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Upland rush management advocated by agri-environment schemes increases predation of artificial wader nests

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Keywords

agri-environment schemes; common snipe; Eurasian curlew; farmland birds; land use; mesopredator; rush pasture; predation risk.

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Abstract

Farmland birds, including breeding waders, have declined across Europe. One frequently advocated strategy to facilitate population recovery is using agri-environment schemes (AES) to improve vegetation structure. A key example is cutting dense rush *Juncus* to open the sward which aims to increase the abundance of wading birds, for example by improving foraging conditions. Effects on breeding success are, however, unknown. This is a critical knowledge gap as high nest and chick predation rates are a key driver of wader declines. For wader species that nest across a range of sward structures, for example Eurasian curlew *Numenius arquata* and common snipe *Gallinago gallinago*, converting denser swards to more open ones may reduce opportunities for nest concealment and thus increase predation risk. Due to the difficulties of locating large numbers of wader nests, we assess rush management impacts on nest predation risk using artificial wader nests ($n = 184$) in two upland areas of England, using fields in which rush is managed according to AES prescriptions (treatment; $n = 21$) or un-managed (control; $n = 22$) fields. Daily nest predation rates (DPRs) were twice as high in treatment (0.064 day^{-1}) than control fields (0.027 day^{-1}). Within treatment fields, DPRs were twice as high for nests in cut rush patches (0.108 day^{-1}) than in uncut rush (0.055 day^{-1}). Modelling links higher DPRs associated with rush cutting to the resultant shorter and less dense vegetation. Our results highlight the need to assess how AES prescriptions that alter vegetation structure impact all aspects of the target species' fitness and thus determine population recovery. Studies using real wader nests should test whether AES rush management inadvertently creates an ecological trap by altering vegetation structure, and identify the sward structure and configuration that optimizes trade-offs between foraging conditions and nest predation risk.

Introduction

Widespread declines in European farmland birds have arisen from changes in agricultural practices, in particular intensification (Donald, Green & Heath, 2001; BirdLife International, 2015). Despite three decades of conservation interventions, principally agri-environment schemes (AES), that attempt to reverse these declines many previously common species are still declining (Kleijn & Sutherland, 2003; BirdLife International, 2015). Targeted AES interventions can benefit locally distributed, threatened species (e.g. corn bunting *Emberiza calandra*, Perkins *et al.*, 2011) but non-targeted AES typically primarily benefit common and widespread species of least conservation concern (Kleijn *et al.*, 2006; Batáry *et al.*, 2015). Ongoing declines in farmland bird populations are

probably due to insufficient landscape-scale implementation of AES (Franks *et al.*, 2018) combined with limited availability and uptake of detailed prescriptions targeted to the specific habitat requirements of each species (Kleijn *et al.*, 2001; Franks *et al.*, 2018).

A common goal of AES prescriptions is to reverse the trend towards homogenous swards that have become much more common due to agricultural intensification. Sward homogeneity frequently limits avian diversity and abundance (Perkins *et al.*, 2000; Benton, Vickery & Wilson, 2003; Wilson, Whittingham & Bradbury, 2005). Homogenous swards drive avian population declines as vegetation structure determines food availability and nest predation risk (of ground-nesting birds), but the optimum structure varies for each species, and many require different structures for feeding and

nest sites (Whittingham & Evans, 2004; Wilson *et al.*, 2005). Shorter and less dense swards enable soil- and surface-foraging birds to access food more easily, but extremely short swards rarely provide suitable nesting sites as predators can locate nests more easily. Taller or denser swards provide more concealment for nests, but very tall or dense swards may be avoided as nesting sites because incubating parents cannot readily detect approaching predators, thus increasing their predation risk (Vickery *et al.*, 2001; Whittingham & Evans, 2004). Changing vegetation structure through AES to generate more diverse sward structures, whilst avoiding a dominance of extremely short, tall or dense swards, is one widely advocated approach to tackling farmland bird declines (Wilson *et al.*, 2005).

Breeding waders are experiencing widespread and marked population declines across Europe (BirdLife International, 2015; BirdLife International, 2017) despite being targeted by AES (Natural England, 2012a; Franks *et al.*, 2018). The primary driver of wader declines is low breeding productivity, mainly due to high nest and chick predation rates that arise through numerous factors including land use change (Roodbergen, van der Werf & Hötter, 2012; Douglas *et al.*, 2014; Roos *et al.*, 2018). Habitat loss and degradation have also contributed to population declines (Franks *et al.*, 2018). Waders have a diverse range of requirements regarding sward structure. Some species mainly nest in tall, denser vegetation (e.g. common redshank *Tringa totanus* – threatened within some European countries including the UK; Smart *et al.*, 2006; Eaton *et al.*, 2015), or short, more open vegetation (e.g. northern lapwing *Vanellus vanellus* – globally Near Threatened; Milsom *et al.*, 2000; IUCN, 2020). Other species, including Eurasian curlew *Numenius arquata* (globally Near Threatened; IUCN, 2020) and common snipe *Gallinago gallinago* (threatened within some European countries including the UK; Eaton *et al.*, 2015), use nest sites across much of the gradient in vegetation structure from short, open swards to tall, denser patches of vegetation (Valkama, Roberston & Currie, 1998; Fisher & Walker, 2015; Wentworth, 2015; Zielonka *et al.*, 2019).

The UK uplands support important breeding populations of declining wader species (Balmer *et al.*, 2013). These regions are targeted by AES that attempt to create more favourable vegetation structures by promoting management of dense *Juncus* spp. (hereafter termed 'rush') swards and other rank vegetation. This management aims to generate less homogenous swards that contain patches of uncut rush as well as cut rush patches that provide shorter, more open vegetation. In theory, this provides open swards that are suitable for foraging and a variety of sward structures that provide suitable nesting sites for upland waders (Natural England, 2012a). This system thus provides a useful framework for assessing the consequences of AES-induced changes in vegetation structure on wader nest predation rates.

