover and crop categories included (Y) and omitted (–) from analyses of Eurasian Stone-curlew *Burhinus oedicnemus* foraging-site selection (separately during nesting and post-breeding; DF, diurnal foraging model; NF, nocturnal foraging model). Initial crop categories [autumn-sown (A), spring-sown (S) or both (B)] were combined according to phenology and structure and further merged (denoted by shading) following cross-validation against a sample of ground-truthed fields ($n = 561$; Supporting Information, Table S1). Omitted categories were known to be unsuitable for Stone-curlews (Supporting Information, Table S2), frequently misclassified by remote sensing (crop categories only; judged from cross-validation, Supporting Information, Table S1), or used too infrequently to reliably model resource selection (judged separately for each analysis, Supporting Information, Table S2)

Initial categories	Categories merged by phenology and structure	Final categories	Categories included in analysis		
			Nesting period		Post-breeding
			DF	NF	NF
Grassland ^a	Grassland	Grassland	Y	Y	Y
Disturbed-grassland ^{b,c}	Disturbed-grassland	Disturbed-grassland	Y	Y	Y
Sugar beet (S) ^d	Sugar beet or maize (S)	Sugar beet or maize (S)	Y	Y	Y
Maize (S) ^d					
Pig field or manure heaps ^{b,c}	Pig field or manure heaps	Pig field or manure heaps	—	Y	Y
Carrot (S) ^d	Vegetable or root crops (S)	Vegetable or root crops (S)	—	Y	Y
Onions (S) ^d					
Parsnips (S) ^d					
Cabbage (S) ^d					
Potatoes (S) ^d					
Arable fallows ^{b,e}	Arable fallows	Arable fallows	—	—	Y
Barely (S) ^d	Cereals (S)	Cereals (B)	—	Y	Y
Wheat (S) ^d					
Barely (A) ^d	Cereals (A)				
Wheat (A) ^d					
Rye (A) ^d					
Field beans (B) ^d	Field beans (B)	Field beans (B)	—	—	—
Linseed (S) ^d	Linseed (S)	Linseed (S)	—	—	—
Rape (A) ^d	Rape (A)	Rape (A)	—	—	—
Peas (S) ^d	Peas (S)	Peas (S)	—	—	—

Landcover was identified from: ^athe Center of Ecology and Hydrology Land Cover Map 2015 (Rowland *et al.*, 2017); ^bsatellite images (obtained from the Sentinel-2, available at; <https://scihub.copernicus.eu/dhus/#/home>); ^cfield-based surveys (see Supporting Information, Figure S2); and ^dremote sensing (obtained from the Crop Map for England, Rural Payments Agency, 2019). ^eArable fallows comprised Eurasian Stone-curlew nest plots within arable crops ^{b,c} and arable fields left uncropped^d.

reliably model (<2% for each of diurnal nesting, nocturnal nesting and nocturnal post-breeding foraging locations; Supporting Information, Table S2). These categories were omitted from subsequent analysis (Table 1).

Analysis of resource selection, movement behaviour and subplot use

To investigate resource selection, we compared habitat at used locations with availability at the scale of each individuals' home-range (third-order selection; Johnson, 1980). To control for central place foraging when sampling habitat availability, we paired each foraging location with four random locations positioned the same distance from the nest-site (during nesting) or day-roost (post-breeding), but in random directions (see Supporting Information, Figure S3). By constraining random locations this way, the modelled sample represented used and unused sites equally available for the same travel investment. An alternative approach, whereby

random points are allocated within each birds' home range (e.g. quantified using a Minimum Convex Polygon, MCP) would over-sample less accessible distant locations.

We used Generalized Estimating Equations (GEE) from the package 'geepack' (Halekoh, Højsgaard & Yan, 2006) with a binomial response variable (used locations, random locations) and logit link to model: (1) foraging-site selection during nesting (separate models considered diurnal and nocturnal locations, as response to human disturbance, Taylor, Green & Perrins, 2007, anti-predator vigilance, and prey availability, may all differ between day and night); and (2) nocturnal foraging-site selection post-breeding. GEEs are suited to resource selection analyses because they model robust standard error estimates that account for repeated observations of the same individual by replacing the assumption of independence with a defined correlation structure (Koper & Manseau, 2009). For each model, habitat was entered as a fixed effect (Table 1), with undisturbed grassland set as the reference category and locations (used/random) clustered by

