Placement, survival and predator identity of Eurasian Curlew *Numenius arquata* nests on lowland grass-heath.

Natalia B. Zielonka[1]
Robert W. Hawkes[2]
Helen Jones[3]
Robert J. Burnside[2]
Paul M. Dolman[2]

[1] School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK
[2] School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK
[3] RSPB Centre for Conservation Science, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK

Short title

Eurasian Curlew breeding ecology

Keywords

Nest predation, nest survival, Red Fox, *Vulpes vulpes*, wader, ground-disturbance management

Correspondence author: Natalia Zielonka (n.zielonka@uea.ac.uk)

Summary

Capsule

Within the UKs largest lowland Eurasian Curlew *Numenius arquata* population, Curlew preferentially nested on physically-disturbed (treated) than undisturbed (control) grassland, and low nest survival rates were primarily attributable to Red Fox *Vulpes vulpes.*

Aims

To inform conservation interventions for Curlew within semi-natural lowland dry-grassland landscapes.

Methods

Across a 3,700 ha lowland dry-grassland landscape, over two years, effects of ground-disturbance management on Curlew nest placement (n=41) were examined using GLMs controlling for vegetation strata; effects of site and management on nest survival (n=44) were examined controlling for lay date and year. Nest predator identity was investigated using temperature sensors (n=28) and nest cameras (n=10).

Results

Curlews were five times more likely to nest on physically-disturbed than undisturbed grassland. Nest survival (overall mean 0.24 ± 0.07, SE) was not influenced by year or ground-disturbance but declined with lay date and differed markedly between the two sites, consistent with predator control. Predation accounted for 29/32 of failed nests and was predominantly at night (17/23 cases where timing was known, $p<0.001$), consistent with mammalian predators. Cameras indicated Foxes to be the main predator (4/5 cases). Overall breeding productivity was 0.16 ± 0.01 (SE) chicks per nesting attempt.

Conclusion

Curlew suffered from unsustainably high rates of nest predation primarily attributable to Foxes. A combination of perimeter fencing and lethal predator control appeared to improve nest success at one site. Ground-disturbance treatment could encourage nesting attempts in areas managed to minimise predator density.

Introduction

Global wader (shorebird) populations are declining (Butchart *et al.*, 2010), primarily due to habitat loss and degradation through agricultural intensification and climate change (Pearce-Higgins *et al.*, 2017, Franks *et al.*, 2017). Almost half of European wader populations for which trends are known are either IUCN Threatened or declining (Stroud *et al.,* 2006) and in the UK, 16 of 20 breeding wader species are classified nationally as IUCN Threatened (Stanbury *et al.,* 2017). One such species is the Eurasian Curlew *Numenius arquata* (hereafter ‘Curlew’), which has been recently classified nationally as Threatened. As a result of the species’ global conservation status (IUCN Near Threatened; BirdLife International 2017), the international significance of the UK breeding population (~68,000 breeding pairs, accounting for over a quarter of the global breeding population; Musgrove *et al.* 2013, Hayhow *et al.*, 2017), and its long-term decline (65% between 1970-2015; Hayhow *et al.*, 2017), Curlew are considered to be the UK’s highest bird conservation priority (Brown *et al.*, 2015). Although the number of Curlew in the UK uplands (including moorland: upland heath, bog and unenclosed grassland; and enclosed upland grassland) is not known with precision, these hold the majority of the population, where considerable research has focused on their breeding ecology and conservation (Douglas *et al.,* 2017; Johnstone *et al.,* 2017). Although lowland Curlew are less studied, their loss would reduce the species’ breeding range, increasing the dependence on vulnerable upland populations (Baldock *et al.*, 2017).

The main driver of UK Curlew decline is low breeding productivity, attributable to predation and reduced quality of breeding habitats (Franks *et al.*, 2017; Hayhow *et al.*, 2017). Research from the uplands has informed habitat provision (e.g. controlled cutting of moorland to provide a mosaic of vegetation heights and creation of pools, Fisher & Walker 2015) and demonstrated that legal predator control (of Red Fox *Vulpes vulpes,* hereafter 'Fox', Carrion Crow *Corvus corone*, hereafter 'Crow', Stoat *Mustela erminea* and Weasel *M. nivalis*) can increase Curlew breeding success and abundance (Fletcher *et al.*, 2010; Ludwig *et al.*, 2019); however, lethal control does not work in all cases (e.g. Bodey *et al.,* 2011, Bolton *et al.* 2007b). In lowland regions of the UK, recent monitoring (Smart, 2017; Curlew Call, 2017) has confirmed low breeding productivity with a mean across studies (weighted by square-root of sample sizes) of 0.23 ± 0.13 SD fledged chicks nesting attempt^{-1} year^{-1} (Table S1), considerably less than the 0.48 - 0.62 pair^{-1} year^{-1} required for population stability (Grant *et al.*, 1999). Previous research into the predator assemblage and efficacy of anti-predator solutions (e.g. lethal control and anti-predator fencing, Bolton *et al.,* 2007b; Malpas *et al.,* 2013) in lowland habitats, which has focused on other wader species, particularly Northern Lapwing *Vanellus vanellus* (hereafter 'Lapwing')*,* Common Redshank *Tringa totanus* and Common Snipe *Gallinago gallinago*, has demonstrated that nocturnal mammalian predators are the main cause of nest failure (MacDonald & Bolton 2008, Teunissen *et al.,* 2008). However, these findings may not be applicable to lowland Curlew due to differences in nest exposure (Curlew nests are less concealed compared to Common Redshank or Snipe), adult size, social aggregation and habitat preferences (Bolton *et al.,* 2007b). This, along with the vulnerability of Curlew breeding populations, emphasises the need for a study into nest predation (Leyrer *et al.,* 2018).

Most lowland Curlew breed on dry grasslands and heathland (Table S1, Johnstone *et al.,* 2017) where conservation management can radically alter habitat structure. Within these habitats, physical ground-disturbance is increasingly advocated as a land management intervention for other rare, scarce and threatened species, such as Stone-Curlew *Burhinus oedicnemus* and Woodlark *Lullula arborea* (Fuller *et al.*, 2017; Hawkes *et al.*, 2019b); however, it is not known whether this influences Curlew nest placement or breeding success. Understanding whether Curlew nests on disturbed grassland are easily visible to corvid nest predators, or conversely, whether placement of disturbed-plots can be used to manipulate nest placement into areas protected from mammalian predators, would better inform such management on sites with breeding Curlew.