In the UK uplands, rush encroachment on grasslands has increased in recent decades (Silcock, Brunyee & Pring, 2012; Ashby *et al.*, 2020). Rush encroachment is facilitated by high livestock densities due to grazing of other more

palatable vegetation (Tweel & Bohlen, 2008) and trampling creating patches of bare ground that enables rush seeds to germinate and establish (Agnew, 1961; Bilotta, Brazier & Haygarth, 2007). Other potential catalysts include increased soil wetness due to inadequate drainage and soil compaction; insufficient grazing by traditional cattle and pony breeds which are more likely to eat rush (e.g. arising from a switch from mixed grazing to sheep grazing) and land abandonment, reduced fertilizer and lime application and increased precipitation and warmer winters (Silcock *et al.*, 2012; Ashby *et al.*, 2020). Rush encroachment generates tall, dense swards that will limit wader foraging opportunities and reduce the availability of nesting sites, especially for those species that prefer to nest in more open areas (see above). This has been tackled by incorporating rush management within AES prescriptions to improve foraging and nesting conditions for waders (Natural England, 2018).

As of 2009, 83% of the eligible area of purple moor grass *Molinia caerulea* and rush pasture priority habitat in England was managed under AES prescriptions (Natural England, 2009). Current broad AES prescriptions incorporating rush management in the UK (precise prescriptions deviate slightly between component countries) require at least one-third of a field to be covered in rush for a field to qualify for the prescriptions. Within a qualifying field, one-third of the total area of rush needs to be cut annually in rotation (e.g. Natural England, 2012a), although farmers may often cut more than this. The overall objective is to reduce rush cover to <30% of the field, with continued management over a minimum of 2 years required due to the high regrowth capacity of rush (Nielsen, Hald & Nissen 2014; Natural England, 2018; Shellswell & Humpidge, 2018; Kaczmarek-Derda *et al.*, 2019). Targeted prescriptions can vary the extent of rush cutting and desired rush cover depending on the target wader species (Natural England, 2012b; Welsh Government, 2017), with lower rush cover typically desired for lapwing than curlew (Glastir Advanced Management Options 164 and 168; Welsh Government, 2017). Supplementary rush management techniques involve aftermath grazing following cutting to reduce the rate of regrowth (livestock type and number is highly variable and there are no clear guidelines; Natural England, 2018; Shellswell & Humpidge, 2018) and occasionally herbicide application (Natural England, 2018).

Although rush management is a major component of UK upland AES prescriptions, research assessing its effectiveness for reversing wader population declines is limited. Wader abundance may increase following targeted rush management (Holton & Allcorn, 2006; Robson & Allcorn, 2006) or cutting of rank moorland vegetation that includes rush (Fisher & Walker, 2015; Douglas *et al.*, 2017). However, the mechanisms through which rush management influences wader populations remain unclear. A key unanswered question, which is especially important given the role of nest predation as a driver of wader population declines, is how rush management influences breeding success. Evidence from other agricultural systems strongly suggests that simpler and more open swards arising from rush management may increase nest predation (Whittingham & Evans, 2004).

Detecting and monitoring a large sample of wader nests is logistically extremely challenging but the relative predation rates of artificial nests that closely mimic real nests, and attract similar predator guilds, can provide useful information for evaluating conservation interventions (Major & Kendal, 1996; Villard & Pärt, 2004). We thus use predation rates of artificial wader nests as an index of predation pressure in treatment fields that follow or emulate AES prescriptions for rush cutting and in nearby untreated control fields. Artificial nests are located in vegetation patches with a wide range of vegetation structures and our results are thus most applicable to waders that nest across this gradient in vegetation structure, such as snipe and curlew (see above). We first test how rush management influences wader nest predation rates by assessing if (1) artificial nests in treatment fields, that is those with rush management, have higher daily nest predation rates (DPRs) than those in control fields without rush management, and (2) artificial nests in cut rush patches within treatment fields have higher DPRs than those in uncut rush patches within the same fields. We then test if the structure of vegetation surrounding nests varies between nests located in treatment and control fields, and between cut and uncut rush patches within treatment fields. These results enable us to confirm that rush management influences vegetation structure. Finally, we model DPRs as a function of vegetation structure and other potentially confounding environmental variables.

Materials and methods

Study areas

Research was conducted in two English upland regions during the wader breeding season (April–June 2019) in the south-west of the Peak District National Park (South West Peak, hereafter ‘SWP’) and Geltsdale reserve (hereafter ‘Geltsdale’) in Cumbria (Fig. 1), which is jointly owned by the Royal Society for the Protection of Birds and the Weir Trust. Both regions are representative of UK upland farmed landscapes (a mosaic of grassland and moorland) in terms of land management and use, and support populations of breeding waders including curlew and snipe. Study fields were mostly semi-improved pasture with additional unimproved pasture, hay meadow and ‘white moor’ fields (rough grassland with a mixture of rush and *Molinia*). Rush cutting within treatment fields had been managed between autumn 2018 and spring 2019 following or emulating the EK4 and EL4 Entry Level Stewardship prescriptions (Supporting Information, Table S1; Natural England, 2012a). These AES prescriptions are available throughout the UK regardless of whether they are located within a National Park or a reserve. All treatment fields had at least one-third rush cover prior to management, in accordance with AES prescription requirements, and received rush management in the preceding autumn/winter. All control fields had not been managed for rush in the 2 years prior to the study but had a similar range of rush cover as treatment fields (*c.* 30%, although three fields had 10–30%) to limit the potential for other environmental variables to differ between control and treatment

fields and generate confounding factors. Control fields were located close to treatment fields [mean distance = 90 m (95% CI 23.36–156.64 m)] and were similar in size (Fig. 1; Supporting Information, Table S2). In the SWP, we used 12 treatment fields and 13 control fields across 10 farms. At Geltsdale, we used nine treatments and nine control fields.