bird identity to control for repeat observations from the same individual. An interaction between date and habitat was not considered because the start and end of each tracking period varied considerably (Supporting Information, Figure S4); thus date would have been confounded with individual. After assessing model fit by comparing the quasilielihood information criterion of models with alternative correlation structure (autoregressive, exchangeable, or independent, following Pan, 2001), we selected an autoregressive structure – which assumes correlations between locations decrease progressively with time – for every model; though importantly, GEEs are still reliable with mis-specified correlation structures (Hardin & Hilbe, 2002; Dormann *et al.*, 2007; Koper & Manseau, 2009). Following usual practice (Keating & Cherry, 2004; Hebblewhite *et al.*, 2005) we evaluated the probability of selection of each habitat relative to grassland (model intercept) using odds ratios derived from the beta coefficients. Habitat categories were considered to be selected similarly to grassland when their odds ratio confidence interval (CI) overlapped one, and similarly to another habitat when CIs overlapped. Note, because tags were accurate to ± 15 m, selection coefficients are slightly biased in favour of larger landcover categories (e.g. arable crops or undisturbed grassland) where the consequence of any error is negligible. Selection coefficients may also be biased towards long established landscape features (e.g. arable nest plots); however, most landcover categories were either recently established (ground-disturbance plots) or rotate around the landscape (arable crops, pig fields), which probably limits any site fidelity bias. All analysis was undertaken in R (R Core Team, 2015).

Following Boyce *et al.* (2002), we validated each model through a *k*-fold cross-validation, at each iteration withholding 20% of both used and available data (randomly, pooling data across individuals) while using the rest to develop a new cross-validation set (the trained model, producing five sets). For each set (trained model), we examined the Spearman's rank correlation between 10 equal-sized categories of odds ratio 'scores' (hereafter 'bins'; 0–10, increasing from the lowest to highest score) and the area-adjusted frequency of each bin (for a detailed overview, see Roberts *et al.*, 2017). A significant ($P < 0.05$) positive correlation between area-adjusted scores and odd ratio bins (i.e. the area-adjusted frequency increases progressively with bin rank) across all sets, indicates a model with good predicative performance (Boyce *et al.*, 2002).

To determine whether Stone-curlews travelled further from the nest- or roost-site to forage within certain habitats, we used linear mixed models from the package 'lme4' (Bates *et al.*, 2017). Separately for diurnal nesting, nocturnal nesting and nocturnal post-breeding, distance travelled to each foraging location (log transformed) was included as the dependent variable, with habitat type as a categorical fixed effect (Table 1) and bird identity as a random effect. Habitat category means were compared by Tukey's pairwise comparison in the package 'multcomp' (Hothorn, Bretz & Westfall, 2008).

We examined the use of treated plots in greater detail, separately for foraging locations during nesting (pooling diurnal and nocturnal) and nocturnal post-breeding, considering only those plot complex-mosaics with at least one location during the relevant period. Homogenous plots were excluded from this analysis because only one treatment type was available, prohibiting any assessment of subplot choice. We calculated the number of locations within each subplot (three categories: first-time cultivated, repeat-cultivated and fallow), but discarded 18 nesting-period foraging locations from one individual to avoid over-inflating subplot use on the plot where they nested (but retaining their locations from other plots, and all post-breeding locations). Whether the frequency of use of the three subplot categories differed from a uniform distribution was examined using Fisher's exact tests, separately for deep- and shallow-cultivated complex-mosaics. Where overall subplot use differed significantly from uniform (Fisher's exact $P < 0.05$), we performed three pairwise comparisons (Fisher's exact tests) with Bonferroni-adjusted correction for multiple tests (MacDonald & Gardner, 2000).

Results

Three male and two female Stone-curlews were tracked for a mean duration of 84 days (range: 67–103 days). During the nesting period, 287 diurnal (37–101) and 223 nocturnal (39–75) foraging locations were recorded across four individuals (three males and one female from a different pair, from one breeding attempt each). Two nested on disturbed-grassland, and the other two on an arable crop (one on each of sugar beet and maize) immediately adjacent to grassland and close to disturbed-grassland (120 and 350 m respectively). Post-breeding, 1371 nocturnal foraging locations (110–476) were recorded across all five individuals. During each period, 96% (during nesting) and 94% (post-breeding) of foraging locations were within 100 m of another foraging location (from the same individual, from the same period). However, omitting one individual that was only tracked post-breeding, just 17% of post-breeding foraging locations were within 100 m of a nesting period foraging location (from the same individual). Each individuals nesting and post-breeding home range either completely or partially overlapped, but the latter was always larger (inferred from MCPs, Fig. 1).