To inform conservation interventions for Curlew, we studied nest placement, nest survival and nest-predator identity within the UK's largest lowland Curlew population (Breckland, Eastern England, Balmer *et al.,* 2013; holding at least 100 breeding pairs but likely more, H. Ewing pers. comm.), across two extensive grass-heath sites (total c. 3,700 ha) that differed in predator density and management. Across both sites, vegetation structure was diversified prior to this study with ground-disturbance plots as part of a wider multi-taxa experiment (see Hawkes *et al.*, 2019a,b), which may influence Curlew nest site selection and productivity. We *a priori* predicted that: (1) Curlew would select undisturbed grassland over disturbed grassland as nesting habitat (given that Curlew prefer rougher habitats with longer swards for nesting: Baines 1988; Ewing *et al.,* 2018), (2) nest survival would be higher on the site with lower predator density and decrease through the season (informed by Franks *et al.* 2017 and MacDonald & Bolton 2008), and (3) predation events would be attributable to nocturnal mammalian predators (as with other lowland wader species, MacDonald & Bolton 2008).

Materials and methods

Study site

The study was carried out in 2017 and 2018 in Breckland across the Stanford Military Training Area (hereafter 'STANTA', 52.50°N, 0.71°E) and Brettenham Heath NNR (0°83'E, 52°43'N). Both sites contain extensive areas of dry grassland and grass-heath (hereafter 'grassland', STANTA 3,500 ha; Brettenham Heath, 200 ha) surrounded by arable farmland and woodland (Fig. 1). Generalist predator control on STANTA was focussed around pheasant release pens (approximately 130 Foxes were removed annually; 0.03 ha^{-1} $year^{-1}$) but was lacking across remaining parts of STANTA and most of the surrounding arable and woodland. In contrast, Brettenham Heath was subject to continuous predator control across the whole site (10-20 Foxes were removed annually; 0.05-0.1 ha^{-1} $year^{-1}$) with similar levels of intensive control across the surrounding arable farmland (but not woodland). Brettenham Heath is also enclosed by a two-meter high deer fence with a single electric strand set half meter above the ground. Although we lacked the time and resource to compare generalist predator densities between the two sites, we saw at least one Fox during each of seven of the 75 fieldwork days on STANTA, compared to none during 23 fieldwork days on Brettenham Heath (though this ratio did not differ significantly, Fisher Exact test, $p=0.194$). Both sites are sheep-grazed (approximately one ewe ha^{-1}) with regular scrub and bracken *Pteridium aquilinum* control (see Appendix S1 for additional site management details). STANTA is subject to regular vehicle and soldier movements.

We used the Centre for Ecology and Hydrology Land Cover Map 2015 (LCM2015, Rowland *et al.,* 2017) to identify areas of grassland and dwarf shrub heath across both study sites (hereafter collectively 'grassland', Fig. 1). Grassland was then categorised based on underlying soil type (NSRI, 2014) and age since last cultivation

(Sheail, 1979) to give two vegetation strata which differed in structure and vascular plant composition; ‘calcareous/young’ and ‘older acidic’ grassland. Calcareous/young grassland was characterised by shorter swards (4.15 cm, 3.77 - 4.58 95% CI; Hawkes *et al.,* 2019b), comprising a mixture of calcicolous and acidiphilous plant species developed on rendzina or following arable abandonment (73-113 years ago), whilst older acidic grassland (at least 114 years since arable cultivation) was characterised by taller swards (5.14 cm, 4.66 - 5.67 95% CI) mainly comprising acidiphilous plant species (see Appendix S1 for details).

Across both sites, 64 experimental ground-disturbance plots (32 deep-cultivated and 32 shallow-cultivated; see Hawkes *et al*., 2019a for details) were established in early 2015 and subsequently disturbed annually to create: (i) 25 2 ha ‘homogenous’ plots (13 deep- and 12 shallow-cultivated, repeated annually in the same location), and (ii) 39 4 ha ‘complex-mosaic’ plots (19 deep- and 20 shallow-cultivated) cultivating half-overlapping and half freshly-disturbed sections building up a mosaic of 1 ha subplots varying in fallow age and disturbance frequency. Potential for unexploded ordnance excluded ground-disturbance plots in the central ‘impact area’ of STANTA (1,180 ha), restricting treatment plots to Brettenham Heath and outer areas of STANTA (Fig. 1). In analyses, ground-disturbance treatments were combined as a single ‘disturbed grassland’ category, with aggregate area of 206 ha in both years of study, comprising ~5.6% of the available grassland extent (~8.2% of available grassland outside the impact area). We did not attempt to model relative preference for deep- or shallow-cultivation, homogenous or complex-mosaic owing to limited statistical power and also as different treatments were not available in each Curlew home range.

Tests of wader nest placement and nest survival frequently consider landscape context (Bertholdt *et al.*, 2017; Laidlaw *et al.,* 2015), however this is problematic in this study. Although woodland may harbour mammalian predators, Foxes also den in rabbit warrens, bracken, scrub and hedgerows, so that distance to woodland is not a reliable proxy for their activity. Woodland may offer perches but Crows also perched on individual trees that were scattered throughout the entire landscape. Arable farmland may also be a source of predators (Roos *et al.,* 2019) and cause disturbances that affect the distribution of nests. However, exploratory modelling showed no effects on nest placement or survival of either distance to woodland or arable farmland; these variables were therefore omitted from subsequent analysis to avoid over-fit models.