Artificial nest deployment and predation rates

Artificial wader nests were deployed within the typical breeding season of upland waders (Joys & Crick, 2004) from 1 April–28 April (early breeding season) and 28 May–18 June (late breeding season) in the SWP and 3 May–20 May (early breeding season) at Geltsdale (late season nests were not deployed in Geltsdale due to logistical constraints). Nests contained three fresh Japanese quail *Coturnix japonica* eggs and a plasticine egg (to aid separation of avian and mammalian predators). The latter was made by adapting the methods of Martin, Dueser & Moncrief (2010; Supporting Information, Figure S1) using Newplast modelling clay (Newclay Product Ltd, Devon, UK) and PlastiDip® coating (PlastiDip UK Ltd, Hampshire, UK) to minimize plasticine scent which could influence predators (Purger *et al.*, 2012). The markings of plasticine and quail eggs were similar to each other and those of curlew and snipe, and their dimensions are close to those of snipe eggs (Cramp & Simmons, 1982; Robinson, 2005; Smith, Gilchrist & Smith, 2007; Supporting Information, Figure S2). Green garden twine (30 cm) was embedded in each plasticine egg and ground-tethered to hinder removal by predators.

Latex gloves were worn to minimize human scent and disturbance of vegetation around nests was minimized. The number of nests varied with field size using estimates of snipe nest densities (Green, 1985) which are typically intermediate between those of more colonial lapwing and less aggregated curlew (Cramp & Simmons, 1982). Fields <4 ha received two nests (22 fields; median = 2.03 ha; range = 0.40–3.55 ha; four <1.05 ha fields within the same landholding (two treatment and two control) in the SWP received only one nest), and fields >4 ha (21 fields; median = 7.06 ha; range = 4.16–40.64 ha) received four nests (Supporting Information, Table S3).

Nest placement was conducted using an approach that ensured that there was no systematic bias in nest placement which could confound our analyses. In control fields, nests were placed in patches of uncut rush (the only type of rush available). In treatment fields, nests were placed in patches of cut rush except for fields >4 ha where one nest was placed in uncut rush (Supporting Information, Table S4). Placing nests in cut and uncut rush patches within the same field provides an additional check that differing nest predation rates between treatment and control fields is due to rush cutting rather than unrelated attributes of treatment fields. Upon entering a field, patches of cut and/or uncut rush were identified via a scan of the field. To select precise nest locations, the number of paces required to stop in one of the rush patches, without bias towards the centre or edge of the

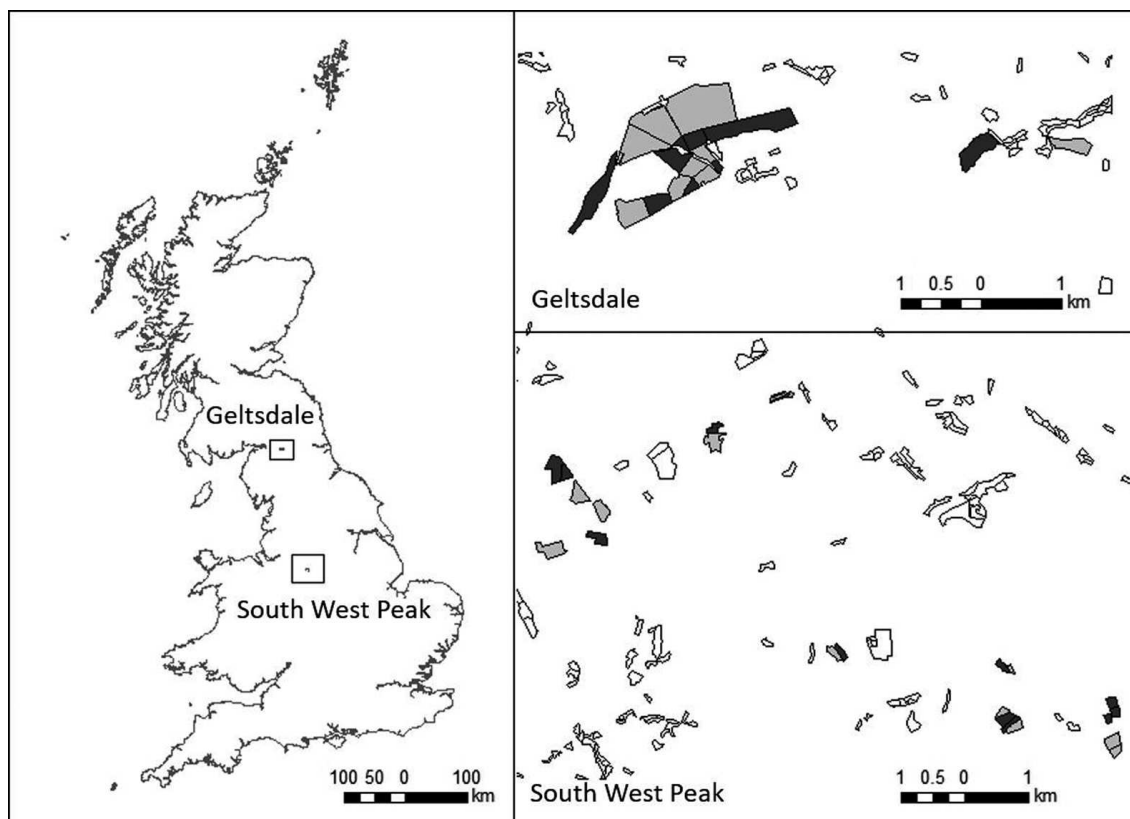


Figure 1 Locations of treatment (light grey) and control (dark grey) fields, with blocks of woodland (white; defined as areas with >20% tree cover, from Land Cover Map 2015; Rowland *et al.*, 2017) in the surrounding landscape.

patch, was estimated. After walking this number of paces, a natural depression in the immediately adjacent ground was selected for the nest scrape. If a natural depression was unavailable, a scrape (15 cm diameter \times 5 cm depth) was created using a small trowel. Eggs were placed in the scrape which was lined with a handful of dried vegetation; artificial nests were thus similar in appearance and location to real wader nests including those of snipe and curlew (Cramp & Simmons, 1982; Supporting Information, Figure S2). To aid relocation, a blue wooden golf tee was discreetly placed flush to the ground and a 60 cm bamboo cane topped with red tape was placed 10 m away in a random direction (Smith *et al.*, 2007; Pedersen *et al.*, 2018); the use of such canes does not alter wader nest predation rates (Zámečník, Kubelka & Šálek, 2018). The mean distance (95% CI) between nests within a field was 80.97 m (75.80–86.14 m), and from each nest to the nearest field boundary was 50.66 m (47.49–53.84 m).