Nesting period foraging-site selection

During nesting, 90% of foraging locations were within 1 km of the nest (furthest was 4.1 km, Fig. 2). Birds travelled further to forage at night (nocturnal foraging, median distance travelled = 523 m, IQR 157–842 m; diurnal foraging, 109 m, IQR 68–305 m; Mann–Whitney, $P < 0.001$). The most distant nocturnal foraging locations were on 'pig fields or manure heaps' (Fig. 3). Diurnally, three habitats had enough foraging locations (>2%) for analysis of habitat selection (Table 1), but 'cereals', 'pig fields or manure heaps', rape, arable fallows and 'vegetable or root crops' were rarely used and therefore excluded (Supporting

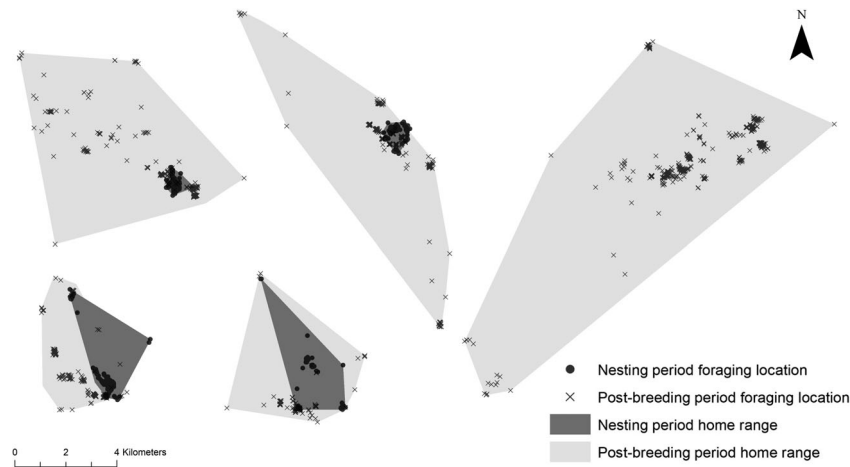


Figure 1 The home range (Minimum Convex Polygon) and individual foraging locations of five adult Eurasian Stone-curlews *Burhinus oedicnemus*, shown separately for the nesting and post-breeding period. Note, one individual (far right panel) was only tracked during the post-breeding period. We excluded foraging locations <50 m from the nest-site (but not the day-roost) to avoid over-representing periods of inactivity. We also excluded nesting and post-breeding foraging locations that were: (1) within habitats known to be unsuitable for Stone-curlews (Supporting Information, Table S2); (2) frequently misclassified by remote sensing (Supporting Information, Table S1) or (3) used too infrequently to reliably model resource selection (Supporting Information, Table S2).

Information, Table S2). Nocturnally, individuals foraged across a greater range of habitats, but rape and arable fallows were again excluded.

Accounting for central place foraging when sampling habitat availability, nesting Stone-curlews were two to three times more likely to select disturbed-grassland over grassland for both nocturnal (odds ratio = 1.9, 95% CI: 1.2–3.4, Table 2) or diurnal foraging (odds ratio = 3.4, 95% CI: 1.3–8.9). Nocturnally and diurnally, ‘sugar beet or maize’ was also preferred relative to unmodified grassland and was selected with similar preference to disturbed-grassland. Nocturnally, Stone-curlews were ten times more likely to select ‘pig fields or manure heaps’ over grassland (odds ratio = 10.0, 95% CI: 3.9–27.4), which they also selected over every remaining habitat except ‘sugar beet or maize’. Neither ‘cereals’ nor ‘vegetable or root crops’ were selected relative to grassland, either diurnally or nocturnally. Model validation (*k*-fold cross-validation) showed the predictive performance of the nocturnal model was good (Supporting Information, Figure S5). For the diurnal model, there was no positive correlation between the area-adjusted scores and odds ratio bins for two of the five trained sets, attributable to the low number of habitat categories considered by this model (Table 1); nevertheless, because every set gave similar inference, we consider the overall model robust.