Nest searching and monitoring

Our approach to locating Curlew territories differed between 2017 and 2018. In 2017, territory-searches focused initially on the 64 ground-disturbance plots, plus 38 4 ha untreated grassland control plots (Hawkes *et al.,* 2019a; see Fig. 1), with at least three 40-minute visits to each plot between 14 March and 26 June (days between visits: mean 27 ± 7 SD) during still, dry mornings (Beaufort wind force <4) between dawn and 11:00. Additional opportunistic searches were made in 2017 on any grassland areas where Curlew were detected. We are confident that detectability of territories was comprehensive on both Brettenham Heath and outer areas of STANTA. As unexploded ordinance precluded ground-disturbance treatments from the STANTA ‘impact area’ (Fig. 1) and furthermore, in 2017 searches in this area were largely restricted to 20 control plots and were not comprehensive; impact area nests were excluded from analyses of nest placement relative to random points (see below). In contrast, in 2018 we conducted systematic searches for Curlew territories across the entire grassland extent (including the impact area), conducted by one observer walking linear transects spaced 250 m apart (following Brown and Shepherd, 1993) repeated three times between 1 April and 8 June (days between visits: 18 ± 6 SD), between dawn and dusk. In both years, the location and behaviour of any detected Curlew was recorded.

In both years, nests were located between mid-April and late June, visiting any area where Curlew had been seen and looking for adults sitting on, or walking back to, the nest. To determine the date and timing of nest failure, temperature sensors were placed under nests (iButtons thermocrons, Maxim Integrated Products Ltd, CA, USA; set to record the temperature every 10 minutes, following Berg, 1992). Nests were remotely checked every three-to-seven days to confirm adults were still incubating, and the scrape was visited once a week to record any predation events (e.g. partial clutch predation). To avoid leaving tracks that could lead predators to nests, observers adopted a different meandering path during subsequent nest visits. It is also important to note that, particularly at STANTA, our activity was superimposed on ubiquitous tracks and scent trails from frequent ground troop and shepherd movements, further reducing the likelihood that Foxes would follow our tracks. From three days before the predicted hatch date (calculated from egg measurements at STANTA only in 2018, following Grant, 1996) nests were remotely monitored daily to accurately determine their fate.

Nest outcome was inferred from visits and temperature sensor data. Successfully hatched nests were characterised by the presence of small shell fragments within the nest cup and the presence of chicks or alarming adults in the area. Nest failure was assumed if nests were found empty before the predicted hatching date and if no adult birds or chicks were seen around the nest site. Failure was attributed to predation if the nest contained shell remains or no eggs (larger predators, particularly Foxes, remove intact eggs, Guilherme *et al.,* 2018) and a sharp permanent decline in temperature (when temperature sensor data were available). Destroyed nests were identified by obvious signs of sheep trampling or freshly cut grass. When temperature sensor data were not available, due to the sensor being removed from the nest (5/28 cases), failure date was calculated as the mid-point between the final two visits (Johnson, 1979). After hatching, the nest site was visited every three-to-five days to observe adults and chicks from a vehicle at a distance, continuing until the chicks fledged (determined by observing chicks flying or their survival to 35 days post-hatching), or the breeding attempt had failed.

Laying date of the first egg (hereafter 'lay date') was estimated in one of three ways. For successful nests with known hatch date, or when expected hatch date of a failed nest was available from egg measurement, lay date was back-estimated allowing for a 29-day incubation (Berg, 1992) and n x 1.5-day laying period (where n = number of eggs in the clutch). When the nest was found during-laying (with clutch size incrementing by the second nest visit), lay date was estimated allowing 1.5 days per egg present at the find date. In remaining cases (n = 16, 33%), when the nest was found after incubation commenced, eggs were not measured and the clutch failed prior to hatching, the lay date was estimated as the mid-point of the earliest and latest possible lay dates, based on find and failure dates (following Mallord *et al.*, 2007; Koshkin *et al.,* 2016).

Where available, temperature sensor data informed classification of diurnal (after sunrise, before sunset), crepuscular (between dawn and sunrise, and between sunset and dusk) and nocturnal (between dusk and dawn) predation events, with nocturnal and crepuscular events attributable to mammalian predators (most likely Fox or Badger *Meles meles*, but potentially also European Hedgehog *Erinaceus europaeus*, as found by Jackson 2001) and diurnal events unattributable (MacDonald & Bolton, 2008). To further validate predator identity, in 2018 infra-red nest cameras were placed at 10 nests on STANTA (as 2017 monitoring indicated a higher incidence of nest predation at STANTA than at Brettenham Heath) following Bolton *et al.* (2007a). The camera (~3.6mm lens, ~30x20x20mm camera head including the hood and infrared array) was placed about a meter from the nest and c. 15 cm above the ground within vegetation (to help concealment), with the battery (between 180x76x167mm and 269x174x225mm) and recording unit buried seven-to-ten meters away to reduce disturbance, trampling or scent in the vicinity of the nest (that could potentially attract a predator) whilst changing batteries. Cameras triggered by movement were set to save five consecutive images within two seconds, with one image before triggering (the device continuously records and temporarily stores frames, but only saves these frames if triggered), and four after, with a five-second pause before it could be triggered again.

Data analysis

To examine nest placement in relation to ground-disturbance treatments and vegetation strata, we compared characteristics of nest locations to those of random points sampled in ArcGIS 10.3 (ESRI, 2014; ‘used-available’ design), using Generalised Linear Models (GLMs) with binomial error and log-link, conducted in R (R Core Team 2017). We excluded nests within the STANTA central ‘impact area’, thereby restricting analyses to areas with both disturbed and undisturbed grassland available (Fig. 1), and that were comprehensively surveyed in both years. Analyses were conducted separately at the ‘study-area’ scale, considering the entire grassland area, and the ‘home-range’ scale, considering grassland with a 164 m radius of each nest site (the distance within which >85% of breeding adults or broods were observed foraging; threshold follows Odum & Kuenzler 1955, see Appendix S2). At both scales, we sampled three times as many random points as nests. At the study-area scale, the placement of control points was restricted to outside the STANTA impact area, and GLMs examined fixed effects of treatment (two levels: disturbed vs. undisturbed grassland) and vegetation strata (two levels: calcareous/young grassland vs older acidic grassland). We did not examine the effects of site on nest placement as the two study sites both contained experimental ground-disturbance plots and were comparable in terms of vegetation structure (Hawkes *et al.,* 2019b). For the home-range scale, we sampled three random points within a 164 m radius (of each nest) and GLMs examined fixed effects of treatment (two levels) but not vegetation strata, as most (38/41) home ranges contained only a single stratum.