Nests were deployed until predated, or for 15 days. The length of this maximum exposure period was determined by a trade-off between the use of a longer exposure period that would provide a closer match to wader incubation periods (e.g. 18–20 days for snipe; Robinson, 2005) and maximizing the number of nests that could be deployed and monitored; the duration of our maximum exposure period is sufficient to generate a reliable estimate of DPRs. Nests were checked

every 5 days (± 1 day in both cases depending on weather conditions to avoid disturbing real wader nests in these fields during inclement weather). Nests were classified as predated if at least one egg was missing, damaged or outside the nest scrape in the immediate surroundings (Smith *et al.*, 2007; Pedersen *et al.*, 2018). Trampled nests (7.1% of 184 nests; crushed eggs with contents remaining in the shell or on surrounding ground) were excluded from further analyses and trampling rates were similar in treatment (7.1% of 98 nests) and control fields (7.0% of 86 nests).

For predated nests, the plasticine eggs (if found) were assigned to predator type using bill or tooth marks following Trnka, Prokop & Batáry (2008) and Bocz *et al.* (2017). Two assessors working independently classified each plasticine egg predator as unknown, avian, mammalian or signs of both avian and mammalian predators.

Environmental variables

Habitat around nests was recorded during the first monitoring visit. Vegetation height (to the nearest 1 cm) and density were measured at four equally spaced points on the nest scrape edge, and four equally spaced points 1 m away from the nest. Mean values were calculated from all eight measures. Vegetation density was the number of concealed white bands – five 2-cm-wide bands at 10 cm intervals from 0 to

40 cm on a pole – and was measured visually by viewing the upright pole at a height of *c.* 85 cm from a point *c.* 45 cm horizontally from the pole (Sansom, Pearce-Higgins & Douglas, 2016). More concealed bands indicate denser vegetation. Rush cover within a 5 m radius of each nest was estimated visually to the nearest 5%.

Field size (ha) was measured from 1:25 000 maps (Ordnance Survey, 2019) using ArcMap™ (v10.4.1; Esri, Redlands, CA, USA); some fields had identical sizes. Straight-line distance (m) from each nest to the nearest field boundary was measured using the ‘Near (Analysis)’ tool to account for potential edge effects in nest predation risk. Similarly, we measured the straight-line distance from each nest to the nearest block of woodland (defined as areas with >20% tree cover, from Land Cover Map 2015, Rowland *et al.*, 2017) as this represents a metric of real or perceived nest predation risk for waders (e.g. Wilson *et al.*, 2014). We used a straight-line distance, rather than a metric which attempts to measure routes potentially taken by predators (such as through gates) as many important mammalian predators of wader nests (mustelids and rodents) can pass through gaps in field boundaries (fence lines, small gaps in dry stone walls, etc.) and avian predators are not constrained by boundary features.

Predator control

Predator control was classified across each of the 11 landholdings in which our study fields were located using a semi-structured interview with land managers and owners (Supporting Information, Table S5) following approval from the University of Sheffield Research Ethics Committee (application number 030271). Informed consent was gained from all interviewees. ‘Regular’ predator control comprised 3–4 nightly patrols for red foxes *Vulpes vulpes* per week (January–June inclusive) and daily Larsen trapping of corvids (March–April inclusive) with a full-time contractor (with one landholding also conducting daily mustelid trap checks; January–June inclusive). ‘Negligible/no’ control comprised no corvid control and no fox control, except one landholding with occasional fox control.

Avian predator abundance

Avian predator surveys were conducted in each study field – two during the early breeding season in all fields and two during the late breeding season in SWP fields only. Surveys were not undertaken in the first hour after sunrise or last hour before sunset, during heavy rain, in fog (<250 m visibility) or if wind speed was greater than Beaufort Force 5. The entirety of each study field, to within a distance of 50 m, was walked during each survey and all avian predators (regardless of their activity) were recorded except those flying more than 30 m above the ground (which were considered unlikely to be using or searching for resources in the field). We calculated two indices of potential avian predator activity: corvid abundance (carrion crow *Corvus corone*; rook *Corvus frugilegus*; Eurasian jackdaw *Corvus monedula*;

Eurasian magpie *Pica pica*; unidentified corvid; Leigh, Smart & Gill, 2017) and total avian predator abundance (corvids, gulls, raptors and herons). The indices were generated for the early and late breeding seasons separately by calculating the mean number of individuals observed over the two surveys per study field. Because gulls, raptors and herons were rarely observed, corvid abundance and total avian predator abundance were highly correlated (early breeding season: $r_s = 0.971$, $P = 2.2^{-16}$; late breeding season: $r_s = 0.980$, $P = 2.2^{-16}$). Therefore, corvid abundance was the only measure included in further analyses (carrion crow are the primary avian predator of wader nests; MacDonald & Bolton, 2008; Teunissen *et al.*, 2008). Mammalian predator surveys were logistically unfeasible due to time constraints.