Post-breeding period foraging-site selection

Post-breeding, 90% of foraging locations were within 5 km of the day-roost (the furthest was 13 km, Fig. 2). Birds travelled further to forage than they did at night during nesting (nocturnal foraging post-breeding, median distance

travelled = 1267 m, IQR 351–2662 m; Mann–Whitney, $P < 0.001$). Seven habitats contained enough nocturnal foraging locations for inclusion in analysis of habitat selection (Table 1); but rape was rarely used and therefore excluded (Supporting Information, Table S2).

Accounting for central place foraging, post-breeding Stone-curlews were *c.* 15 times more likely to select either disturbed-grassland (odds ratio = 14.3, 95% CI: 7.5–26.8) or arable fallows (odds ratio = 15.8, 95% CI: 7.8–31.5) than undisturbed grassland for foraging (Table 2); both were also preferred relative to every crop. ‘Pig fields or manure heaps’ was also selected relative to undisturbed grassland, to a similar degree as disturbed-grassland and arable fallows, and above two of the three considered crops (‘cereals’ and ‘vegetable or root crops’, but not ‘sugar beet or maize’). ‘Sugar beet or maize’ and ‘vegetable or root crops’ (but not ‘cereals’) were selected over grassland. Model performance was good (Supporting Information, Figure S5).

Subplot selection

Stone-curlews were recorded foraging in four complex-mosaic plots during nesting (all shallow-cultivated, none deep-cultivated). Post-breeding, foraging was recorded in eight (six shallow-cultivated, two deep-cultivated) complex-mosaic plots. Within the shallow-cultivated complex-mosaics, nesting period foraging locations were uniformly distributed across all subplot types (Fisher’s exact $P > 0.47$); however, post-breeding, first-time-cultivated and repeat-cultivated subplots both held more foraging locations than fallows (Table 3). Within deep-cultivated complex-mosaics, first-time-cultivated subplots held more post-breeding foraging locations than fallows or repeat-cultivated subplots.

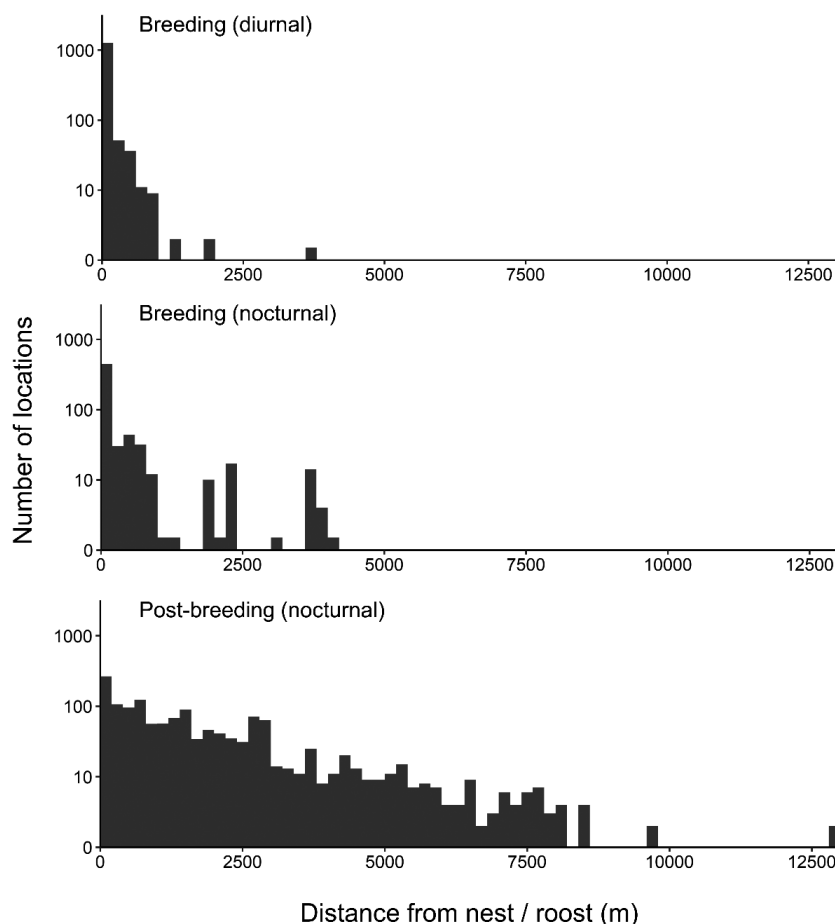


Figure 2 Distribution of nesting period (diurnal and nocturnal) and post-breeding (nocturnal only) locations from tracked Eurasian Stone-curlews, relative to the breeding period nest-site ($n = 4$ adults) or post-breeding day-roost ($n = 5$ adults) respectively. In subsequent analysis, locations <50 m from the nest-site (but not the day-roost) were excluded to avoid over-representing periods of inactivity. We also excluded nesting period and post-breeding locations that were: (1) within habitats known to be unsuitable for Stone-curlews (Supporting Information, Table S2); (2) frequently misclassified by remote sensing (Supporting Information, Table S1); or (3) used too infrequently to reliably model resource selection (Supporting Information, Table S2).