To examine factors influencing daily nest survival, GLMs were performed with the number of binomial trials of each nest determined by the number of ‘nest days’ it was active and monitored, incorporating fixed effects of year (two levels), treatment (two levels), vegetation strata (two levels), site (two levels, reflecting differing predator control effort across sites) and lay date (following Dinsmore *et al.,* 2002), using the RMark 2.2.5 package (Dinsmore & Dinsmore, 2007). Analysis considered all monitored nests as independent observations, as: (i) lack of treatment plots within the impact area affects settlement options but does not bias failure relative to nest-site characteristics; (ii) failure was assumed to be largely caused by stochastic factors independent of parental quality, and (iii) within each year most nests were from different pairs (90% in 2017; 92% in 2018) with few re-nesting attempts. The mean probability of nest success (hatching at least one egg) per nesting attempt was calculated from the product of daily clutch survival rates across the 29-day incubation period. Breeding productivity was quantified as the number of fledglings per nesting attempt, including any re-nesting attempt, as independent observations; it was not possible to estimate productivity per pair per year as adults were unmarked and we could not reliably allocate re-nests to individual pairs. For analysis of nest placement and nest survival, candidate model sets comprising all possible variable combinations were examined using the 'lme4' package. The model with the lowest value of Akaike Information Criterion adjusted for small sample size (AICc) was accepted as 'best' if the difference (ΔAICc) relative to all other candidate models was >2. When multiple models were within two AICc units of the 'best' model, multimodal inference was conducted to estimate model-averaged coefficients across these competing models (following Burnham & Anderson, 2002), using the MuMIn package (Barton, 2019). Candidate variables were considered to be supported where their 95% CI did not span zero (following Burnham & Anderson, 2002; Boughey *et al.,* 2011). Where the fixed effect of treatment was supported in nest placement models, we quantified the probability of selection of disturbed grassland relative to undisturbed grassland (model intercept) using odds ratios derived from the model coefficients. For each analysis, spatial autocorrelation of residuals (from the best or averaged model, as appropriate) was examined, calculating Moran's I in the 'Ape' package (Paradis *et al.*, 2004).

For nests where the timing of nest predation failure was known (through temperature logger or nest camera data) we examined whether predation events were more likely during the night (nocturnal and crepuscular) or day, relating the ratio of observed night/day predation events to the numbers of night/day hours summed across all monitored nest-days (as day length varies through the season), using a 2x2 Fisher Exact test.

Finally, considering all predated nests for which the date and time of failure were known, we used a Fishers Exact test to determine whether nest predation was more likely during the 24 hours following a direct monitoring visit (2x2 Fishers Exact: the number of predation events in relation to the number of nights within 24 hours of a disturbance event, against the numbers of predation events in relation to the number of other nights monitored).

Results

Nest placement

Across the two years of study 46 Curlew nests were located (2017, 20 including two re-nests; 2018, 26 including two re-nests). Of these, 41 were outside the impact area (2017, 17 nests; 2018, 24 nests), with 20 (49%) on disturbed grassland (17 on shallow-cultivated and three on deep-cultivated treatments) and 21 (51%) on undisturbed grassland.

For models of nest placement, at the study-area scale multi-model inference was undertaken across two candidate models within <2 AICc units (Table S2) and at the home-range scale the best-supported model was >2 AICc relative to all other models. At both spatial scales, Curlew were five- to six-times more likely to select disturbed than undisturbed grassland as nesting habitat (Fig. 2; study-area scale, odds ratio = 5.16, 95% CI: 2.0 – 13.3; home-range scale, odds ratio = 6.3, 95% CI: 2.8 – 14.6). No effect of vegetation strata was found in the study-area scale averaged model (vegetation strata was not considered in the home-range scale analysis). Modelled residuals from nest placement analyses were not spatially autocorrelated.

Nest survival

Excluding two nests with zero observation days (found at or after failure or hatching), 44 nests were monitored (for 557 nest-days) of which 32 failed (Brettenham Heath: 3 of 11, STANTA 29 of 33), with 29 predated (Brettenham Heath: 3, STANTA: 26), one trampled by livestock (STANTA), one destroyed by grass cutting (STANTA) and one deserted (a single-egg re-nest late in the season at STANTA). Mean overall nest survival probability from start of incubation to hatching was 0.24 ± 0.07 SE

(Brettenham Heath: 0.70 ± 0.18 SE, STANTA: 0.16 ± 0.06). Overall breeding productivity was 0.16 ± 0.01 SE fledged chicks per nesting attempt.

For analysis of daily nest survival rate, multi-model inference was undertaken across four candidate models within <2 AICc units (Table S2). The effects of lay date and site were supported; daily nest survival rate decreased through the nesting season and was greater at Brettenham Heath than at STANTA (Fig. 2, Fig. 3). No support was found for effects of treatment, vegetation strata or year (Fig. 2). Residuals of the averaged-model were not spatially autocorrelated.

Timing of nest failure and predator identity

Of the ten 2018 nests with nest cameras: three survived to hatching; four were predated by Fox (one diurnal and three nocturnal; Fig. 4, Digital material 1); one was predated by an unknown predator (following camera malfunction); one was predated by a Sheep *Ovis aries* (two out of four eggs remained but incubation was not resumed and the clutch was classified as failed; Digital material 2) and a single-egg late-season re-nesting attempt was abandoned three days after camera deployment (with failure therefore not directly attributable to the installation). For all four confirmed fox-predation events, the scrapes were undisturbed, and no shell fragments remained. In one predated nest without a camera, large shell fragments were found with teeth marks, which suggested a further predation event attributable to a Fox (following Green *et al.,* 1987). Cameras also recorded an unsuccessful predation attempt by a Crow, fended off by the incubating Curlew (Digital material 3), and two instances of Crows scavenging abandoned clutches; one 29 hours after the partial-predation by a sheep (that had already resulted in complete clutch failure), the second five hours after the late-season desertion of a re-nesting attempt. There was no effect of nest cameras on daily nest survival rate (see Appendix S3).