Statistical analyses

All analyses were conducted in R 3.6.3 (R Core Team, 2020). Our general approach is to use full models to test our core hypotheses that (1) rush management and (2) metrics of vegetation structure influenced by rush management (vegetation density, vegetation height and rush cover) influence nest predation rates whilst taking into account potentially confounding variables (Supporting Information, Table S6). This full model approach is a suitable method, especially in experimental settings (Burnham & Anderson, 2002), and superior to selection of a single best model through stepwise model selection techniques which can generate biased parameter estimates (Whittingham *et al.*, 2006; Mundry & Nunn, 2009).

We modelled DPRs using Mayfield logistic regressions following the Hazler (2004) method and constructed generalized linear mixed effects models (GLMMs; fit by maximum likelihood with Laplace approximation) using the lme4 package (Bates *et al.*, 2015). The response variable was DPR i.e. nest outcome (1 = predated; 0 = not predated)/exposure days. Exposure days was the number of days between nest establishment and failure date, or date of final monitoring visit. Failure date was calculated as the mid-point between the monitoring visit when the nest was last observed intact and the subsequent visit when the nest had failed. Thus, exposure days could have non-integer values. These were converted to integer values by rounding up for odd numbered nests and down for even numbered nests to avoid problems generated by consistently over-estimating exposure days if 0.5 values were consistently rounded upwards (Johnson, 2007). All models of DPRs were constructed with a binomial error structure (logit link) and field identity as a random effect as each field contained more than one artificial nest. Continuous predictor variables were centred and scaled using the scale function. Theoretical conditional R^2 values were calculated for each model using the MuMIn package (Barton, 2019) and represent model fit (Nakagawa & Schielzeth, 2013; Nakagawa, Johnson & Schielzeth, 2017). We report profile and bootstrap 95% CIs of parameter estimates.

Table 1 Structure of the four generalized linear mixed effects models (binomial (logit)) of daily nest predation rate (DPR), the dataset used, the optimizer used, the model distribution and link function and the predictor variables (fixed and random) included. The bobyqa optimizer was used for model iii following the recommendation of lme4 package author, Ben Bolker, as the model failed to converge with the default optimizer (combination of Nelder-Mead and bobyqa). For a detailed breakdown of sample sizes, see Supporting Information, Tables S3 and S4

Model	Dataset	Optimizer	Distribution (link)	Predictor variables
Objective – test effect of rush management on DPRs				
i	All fields ($n = 43$) 91 treatment nests; 80 control nests	Combination of Nelder-Mead and bobyqa	Binomial (logit)	Treatment + Woodland distance + Boundary distance (square root transformed) + Deployment date + Field size (natural logarithm transformed) + Predator control + Corvid abundance (natural logarithm ($x + 1$) transformed) + Region + (1 Field identity)
ii	Treatment fields >4 ha ($n = 13$) 50 nests in cut rush; 17 nests in uncut rush	Combination of Nelder-Mead and bobyqa	Binomial (logit)	Cut or uncut rush + Woodland distance + Boundary distance (square root transformed) + Deployment date + Region + (1 Field identity)* *Note that the three variables measured at the field level (field size, predator control and corvid abundance) were excluded from this model because it is comparing nests within the same field. Field identity was retained as a random factor
Objective – test effect of vegetation structure on DPRs				
iii	All fields ($n = 43$) 171 nests	bobyqa	Binomial (logit)	Vegetation density + Rush cover + Woodland distance + Boundary distance (square root transformed) + Deployment date + Field size (natural logarithm transformed) + Predator control + Corvid abundance (natural logarithm ($x + 1$) transformed) + Region + (1 Field identity)
iv	All fields ($n = 43$) 171 nests	Combination of Nelder-Mead and bobyqa	Binomial (logit)	Vegetation height + Rush cover + Woodland distance + Boundary distance (square root transformed) + Deployment date + Field size (natural logarithm transformed) + Predator control + Corvid abundance (natural logarithm ($x + 1$) transformed) + Region + (1 Field identity)

Effect of rush management on DPRs

We first modelled DPRs, using data from all artificial nests, as a function of location in treatment or control fields whilst accounting for region, field identity (random factor), deployment date and other environmental variables (woodland distance, boundary distance, field size, predator control and corvid abundance) except those relating to vegetation structure (Table 1, model i). We then used data from treatment fields >4 ha and modelled DPRs as a function of artificial nest location in cut or uncut rush whilst accounting for region, field identity (random factor), deployment date and other nest level environmental variables except those relating to vegetation structure (Table 1, model ii).

Associations between rush management and environmental variables

We conducted subsidiary analyses to test whether vegetation structure differed between nests in treatment and control fields and whether other environmental variables (woodland distance, boundary distance, field size and corvid density) differed between treatment and control fields. Similarly, we tested whether there were differences in the structure of vegetation surrounding nests in cut and uncut rush patches within treatment fields that contained nests in both habitat types (fields >4 ha). We used GLMMs (lme4 package; Gaussian error structure and identity link) when there was more

than one data point per field (nest level variables; with field identity as a random factor) and generalized linear models (GLMs; Gaussian error structure and identity link) in other cases (field level variables; see Supporting Information, Tables S7 and S8).

Effect of vegetation structure on DPRs

Finally, we modelled DPRs as a function of vegetation structure whilst accounting for other environmental variables. Vegetation density and vegetation height were highly correlated so could not be included in the same model ($r = 0.74$; Dormann *et al.*, 2013). We first used GLMMs (lme4 package) to model DPRs, using data from all artificial nests, as a function of vegetation density and rush cover whilst accounting for region, field identity (random factor), deployment date and other environmental variables (Table 1, model iii). We repeated this model replacing vegetation density with vegetation height (Table 1, model iv) as this is an easier metric to obtain in the field and may be more practical for conservation managers.