Discussion

Consistent with our *a priori* expectation our study showed that physically disturbing semi-natural grassland to create suitable nesting habitat safe from arable farming operations also provided foraging habitat. Pig fields, manure heaps and sparse spring-sown crops were also selected across the wider landscape. Stone-curlews are known to select open habitats (Green *et al.*, 2000; Caccamo *et al.*, 2011), but this is the first study to demonstrate that creating bare or sparsely vegetated ground through rotational physical ground-disturbance increases foraging opportunities.

The only previous study to track Stone-curlews in the UK found that short semi-natural grassland (<5 cm) provided suitable foraging habitat (Green *et al.*, 2000). However, in this study, conducted in the same region three decades later, other habitats were preferred. Over the intervening period rabbit populations have collapsed, with a concurrent

reduction in very short grassland (<2 cm) (Supporting Information, Appendix S1). We are confident that sward growth, which is known to reduce nest habitat quality (Green & Griffiths, 1994; Bealey *et al.*, 1999), also explains why unmodified grassland was rarely used for foraging. While previous attempts to address this problem have focused on livestock or rabbit enhancement, our study demonstrates that ground-disturbance interventions immediately and effectively create foraging habitat.

Although Stone-curlews selected disturbed-grassland over undisturbed-grassland throughout the breeding season, this selection preference was stronger post-breeding; probably because sward and crop growth (see Supporting Information, Figure S6) render grassland and most arable habitats unsuitable later in the season, limiting foraging to habitats that stay bare and short for longer. Arable fallows were used to a similar extent as disturbed-grassland post-breeding, probably because they too were sparsely vegetated later in the season.

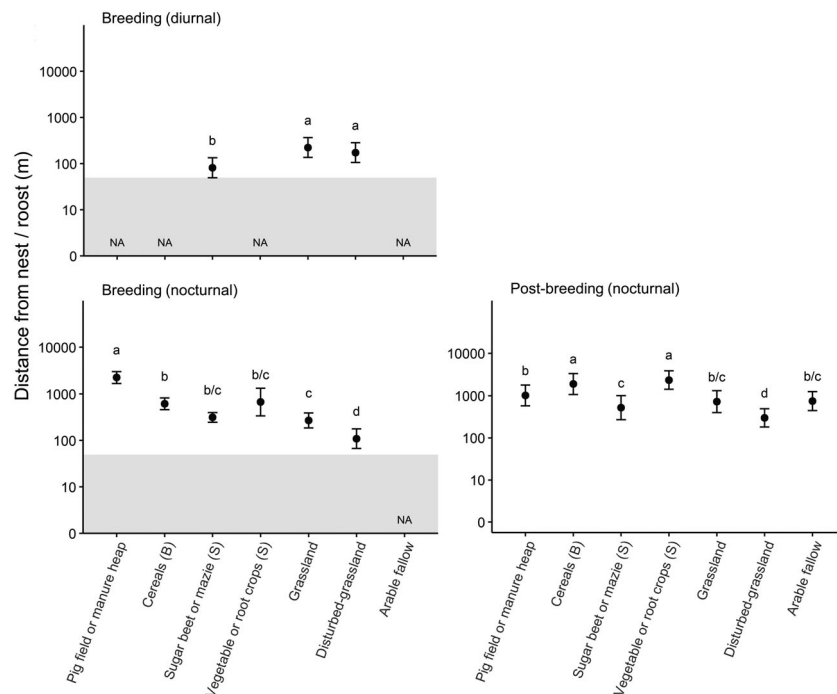


Figure 3 Distance travelled by Eurasian Stone-curlews from their nest-site or day-roost, for diurnal nesting, nocturnal nesting and nocturnal post-breeding foraging locations in different habitats. Shown are estimated means (black circles, bars represent 95% CIs) from linear mixed models including the fixed effect of habitat (see Table 1 for included categories); means that share a superscript do not differ significantly (Tukeys pairwise comparisons $P > 0.05$). NA denotes habitats omitted from analysis as they were used too infrequently to model reliably (Supporting Information, Table S2; note, rape was omitted from every model and therefore excluded from each panel). For crop categories, letters in parentheses denote whether it was autumn-sown (A), spring-sown (S) or both (B). For the nesting period panels, shading represents the first 50 m from the nest where locations were excluded to avoid over-representing periods of inactivity.