The timing of failure was known for 23 predated nests (28/29 predated nests were fitted with temperature loggers but five were removed from the nest by the bird) of which 17 events were during the night (13 nocturnal, four crepuscular) and six during the day (Fig. 4). Relative to the ratio of night/day hours monitored (pooled across each nest-day monitored, ratio 0.50) predation more often occurred at night (night/day ratio, 2.83) than expected by chance (Fisher Exact test, $p<0.001$). Nest predation did not occur more frequently during the 24 hours following a disturbance event caused by monitoring (three predation events <24 hours after a disturbance event, $n=52$, 20 predation events >24 hours after disturbance, $n=164$; Fisher Exact test, $p=0.303$).

Discussion

Through a two-year study on one of the UK's largest remaining semi-natural grassland sites, we have demonstrated that breeding Curlew selectively placed nests on physically-disturbed grassland (deep-cultivated by ploughing, or shallow-cultivated by rotovation) over undisturbed grassland. Overall breeding productivity was low due to high rates of nest predation, primarily attributed to Foxes. While nest survival was not influenced by ground-disturbance treatment, it decreased with lay date and was substantially lower at STANTA than at Brettenham Heath; probably due to differences in Fox activity between these two sites (though this was not directly measured). As far as we are aware, this is the first study to simultaneously investigate Curlew nest placement, survival and predator identity within a lowland system.

Nest placement

Contrary to our predictions, Curlew were five- to six-times more likely to select nest-sites on physically-disturbed than undisturbed grassland, with 48.7% of nests located on disturbed grassland across both years, which only occupied ~8.2% of the grassland area. Curlew are long-lived and site-faithful (Currie *et al.*, 2001); as ground-disturbance was first applied two years prior to this study, treated plots may have been created within already-established breeding territories, rather than influencing territory settlement. However, analysis of nest placement relative to random locations within home-ranges showed nests were more frequently placed on disturbed than undisturbed grassland relative to availability.

Disturbed grassland is characteristically bare and short compared to uncultivated grassland (Dolman & Sutherland, 1994; Hawkes *et al.,* 2019b). Curlew may have placed nests on this habitat because it allows greater vigilance (to facilitate and evade predator detection, Amat & Masero, 2004) and a greater abundance of some important prey (confirmed experimentally by Hawkes *et al.,* 2019b) than the surrounding grassland. Although we did not examine whether ground-disturbance detail matters (to avoid overparameterizing the models), most nests were on shallow-cultivated plots (n = 17, 41.5%), with few on deep-cultivated plots (n = 3, 7.3%). It is possible that the likelihood of attracting nest placement is greater on shallow-cultivated grassland, though further work is needed to establish this.

Nest survival

Nest survival was low and re-nesting following failure appeared infrequent. Annual productivity was lower than found in other lowland UK Curlew populations (Call of the Curlew 2017, Table S1), and is likely to be substantially below that required to maintain a stable population. Consistent with other passerine and non-passerine species (Gunnarsson *et al.,* 2006), daily nest survival rate decreased during the breeding season (by 39% from start to end). For Lapwing and Common Redshank, this is related to predator phenology, particularly as Foxes become more active once their cubs require more prey (Kentie *et al*., 2015; Mason *et al*., 2017). Seasonal declines in nest survival may also be attributable to decreasing visibility of predators as vegetation grows taller (Whittingham & Evans, 2004; MacDonald & Bolton, 2008). Importantly, nest survival was not influenced by ground-disturbance, which suggests that this management intervention (which positively influenced nest placement) did not increase nest exposure to predators.

Predator identity

Predation accounted for most nest failures in this study, similar to predation rates reported in other Curlew (Grant *et al.,* 1999) and wader populations (MacDonald & Bolton, 2008). Timing of nest predation was disproportionately higher during the night (nocturnal or crepuscular), consistent with mammalian rather than avian predators. Although predator identity was confirmed by camera for only five nest predation events, Foxes where responsible for all three nocturnal and one of two diurnal events, with the other confirmed diurnal nest predator a Sheep. In all cases but one, where predator identity was not certain, scrapes were undisturbed and had no shell remains, consistent with confirmed Fox predation events in this and other studies (e.g. Koshkin *et al*., 2016). We found no evidence of activity by other predators; for example, nests predated by Badgers are usually characterised by trampled vegetation and disturbed nest scrapes (Draycott *et al.*, 2008). It is notable that, although Crows were not scared off by cameras and were recorded at nests, they were not found to be predators of Curlew nests and in one instance the sitting adult successfully defended the clutch against a Crow (see Digital material 3); this is unlike other smaller wader species where Crows are frequent nest predators (Teunissen *et al.*, 2008; Ausden *et al.*, 2009). The combined evidence of cameras and timing of predation therefore implicated Fox as the primary nest predator of Curlew in this landscape, consistent with studies that have identified Fox as the major predator of lowland nests of other wader species in the UK (Teunissen *et al.*, 2008; Ausden *et al.*, 2009).

Monitoring protocols were designed to minimise disturbance to the nest site, but in any nest monitoring study there remains a concern as to whether the study has itself affected the fate of nests. However, we found no difference in nest survival rate within the 24 hour periods immediately following direct nest visits, or between nest days with and without nest cameras, consistent with other studies that found no effect of nest cameras on survival of ground-nesting Lapwing (Bolton *et al*., 2007a) or Asian Houbara *Chlamydotis macqueenii* (Koshkin *et al*., 2016). We are therefore confident that reported outcomes were not affected by the study protocols.

In agreement with our *a priori* predictions, nest survival was lower at STANTA than Brettenham Heath. Although this is a quasi-anecdotal contrast between only two sites, it is consistent with greater predator control effort and lower apparent Fox densities at Brettenham Heath. In the UK uplands, predator control can reduce generalist predator abundance and increase Curlew breeding success (Fletcher *et al.*, 2010). However, predator control may be more effective at high initial predator densities (Bolton *et al.,* 2007b), and its effectiveness may be compounded by meso-predator release (Bodey *et al.,* 2011) and replacement of culled individuals by inward dispersal from surrounding habitat. Supplementing lethal control with predator-exclusion fencing along a site boundary reduces the need for shooting (important for ethical reasons) and their combination could reduce Fox activity within the fences towards zero (P. Merrick, pers. comm.). Site-fencing reduces Fox predation of Lapwing clutches (Malpas *et al.,* 2013) and chicks (Rickenback *et al.,* 2011) and in our study, Brettenham Heath, which was both fenced and subject to lethal Fox control, had a breeding productivity well above that considered necessary for replacement (Grant *et al.,* 1999). We recommend further experimental evaluation of whether combined fencing and lethal Fox control consistently increases Curlew productivity in lowland contexts.