Results

Predator type

Marked plasticine eggs ($n = 45$) suggest that mammals were the main nest predators, being identified as the sole predators

in 64% ($n = 39$ eggs assigned to a known predator; assessor #1) and 85% ($n = 41$ eggs assigned to a known predator; assessor #2) of predation events. Equivalent estimates for avian predators were 23% (assessor #1) and 10% (assessor #2), with joint avian and mammalian predation events estimated at 13% (assessor #1) and 5% (assessor #2).

Effect of rush management on DPRs

DPRs were significantly higher in treatment than control fields ($z = 3.038$, $P = 0.002$; Table 2; Supporting Information, Table S9, model i). This equates to 2.35 times higher

DPR in treatment fields (0.064 day^{-1} ; bootstrap 95% CI 0.029 to 0.118 day^{-1}) than control fields (0.027 day^{-1} ; bootstrap 95% CI 0.009 to 0.059 day^{-1} ; Fig. 2a). Within treatment fields in which nests were located in cut and uncut rush patches (fields >4 ha), DPRs were significantly higher in cut rush patches ($z = 1.989$, $P = 0.047$; Table 2; Supporting Information, Table S9, model ii). This equates to 1.96 times higher DPR in cut rush patches (0.108 day^{-1} ; bootstrap 95% CI 0.052 to 0.180 day^{-1}) than uncut rush patches (0.055 day^{-1} ; bootstrap 95% CI 0.021 to 0.106 day^{-1} ; Fig. 2b). No other predictor variable had a consistent significant influence on DPRs (Table 2).

Table 2 Results of generalized linear mixed effects models (GLMMs) investigating the effect of rush management and vegetation structure on daily nest predation rates (DPRs) of artificial nests in all study fields (models i, iii and iv) and treatment fields >4 ha (model ii). For each GLMM, parameter estimates and profile 95% CIs are presented for the predictor variables (see Supporting Information, Table S9 for alternative bootstrap CIs), with significant predictor variables in bold. Control fields are the reference level for treatment; uncut rush patches are the reference level for cut or uncut rush; negligible/no predator control is the reference for predator control; Geltsdale is the reference for region. Theoretical conditional R^2 (Nakagawa & Schielzeth, 2013; Nakagawa *et al.*, 2017), Akaike information criterion with correction for small sample size (AICc) and the dispersion parameter are presented for each GLMM

Model	Predictor variables in models	Estimate (profile 95% CIs)	z statistic	P	R^2	AICc	Dispersion parameter
Effect of rush management on DPRs							
i	Treatment	0.894 (0.310 to 1.501)	3.038	0.002	0.156	409.65	1.218
	Woodland distance	-0.050 (-0.402 to 0.297)	-0.291	0.771			
	Boundary distance (square root transformed)	0.156 (-0.143 to 0.459)	1.022	0.307			
	Deployment date	-0.287 (-0.506 to -0.074)	-2.612	0.009			
	Field size (natural logarithm transformed)	-0.221 (-0.632 to 0.183)	-1.088	0.276			
	Predator control	-0.474 (-1.202 to 0.206)	-1.357	0.175			
	Corvid abundance (natural logarithm ($x + 1$) transformed)	-0.181 (-0.470 to 0.113)	-1.230	0.219			
	Region	0.093 (-0.846 to 1.072)	0.195	0.845			
ii	Cut or uncut rush	0.728 (0.038 to 1.496)	1.989	0.047	0.127	174.42	0.998
	Woodland distance	0.260 (-0.360 to 0.874)	0.864	0.388			
	Boundary distance (square root transformed)	-0.245 (-0.596 to 0.097)	-1.409	0.159			
	Deployment date	0.040 (-0.264 to 0.345)	0.259	0.795			
	Region	0.065 (-1.239 to 1.432)	0.102	0.919			
Effect of vegetation structure on DPRs							
iii	Vegetation density	-0.735 (-1.027 to -0.453)	-5.061	4.165⁻⁷	0.220	387.54	1.264
	Rush cover	-0.051 (-0.324 to 0.217)	-0.372	0.710			
	Woodland distance	-0.106 (-0.421 to 0.201)	-0.693	0.489			
	Boundary distance (square root transformed)	0.209 (-0.093 to 0.515)	1.357	0.175			
	Deployment date	-0.176 (-0.412 to 0.058)	-1.477	0.140			
	Field size (natural logarithm transformed)	-0.113 (-0.489 to 0.267)	-0.597	0.551			
	Predator control	-0.246 (-0.896 to 0.377)	-0.783	0.434			
	Corvid abundance (natural logarithm ($x + 1$) transformed)	-0.206 (-0.478 to 0.067)	-1.506	0.132			
	Region	0.639 (-0.167 to 1.491)	1.571	0.116			
	iv	Vegetation height	-0.766 (-1.105 to -0.432)	-4.483			
Rush cover		0.046 (-0.246 to 0.319)	0.319	0.750			
Woodland distance		-0.101 (-0.411 to 0.197)	-0.676	0.499			
Boundary distance (square root transformed)		0.203 (-0.101 to 0.512)	1.305	0.192			
Deployment date		-0.083 (-0.334 to 0.167)	-0.651	0.515			
Field size (natural logarithm transformed)		-0.119 (-0.493 to 0.254)	-0.640	0.522			
Predator control		-0.406 (-1.051 to 0.205)	-1.312	0.190			
Corvid abundance (natural logarithm ($x + 1$) transformed)		-0.168 (-0.433 to 0.104)	-1.252	0.211			
Region		0.395 (-0.398 to 1.238)	0.991	0.322			