Interestingly, an additional supplementary analysis, which assessed the selection of day-roost sites across all five tagged individuals (Supporting Information, Appendix S2), showed that disturbed grassland and arable fallows also provide suitable roosting habitat; corroborating the findings from the foraging models. We suspect that ground disturbance improved foraging and roosting opportunities because it provides better visibility of prey (an important feature for nocturnal waders, Martin, 1990), higher densities of some prey (Hawkes *et al.*, 2019b), camouflage (Green *et al.*, 2000) and predator visibility. Encouragingly we found a strong selection preference for disturbed grassland only 1 year after the treatments were first implemented; selection may increase in future years as more birds recruit to the local population and learn the exact location of these features.

Thus far we have established that physical disturbance of closed-sward grassland improved foraging opportunities, but does cultivation detail matter? Within our experimental complex-mosaics, foraging locations were evenly distributed across shallow-cultivated subplots during nesting. However, consistent with evidence from Spain where recently tilled fields are more likely to be occupied by Stone-curlew than older fallows (Sanz-Pérez *et al.*, 2019), post-breeding Stone-curlews preferred to forage within first-time-cultivated and repeat-cultivated subplots relative to fallows in the shallow-

cultivated mosaics, and within the first-time-cultivated subplots over fallows in the deep-cultivated mosaics. Within the shallow-cultivated mosaics, it is possible that subplot detail became important post-breeding because the fallows supported short vegetation early but not later in the season, in contrast to the consistently short and sparse repeat-cultivated and first-time-cultivated subplots (Supporting Information, Figure S6). Another explanation for a lack of selection during the nesting period could be that the initial structural suitability of repeat-cultivated and first-time-cultivated subplots (Supporting Information, Figure S6) was offset by a reduction in invertebrate prey following cultivation. Pitfall trapping data (R. W. Hawkes, unpubl. data) suggest that by the post-breeding period the abundance of some important invertebrate groups have recovered (e.g. Carabidae and Scarabaeidae), or at least partially recovered (e.g. Araneae and Silphidae), on the repeat- and first-timed-cultivated subplots. However, we lacked data to confirm whether an initial decline occurred post-cultivation.

At night, when most foraging occurs (Green *et al.*, 2000), Stone-curlews did not exclusively feed in disturbed-grassland, 'sugar beet or maize crops' and 'pig fields or manure heaps' were also important. Green *et al.* (2000) did not find a preference for pig fields, and manure heaps were only selected over other habitats later in the season; however, pig fields were

Table 2. Table Eurasian Stone-curlew foraging site (separately for diurnal nesting, nocturnal nesting and nocturnal post-breeding locations) utilization, showing odds ratios ($\pm 95\%$ CI) of each habitat relative to undisturbed grassland (reference category) estimated from Generalized Estimating Equations with a binomial response and habitat entered as a fixed effect (Table 1). Categories for which the lower CI is greater than one (dashed line) are preferred to grassland (* denotes these cases); NA denotes cases that were omitted from that model because they were never or rarely used (Supporting Information, Table S2; note, rape was omitted from every model and therefore excluded from the table). For crop categories, the letters in parenthesis denotes whether it was autumn-sown (A), spring-sown (S), or included both (B). The number of used and random locations within each habitat category are also shown