Conservation implications

The impact of land management interventions (e.g. rotational moorland burning) on Curlew abundance has previously been studied in upland habitats

(Douglas *et al.,* 2014, Littlewood *et al.*, 2019). Here, for the first time, we have shown that physical ground-disturbance, which is advocated as a conservation measure within lowland dry grassland and grass-heath for many rare, scarce and threatened species (Fuller *et al.,* 2017; Hawkes *et al.,* 2019a,b), also provides suitable Curlew nesting habitat, with no reduction in nest survival. Implementing ground-disturbance, particularly through shallow-cultivating, in areas with few or no mammalian nest predators (e.g. inside anti-predator fenced sites with effective Fox control) could provide a useful management tool for attracting breeding Curlew to safer areas.

Here, nest predation was unsustainably high, and Foxes were the main predator. Given low breeding productivity is an issue across all UK lowland Curlew populations (Table S1), experimental tests which examine the efficacy of different anti-predator options (whether lethal or not) as a way of improving breeding success (not just clutch survival) are urgently needed.

Acknowledgements

Defence Infrastructure Organisation, University of East Anglia and Sir Phillip Reckitt Educational Trust funded this work, along with additional support from the Royal Society for Protection of Birds and Natural England, through the Action for Birds in England programme. We thank Nigel Butcher and Andrew Asque for assistance with nest cameras, and the STANTA bird group, John Black and Tim Cowan for assistance during fieldwork. We also thank Jen Smart for advice and support throughout this study. We are grateful for comments on this manuscript from Ian Hartley and two anonymous reviewers. Cranfield University provided soil data under license.

References

Amat, J. & Maserom J. 2004. Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. *Animal Behaviour* **67:** 293-300.

Ausden, M., Bolton, M., Butcher, N., Hoccom, D.G., Smart, J. & Williams, G. 2009. Predation of breeding waders on lowland wet grassland – is it a problem? *British Wildlife* **October**: 29–38.

Baines, D. 1988. The effects of improvement of upland, marginal grasslands on the distribution and density of breeding wadering birds (Charadriiformes) in northern England. *Biol. Conserv.* **45**: 221-236.

Baldock, D., Buckwell, A., Hart, K. & Maréchal, A. 2017. *EU referendum and implications for UK agriculture and the environment*. Available at: https://www.brexitenvironment.co.uk/policy-briefs/#expertrev (Accessed 1 November 2018)

Balmer, D., Gillings, S., Caffrey, B., Swann, B., Downie, I. & Fuller, R. 2013. *Bird Atlas 2007-11: The Breeding and Wintering Birds of Britain and Ireland*. British Trust for Ornithology, Thetford.

Barton, K. 2019. Multi-model inference. Available at: https://cran.r-project.org/web/packages/MuMIn/ (Accessed 2 July 2018).

Berg, Å. 1992. Habitat selection by breeding Curlews *Numenius arquata* on mosaic farmland. *Ibis* **134**: 355–360.

Bertholdt, N.P., Gill, J.A., Laidlaw, R.A. & Smart, J. 2017. Landscape effects on nest site selection and nest success of northern Lapwing *Vanellus vanellus* in lowland wet grasslands. *Bird Study* **64**: 30–36.

BirdLife International. 2017. *Numenius arquata*. The IUCN Red List of Threatened Species 2017. Available at: http://datazone.birdlife.org/species/factsheet/eurasian-Curlew-numenius-arquata (Accessed 30 June 2018).

Bodey, T., McDonald, R., Sheldon, R. & Bearhop, S. 2011. Absence of effects of predator control on nesting success of Northern Lapwings *Vanellus vanellus*: implications for conservation. *Ibis* **153:** 543-555.

Bolton, M., Butcher, N., Sharpe, F., Stevens, D. & Fisher, G. 2007a. Remote monitoring of nests using digital camera technology. *J. Field Ornithol.* **78**: 213–220.

Bolton, M., Tyler, G., Smith, K.E.N. & Bamford, R.O.Y. 2007b. The impact of predator control on Lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves. *J. Appl. Ecol.* **44**: 534–544.s

Boughey, K.L., Lake, I.R., Haysom, K.A. & Dolman, P.M. 2011. Effects of landscape-scale broadleaved woodland configuration and extent on roost location for six bat species across the UK. *Biol Conserv*. **144:** 2300–2310.

Brown, A.F. & Shepherd, K.B. 1993. A method for censusing upland breeding waders. *Bird Study* **40**: 189–195.

Brown, D.J., Wilson, J.D., Douglas, D.J.T., Thompson, P.S., Foster, S., McCulloch, N., *et al.* 2015. The Eurasian Curlew – the most pressing bird conservation priority in the UK? *British Birds* **108**: 660–668.

Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodal Inference: A practical Information-Theoretic Approach*, Second. Springer, New York.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., *et al.* 2010. Global Biodiversity: Indicators of Recent Declines. *Science.* **328**: 1164-1168.

Call of the Curlew. 2017. Curlew Forum Newsletter 3, 31 August 2017. Available at: http://www.Curlewcall.org/category/newsletters/ (Accessed 3 July 2018).

Currie, D., Valkama, J., Berg, Å.K.E., Boschert, M., Norrdahl, K.A.I., Hanninen, M., *et al.* 2001. Sex roles, parental effort and offspring desertion in the monogamous eurasian Curlew *Numenius arquata*. *Ibis* **143**: 642–650.

Dinsmore, S.J. & Dinsmore, J.J. 2007. Modeling avian nest survival in program MARK. *Stud. Avian Biol.* **34**: 73–83.

Dinsmore, S.J., White, G.C. & Knopf, F.L. 2002. Advanced techniques for modeling avian nest survival. *Ecology* **83**: 3476–3488.

Dolman, P.M. & Sutherland, W.J. 1994. The use of soil disturbance in the management of Breckland grass heaths for nature conservation. *J. Environ. Manage.* **41:** 123-140.