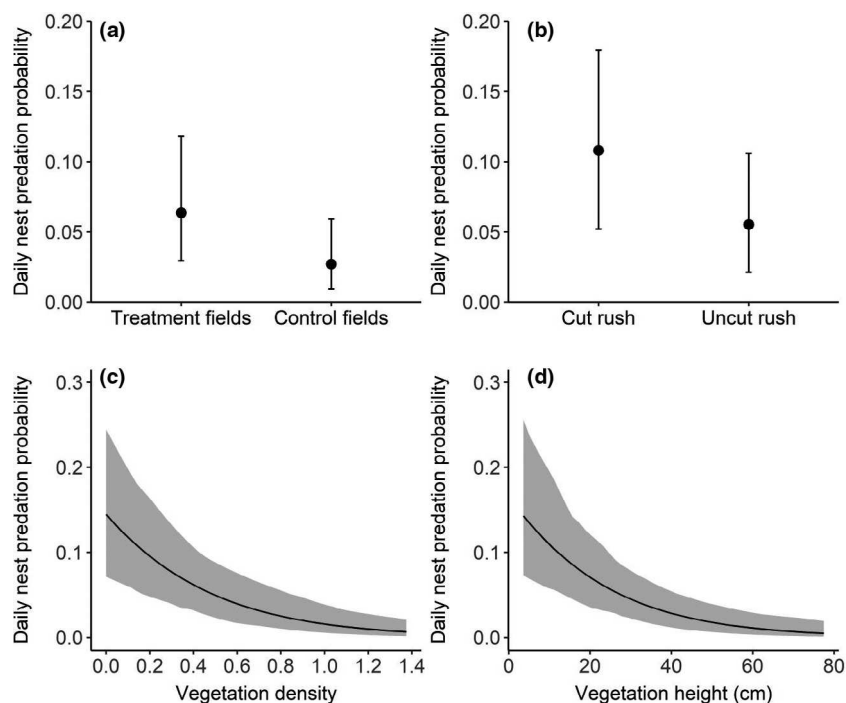


Figure 2 Predicted daily nest predation probability of artificial nests in relation to (a) treatment and control fields, (b) cut and uncut rush patches within treatment fields >4 ha, (c) vegetation density and, (d) vegetation height. In (a) and (b), points represent mean values and vertical lines represent bootstrap 95% confidence intervals from models i and ii presented in Table 2. In (c) and (d), shaded ribbons represent bootstrap 95% confidence intervals from models iii and iv presented in Table 2.

Associations between rush management and environmental variables

Environmental variables (woodland distance and boundary distance) around artificial nests in treatment and control fields were similar except that nests in treatment fields were surrounded by shorter, less dense vegetation and lower rush cover – although the difference in rush cover was marginally non-significant in the late breeding season (Supporting Information, Tables S2, S7 and Figure S3). Within treatment fields >4 ha, artificial nests located in cut rush patches were surrounded by significantly shorter, less dense vegetation and lower rush cover than nests in uncut rush patches (Supporting Information, Tables S8, S10, and Figure S3). Field level variables (field size and corvid density) did not differ significantly between treatment and control fields (Supporting Information, Tables S2 and S7).

Effect of vegetation structure on DPRs

DPRs were significantly higher for nests surrounded by less dense vegetation and shorter vegetation (vegetation density: $z = -5.061$, $P = 4.165 \times 10^{-7}$; vegetation height: $z = -4.483$, $P = 7.367 \times 10^{-6}$; Table 2; Supporting Information, Table S9, models iii and iv). Predicted DPRs and bootstrap 95% CIs across the observed range of vegetation density and vegetation height values are shown in Fig. 2c,d. No other predictor variables had a significant influence on DPRs (Table 2).

Discussion

When taking other environmental variables into account, artificial wader nests located in areas of rush that had been cut in accordance with AES prescriptions had DPRs that were approximately double those of nests in unmanaged areas of rush. This pattern was consistent when comparing nests in treatment and control fields, and when comparing patches of cut and uncut rush within treatment fields. Nests in cut rush were surrounded by shorter and less dense vegetation than nests in unmanaged rush, and the risk of nest predation increased as vegetation height and density decreased.

Artificial nests as indicators of predation risk

Artificial nest experiments require careful interpretation. The absence of parental nest defence could increase artificial nest predation rates (Berg, 1996), especially for species such as lapwing which exhibit strong nest defence, but less so for other waders such as curlew and snipe which exhibit less active nest defence and rely more on nest concealment (Cramp & Simmons, 1982; Vickery *et al.*, 2001). The absence of potential additional camouflage provided by the plumage of incubating adults could also increase artificial nest predation rates relative to actual nests (Troschianko *et al.*, 2016). Conversely, the lack of parental cues (nest visits for incubation, odour of an incubating adult) could reduce

predation rates of artificial nests compared to real nests (Berg, 1996). The deposition of human scent on artificial nests could also influence predation rates and counteract the lack of odour from incubating adults (Zanette, 2002), although our experimental design followed protocols to minimize human scent trails.

Nevertheless, artificial nest predation rates can provide useful information for addressing key questions including relative predation risk between experimental treatments and quantifying variation in predation risk along environmental gradients (Ibáñez-Álamo *et al.*, 2015). This is reinforced when artificial nests closely mimic real nests and attract similar predator guilds (Major & Kendal, 1996; Villard & Pärt, 2004). We believe that our experimental study meets these requirements for three reasons. First, artificial nests were in similar locations to those of snipe and curlew nests including in terms of their vegetation structure (Cramp & Simmons, 1982; Durant *et al.*, 2008; Supporting Information, Figure S2), with snipe and curlew frequently nesting in sward structures across a gradient from short and open swards to relatively tall and/or dense swards (Valkama *et al.*, 1998; Fisher & Walker, 2015; Wentworth, 2015; Zielonka *et al.*, 2019). Notably, we found real snipe and curlew nests during the 2019 fieldwork in rush patches that had been cut the previous winter, and these were found in the early breeding season before any substantial regrowth had occurred (L. Kelly, pers. obs). This demonstrates that some individuals nest in areas managed under AES rush cutting prescriptions despite higher predation rates of artificial nests in such locations. Second, our DPRs (treatment fields = 0.064 day^{-1} ; control fields = 0.027 day^{-1}) are within the range of those reported in studies of real snipe and curlew nests (MacDonald & Bolton, 2008). Finally, the high rate of mammalian predation concurs with research on real wader nests (MacDonald & Bolton, 2008).