Landcover	Coefficient odds ratios ($\pm 95\%$ CIs)	No. used locations	No. random location
Nesting period - diurnal			
Grassland (intercept)		76 (26.5%)	544 (47.7%)
Disturbed-grassland	* 3.4 (1.3, 8.9)	102 (36.3%)	180 (15.7%)
Cereals (B)	NA	NA	NA
Pig field or manure heap	NA	NA	NA
Sugar beet or maize (S)	* 1.7 (1.2, 2.3)	109 (40.0%)	424 (36.9%)
Vegetable or root crops (S)	NA	NA	NA
Arable fallows	NA	NA	NA
Nesting period - nocturnal			
Grassland (intercept)		46 (20.4%)	428 (48.0%)
Disturbed-grassland	* 1.9 (1.2, 3.4)	23 (10.2%)	94 (10.5%)
Cereals (B)	0.8 (0.4, 1.7)	12 (5.8%)	129 (14.5%)
Pig field or manure heap	* 10.0 (3.9, 27.4)	49 (21.7%)	32 (3.6%)
Sugar beet or maize (S)	* 3.7 (2.8, 5.0)	87 (38.1%)	172 (19.2%)
Vegetable or root crops (S)	1.2 (0.4, 3.9)	6 (2.7%)	37 (4.1%)
Arable fallows	NA	NA	NA
Post-breeding nocturnal			
Grassland (intercept)		90 (6.6%)	1989 (36.3%)
Disturbed-grassland	* 14.3 (7.5, 26.8)	257 (18.7%)	298 (5.4%)
Cereals (B)	1.2 (0.8, 1.8)	62 (4.5%)	1093 (19.9%)
Pig field or manure heap	* 10.2 (6.9, 15.5)	450 (32.8%)	714 (13.0%)
Sugar beet or maize (S)	* 2.7 (1.0, 7.1)	96 (7.0%)	691 (12.6%)
Vegetable or root crops (S)	* 2.5 (1.1, 5.8)	43 (3.1%)	321 (5.9%)
Arable fallows	* 15.8 (7.8, 31.5)	373 (27.2%)	378 (6.9%)

scarce in the landscape when this initial research occurred, with few opportunities to test their utilization. Research from Southern England (Taylor, 2006) has also shown that manure heap presence does not improve the likelihood of plot occupancy; but again, these features were scarce in the landscape. Manure heaps, which Stone-curlews utilize for foraging by hunting around the base and climbing the sides (R. E. Green pers. obs.), have been documented as an important foraging resource in other Stone-curlew populations (Giannangeli *et al.*, 2004; Caccamo *et al.*, 2011), attributed to the high densities of prey they likely contain; pig fields were probably selected for the same reason. By way of contrast 'pig fields or manure heaps' were seldom visited during the day (Supporting

Information, Table S2) probably because these features were located at least 1 km any of the nests, a distance rarely exceeded during daylight hours (Fig. 2). It is possible that predation risks from flocks of avian predators' forces both parents to defend the clutch during the day, restricting long-range journeys to night when most predators (foxes *Vulpes vulpes*) search for food on their own. Enhanced prey availability and less human disturbance across the farmed landscape at night (Taylor *et al.*, 2007) may also contribute to differences in diurnal and nocturnal selection.

Although pig fields clearly provided foraging opportunities, they are considered to have a detrimental impact on semi-natural habitats through local atmospheric deposition of

Table 3. Eurasian Stone-curlew utilization of cultivated (but uncropped) subplots (FC, first-time-cultivated; RC, repeat-cultivated; FL, fallow), showing number of foraging locations during nesting and post-breeding, separately for shallow-cultivated and deep-cultivated complexes. Separately for complex type and nesting/post-breeding, subplot categories that share a superscript do not differ significantly (pairwise Fisher's exact, $P < 0.05$, after Bonferroni correction). NA denotes cases where no locations were recorded

	Shallow-cultivated complex mosaics			Deep-cultivated complex mosaics		
	FC	RC	FL	FC	RC	FL
Nesting period foraging locations	22 ^a	15 ^a	12 ^a	NA	NA	NA
Post-breeding foraging locations	48 ^a	21 ^a	0 ^b	41 ^a	1 ^b	0 ^b

ammonia (Chesterton, 2009). Experimental work has shown that the addition of nutrients results in the loss of characteristic lichens, annuals, reduced diversity and dominance of perennial grasses in Breckland grass-heath (Davy & Bishop, 1984), chalk grassland (Bobbink, 1991) and dunes (Boorman & Fuller, 1982). Eutrophication of nutrient-poor ecosystems occurs close to poultry and other intensive animal units (Berendse, Laurijsen & Okkerman, 1988; Pitcairn *et al.*, 1998). Given nutrient deposition poses a significant threat to this habitat, we do not advocate the establishment of new pig units close to grassland; instead, positioning disturbed-ground close to the edge of large grassland blocks would maximize opportunities for breeding Stone-curlews to access this feature. It remains unclear whether manure heaps also pose a similar threat, but this would need to be established before they are advocated as a possible conservation tool.