Douglas, D.J.T., Bellamy, P.E., Stephen, L.S., Pearce-Higgins, J.W., Wilson, J.D. & Grant, M.C. 2014. Upland land use predicts population decline in a globally near-threatened wader. *J. Appl. Ecol.* **51:** 194-203.

Douglas, D.J.T., Beresford, A., Selvidge, J., Garnett, S., Buchanan, G.M., Gullett, P., *et al.* 2017. Changes in upland bird abundances show associations with moorland management. *Bird Study* **64**: 242–254.

Draycott, R.A.H., Hoodless, A.N., Woodburn, M.I.A. & Sage, R.B. 2008. Nest predation of common pheasants *Phasianus colchicus*. *Ibis* **150**: 37–44.

ESRI. 2014. ArcGIS Release 10.3. Redlands, CA.

Ewing, S.R., Scragg, E.S., Butcher, N., & Douglas, D.J.T. 2018. GPS tracking reveals temporal patterns in breeding season habitat use and activity of a globally Near Threatened wader, the Eurasian Curlew. *Wader Study* **124:** 206-214

Fisher, G. & Walker, M. 2015. Habitat restoration for Curlew *Numenius arquata* at the Lake Vyrnwy reserve, Wales. *Conservation Evidence* **12**: 48–52.

Fletcher, K., Aebischer, N.J., Baines, D., Foster, R. & Hoodless, A.N. 2010. Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. *J. Appl. Ecol.* **47**: 263–272.

Franks, S.E., Douglas, D.J.T., Gillings, S. & Pearce-Higgins, J.W. 2017. Environmental correlates of breeding abundance and population change of eurasian Curlew *Numenius* *arquata* in Britain. *Bird Study* **64**: 393–409.

Fuller, R.J., Williamson, T., Barnes, G. & Dolman, P.M. 2017. Human activites and biodiversity opportunities in pre-industrial cultural landscapes: relevance to conservation. *J. Appl. Ecol.* **54**: 459-469.

Grant, M.C. 1996. Predicting the hatching dates of Curlew *Numenius arquata* clutches. *Wader Study Group Bull.* **80**: 53–54.

Grant, M.C., Orsman, C., Easton, J., Lodge, C., Smith, M., Thompson, G., *et al.* 1999. Breeding success and causes of breeding failure of Curlew *Numenius arquata* in Northern Ireland. *J. Appl. Ecol.* **36**: 59–74.

Green, R.E., Hawell, J. & Johnson, T.H. 1987. Identification of predators of wader eggs from egg remains. *Bird Study* **34:** 87–91.

Guilherme, J.L., Burnside, R.J., Collar, N.J. & Dolman, P.M. 2018. Consistent nest-site selection across habitats increases fitness of Asian Houbara. *Auk*, **135:** 192-205.

Gunnarsson, T.G., Gill, J.A., Atkinson, P.W., Gélinaud, G., Potts, P.M., Croger, R.E., *Et Al.* 2006. Population-scale drivers of individual arrival times in migratory birds. *J. Anim. Ecol.* **75**: 1119–1127.

Hawkes, R.W., Smart, J., Brown, A., Jones, H. & Dolman, P.M. 2019a. Experimental evidence that ground-disturbance benefits woodlark. *Ibis* **161**: 447–452.

Hawkes, R.W., Smart, J., Brown, A., Jones, H., Lane, S., Wells, D. & Dolman, P.M. 2019b. Multi-taxa consequences of management for an avian umbrella species. *Biol. Conserv.* **236**: 192–201.

Hayhow, D.B., Ausden, M., Bradbury, R.B., Burnell, D., Copeland, A.I., Crick, H.Q.P., *et al.* 2017. *The State of the UK's birds 2017*. RSPB, BTO, WWT, DAERA, JNCC, NE and NRW, Sandy, Bedfordshire.

Jackson, D.B. 2001. Experimental removal of introduced hedgehogs improves wader nest success in the Western Isles, Scotland. *J. App. Ecol.* **38**: 802-812.

Johnson, D.H. 1979. Estimating nest success: The Mayfield method and an alternative. *The Auk* **96**: 651–661.

Johnstone, I., Elliot, D., Mellenchip, C. & Peach, W.J. 2017. Correlates of distribution and nesting success in a Welsh upland eurasian Curlew *Numenius arquata* population. *Bird Study* **64**: 535–544.

Kentie, R., Both, C., Hooijmeijer, J.C.E.W. & Piersma, T. 2015. Management of modern agricultural landscapes increases nest predation rates in black-tailed godwits *Limosa limosa*. *Ibis* **157**: 614–625.

Koshkin, M., Burnside, R.J., Packman, C.E., Collar, N.J. & Dolman, P.M. 2016. Effects of habitat and livestock on nest productivity of the Asian houbara *Chlamydotis macqueenii* in Bukhara Province, Uzbekistan. *Eur. J. Wildl. Res.* **62**: 447–459.

Laidlaw, R.A., Smart, J., Smart, M.A. & Gill, J.A. 2015. The influence of landscape features on nest predation rates of grassland-breeding waders. *Ibis* **157**: 700–712.

Leyrer, J., Brown, D., Gerritsen, G., Hotker, H. & Ottvall, R. 2018. *International multi-species Action Plan for the Conservation of Breeding Waders in Wet Grassland Habitats in Europe (2018-2028).* Report of Action A13 under the framework of Project LIFE EuroSAP (LIFE 14 PRE/UK/002). NABU, RSPB, VBN and SOF.

Littlewood, N.A., Mason, T.H.E., Hughes, M., Jaques, R., Whittingham, M.J. & Willis, S.G. 2019. The influence of different aspects of grouse moorland management on nontarget bird assemblages. *Ecol. Evol.* **9:** 11089-11101.

Ludwig, S.C., Roos, S. & Baines, D. 2019. Responses of breeding waders to restoration of grouse management on a moor in South-West Scotland. *J. Ornithol.* **160:** 787-797.

MacDonald, M.A. & Bolton, M. 2008. Predation on wader nests in Europe. *Ibis* **150**: 54–73.