Rush management and DPRs

Rush management following or emulating AES prescriptions can generate suitable habitat conditions for breeding waders in locations which would otherwise be unsuitable due to rush encroachment (Holton & Allcorn, 2006; Robson & Allcorn, 2006; Fisher & Walker, 2015; Douglas *et al.*, 2017). Yet, such rush management doubled DPRs compared to a control that lacked rush management, and these differences are attributable to rush management impacts on vegetation structure. These patterns probably arise due to shorter and sparser vegetation increasing the visibility of nests to predators (Whittingham & Evans, 2004) and mammalian predators are more likely to travel through less dense vegetation, increasing the detection of ground nests (Donald *et al.*, 2002). This is particularly pertinent for snipe and curlew as concealment is one of the primary forms of nest defence (Cramp & Simmons, 1982; Vickery *et al.*, 2001).

If breeding waders select areas of recently cut rush for nesting, then rush management that follows or emulates AES prescriptions appears likely to create an ecological trap due to higher nest predation rates in such locations. Such ecological

traps are plausible as it cannot be assumed that waders always select nesting locations that minimize the risk of nest predation (e.g. Hegyi & Sasvári, 1997) as many factors determine nest site choice (Blomqvist & Johansson, 1995; Smart *et al.*, 2013). Indeed, some waders will select nest sites that increase the probability of parents detecting, and thus escaping, approaching predators even though the risk of nest predation is greater at such sites (Whittingham & Evans, 2004; Gómez-Serrano & López-López, 2014). Further evidence for the possibility of ecological traps is provided by their occurrence in other ground-nesting farmland birds (e.g. nest site selection by western yellow wagtail *Motacilla flava*, Gilroy *et al.*, 2011). Ecological traps only arise when suboptimal habitats that reduce fitness are not selected against (Battin, 2004) and demonstration of an ecological trap in our study system thus requires robust data on nest site selection patterns. However, even if rush cutting does not create an ecological trap, it is clear that curlew and snipe do sometimes nest in cut rush and these individuals are likely to experience reduced breeding success that could reduce population growth rates. Indeed, wader population declines are driven largely by poor reproductive output (Roodbergen *et al.*, 2012) and the intended benefits of rush cutting may not occur. This situation is most likely to arise in wader species that nest across a wide range of sward structures, such as curlew and snipe (Valkama *et al.*, 1998; Fisher & Walker, 2015; Wentworth, 2015; Zielonka *et al.*, 2019).

Implications for managing upland sward structure and further research requirements

Our artificial nest experiment meets the conditions required to provide a reasonable indicator of environmental variation in DPRs (see 'Artificial nests as indicators of predation risk' section). It provides evidence that rush management through AES prescriptions could reduce breeding success for individuals nesting in those locations (especially snipe and to a lesser extent curlew due to these species' reliance on nest crypsis for reducing predation risk; although, curlew do exhibit some active nest defence; Cramp & Simmons, 1982; Vickery *et al.*, 2001). This could generate ecological traps but nest site selection studies combined with assessments of predation rates of real wader nests are required to demonstrate this. Achieving this will require a major investment in fieldwork over multiple seasons to achieve sufficient sample sizes, which is why we initially assessed patterns using the more rapid assessment that could be conducted using artificial nests. Our results demonstrate that cut rush is likely to increase nest predation rates, and thus a mosaic of cut and uncut rush will be required to generate heterogeneous swards that breeding waders require.

Future work should, however, explore solutions to the trade-off between the need to manage rush to generate open swards that improve foraging conditions, and the adverse impacts of such swards for breeding success, particularly for wader species which rely on nest concealment. It may also be important to confirm whether rush management provides

a universal benefit to species such as lapwing, which primarily nest in shorter swards (Milsom *et al.*, 2000). This research would require assessing (at a range of spatial scales) how different wader species respond to variation in the relative amounts of cut and uncut rush patches, and their spatial configuration.

Concern over the encroachment of rush and other rank vegetation in upland areas that support important breeding populations of waders and other ground-nesting birds (Silcock *et al.*, 2012; Ashby *et al.*, 2020) suggests that ongoing management of vegetation structure is required. Our study highlights the need, however, for investment in robust evaluation of AES prescriptions targeting vegetation structure in order to ensure that prescriptions balance trade-offs against all demographic factors influenced by vegetation structure, including nest predation risk.

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Authors' contributions

LAK and KLE conceived the ideas and designed the methodology with support from all authors; LAK collected the data; LAK analysed and interpreted the data with advice from KLE and DJTD; LAK and KLE led the writing. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

Data are archived in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.wpzgmsbm8>).

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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. Protocols for creating plasticine eggs.

Figure S2. Images of artificial and real wader nests.

Figure S3. Effects of rush management on vegetation structure metrics.

Table S1. Summaries of the Entry Level Stewardship agri-environment scheme prescriptions.

Table S2. Environmental variables in treatment and control fields.

Table S3. The number of fields and nests within each region, field type, and field size.

Table S4. The number of nests deployed in cut and uncut rush patches within treatment fields >4 ha.

Table S5. Social survey instrument for obtaining information on predator control at the study sites.

Table S6. Descriptions of the predictor variables included as different subsets in the models of daily nest predation rates.

Table S7. Results of generalized linear models and generalized linear mixed effects models exploring differences in environmental variables between treatment and control fields.

Table S8. Results of generalized linear models and generalized linear mixed effects models exploring differences in environmental variables of nests between uncut and cut rush patches within treatment fields >4 ha.

Table S9. Bootstrap 95% confidence intervals for parameter estimates in generalized linear mixed effects models investigating the effect of rush management and vegetation structure on daily nest predation rates for comparison with the profile 95% confidence intervals reported in Table 2.

Table S10. Environmental variables for nests located in cut and uncut rush patches within treatment fields >4 ha.