Consistent with Green *et al.* (2000), our results also show that 'sugar beet or maize', both of which were characteristically bare and open early in the season, were selected during nesting; whereas 'cereals' and rape, which comprised a denser and generally taller crop, were avoided. Post-breeding the 'vegetable or root crops' category was selected over grassland for foraging; however, this is attributable to a single part-fallowed field which contained 22/43 post-breeding foraging locations within this category. Although we did not measure invertebrate prey within farmland habitats, previous work has shown that abundance varies across taxa according to crop type (e.g. Myriapoda are more abundant in sugar beet, whereas Araneae are more abundant in spring-sown cereal; Green *et al.*, 2000). However, while we suspect that prey availability was the main reason why Stone-curlew utilized manure heaps and pig fields, we agree with Green *et al.* (2000) that crop selection is probably influenced predominantly by vegetation structure.

Conclusions

Although our study only considered a limited number of tracked individuals, the precise tracking data, combined with

our experimental manipulations, provide a highly informative assessment of intervention efficacy for this nocturnal and difficult to study species. We conclude that interventions which open-up closed swards create suitable foraging habitat, which all individuals strongly selected relative to its availability. Since recently cultivated ground was selected over fallows during the post-breeding period, annual ground disturbance is probably necessary to maintain suitable habitat throughout the season. Shallow-cultivation may offer a better long-term solution, as the repeat-cultivated subplots in the deep-cultivated mosaics were rarely used.

Consistent with the only other assessments of Stone-curlew movement behaviour during the breeding season (Green *et al.*, 2000; Caccamo *et al.*, 2011), most foraging activity was centered on the nest-site or day-roost. However, in our study, individuals travelled up to 4.1 km (during nesting) and 13 km (post-breeding), further than previously reported. It is possible that the two earlier studies, which used VHF radio tags and manual tracking, overlooked infrequent distant foraging trips. Given central place foraging, conservation strategies aiming to improve nesting habitat through ground-disturbance should ensure sufficient foraging habitat is near to plots (during nesting, 90% of foraging locations were within 1 km of the nest). Targeting interventions close to favoured farmland habitats is not viable, because these rotate around the landscape. Instead, creating extensive areas of disturbed ground within permanent semi-natural grassland adjacent to farmland will create suitable foraging habitat, while allowing access to these other habitats; this could be achieved by creating new plots, or by redistributing existing plots. To help facilitate the widespread adoption of this recommendation, which we believe is applicable to other UK and European Stone-curlew populations, agri-environment schemes should incorporate a bespoke grassland ground-disturbance option.

Previous studies, conducted as an integral part of the same experiment, have demonstrated that disturbed-grassland also benefits Woodlark *Lullula arborea* (Hawkes *et al.*, 2019a), Eurasian Curlew *Numenius arquata* (Zielonka *et al.*, 2019) and priority (rare, scarce or threatened) dry-grassland invertebrates (Hawkes *et al.*, 2019b, 2021). Similar interventions may benefit other disturbance associated grassland waders, such as North American breeding populations of Mountain Plovers *Charadrius montanus* (Augustine & Skagen, 2014) and Upland Sandpipers *Bartramia longicauda* (Sandercock *et al.*, 2015), or Sociable Lapwings *Vanellus gregarius* in Central Asia (Kamp *et al.*, 2009). All three of these waders have suffered medium- or long-term population declines that are at least in part attributable to habitat loss on their breeding grounds (Vickery, Hunter & Melvin, 1994; Augustine *et al.*, 2008; Kamp *et al.*, 2009); though other threats, including pressures on wintering and stopover sites, are also important (Donald *et al.*, 2021).

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Authors' contributions

RH, JS, AB, RG and PD conceived the ideas and designed methodology; RH, JS, RG and HJ collected the data; RH conducted all analyses and wrote the manuscript. All authors contributed to the drafts.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting information

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

Figure S1. UK Stone-curlew population.

Figure S2. Study area.

Figure S3. Sampling habitat availability.

Figure S4. Daily number of foraging locations throughout the tracking period.

Figure S5. Cross-validating foraging- and roost-site selection models.

Figure S6. Grassland and complex-mosaic plot vegetation.

Table S1. Validating crop classification accuracy.

Table S2. Number of foraging and roost locations per habitat.

Appendix S1. Study area, climate and method details.

Appendix S2. Day-roost site selection.