Mallord, J.W., Dolman, P.M., Brown, A.F. & Sutherland, W.J. 2007 Nest site characteristics of woodlarks *Lullula arborea* breeding on heathlands in southern England: are there consequences for nest survival and productivity? *Bird Study* **54**: 307-314 .

Malpas, L.R., Kennerley, R.J., Hirons, G.J.M., Sheldon, R.D., Ausden, M., Gilbert, J.C., *et al.* 2013. The use of predator-exclusion fencing as a management tool improves the breeding success of waders on lowland wet grassland. *J. Nat. Conserv.* **21**: 37–47.

Mason, L.R., Smart, J. & Drewitt, A.L. 2017. Tracking day and night provides insights into the relative importance of different wader chick predators. *Ibis* **160**: 71–88.

Massey, K., Cosgrove, P., Massey, F., Jackson, D. & Chapman, M. 2016. Habitat characteristics of breeding eurasian whimbrel *Numenius phaeopus* on Mainland Shetland, Scotland, UK. *Bird Study* **63**: 500–508.

Musgrove, A., Aebischer, N., Eaton, M., Hearn, R., Newson, S., Noble, D., Parsons, M., Risely, K. & Stroud, D. 2013. Population estimates of birds in Great Britain and the Uniterd Kingdom. *British Birds.* **106:** 64-100.

NSRI, 2014. *National soil map of England and Wales - NATMAP, 1:250,000 scale.* Cranfield University, Bedfordshire. Available at http://www.landis.org.uk (Accessed July 2014).

Odum, E.P. & Kuenzler, E.J. 1955. Measurement of territory and home range size in birds. *Auk*. **72**: 128-137.

Paradis, E., Claude, J. & Strimmer, K. 2004. APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**: 289–290.

Pearce-Higgins, J.W., Brown, D.J., Douglas, D.J.T., Alves, J.A., Bellio, M., Bocher, P., *et al.* 2017. A global threats overview for Numeniini populations: synthesising expert knowledge for a group of declining migratory birds. *Bird Conserv. Int.* **27**: 6–34.

R Core, T. 2017. R Core Team. R: a language and environment for statistical computing. Version 3.2.2. R Foundation for Statistical Computing, Vienna (2015)

Rickenbach, O., Grüebler, M.U., Schaub, M., Koller, A., Naef-Daenzer, B. & Schifferli, L.U.C. 2011. Exclusion of ground predators improves northern Lapwing *Vanellus*

vanellus chick survival. *Ibis* **153**: 531–542.

Rowland, C.S., Morton, R.D., Carrasco, L., McShane, G., O'Neil, A.W. & Wood, C.M. 2017. Land Cover Map 2015 (25m raster, GB). NERC Environmental Information Data Centre.

Sheail, J. 1979. Documentary evidence of the changes in the use, management and appreciation of the grass-heaths of Breckland. *J. Biogeogr.* **6**: 277–292.

Smart, M. 2017*. Curlews in the Severn and Avon Vales*. *Report on a breeding survey in 2016: suggestions on future action.* Southern Curlew Conference, WWT, Slimbridge, 02.02.2017. Available at: http://www.Curlewcall.org/wp-content/uploads/2017/07/Curlews-in-the-Severn-and-Avon-Vales-REV-3.pdf (Accessed 16 November 2018)

Stanbury, A., Brown, A., Eaton, M., Aebischer, N.J., Gillings, S., Hearn, R., ***et al.*** 2017. The risk of extinction for birds in Great Britain. *British Birds* **110**: 502-517.

Stroud, D.A., Baker, A., Blanco, D.E., Davidson, N.C., Delany, S., Ganter, B., ***et al.*** 2006. The conservation and population status of the world's waders at the turn of the millennium. *Waterbirds around the world*. Eds. G.C. Boere, C.A. Galbraith & D.A. Stroud. The Stationery Office, Edinburgh, UK. pp. 643-648.

Teunissen, W., Schekkerman, H., Willems, F. & Majoor, F. 2008. Identifying predators of eggs and chicks of Lapwing *Vanellus vanellus* and black-tailed godwit *Limosa limosa* in the Netherlands and the importance of predation on wader reproductive output. *Ibis* **150**: 74–85.

Appendices

Appendix S1 – Site management

Appendix S2 – Home range of nesting Curlew

Appendix S3 – Effect of camera monitoring on Curlew nest survival

Table S1 – Curlew breeding productivity across Europe

Table S2 – Candidate models MMI

Digital materials: http://eurasiancurlewnestproductivity.simplesite.com

Figure legends

Figure 1. Surveyed grassland (dark grey, c. 3,700 ha) across the study sites (Stanford Training Area and Brettenham Heath). Symbols (not to scale) show the location of experimental ground-disturbance plots (totalling 206 ha) and grassland controls. The dashed line shows the boundary of the Stanford Training Area ‘impact area’ (within which ground-disturbance was precluded). Arable farmland and woodland are also shown.

Figure 2. Coefficient estimates from models relating Eurasian Curlew *Numenius arquata*: i) nest placement at the study-area and home-range scale to treatment (two levels, reference level undisturbed grassland) and vegetation strata (study-area scale model only: two levels, reference level older acidic grassland); and ii) nest survival to treatment, vegetation strata, year (two levels, reference level 2017), site (two levels, reference level Brettenham Heath) and lay date (continuous), showing model coefficients (black dot), standard error (thick grey line) and 95% CI (thin grey line). Variables were deemed to be supported when their 95% CIs did not span zero (dashed line).

Figure 3. Estimated variation in the daily nest survival probability for Eurasian Curlew *Numenius arquata* within the Stanford Training Area (black) and Brettenham Heath (grey) in 2017 and 2018. Estimates are based on multi-model inference (Table S2, see Fig. 2 for included variable). Vertical bars show SE.

Figure 4. Date and time of 23 Eurasian Curlew *Numenius arquata* nest predation events across two years of study. Light shading indicates crepuscular (between dawn and sunrise, and between sunset and dusk) and darker shading indicates nocturnal (between dusk and dawn) periods. Symbols indicate predation events: crosses denote cases where the predator identity was not known, squares denote predation by Red Fox *Vulpes vulpes*, and a triangle predation by a Sheep *Ovis aries*.