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Nest survival of threatened Eurasian Curlew (*Numenius arquata)* breeding at low densities across a human-modified landscape

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Running title

Nest survival of lowland curlew

Targeted management actions to boost key demographic rates can help to restore rare and localised populations but are increasingly required to stabilise or reverse declines of formerly common and widespread species. Many breeding wader populations across Europe are declining because of unsustainably low rates of productivity, and the conservation tools designed to boost wader breeding productivity have been most effectively used for semi-colonial species within protected areas. Targeted management for wader species that breed at low densities across human-modified landscapes, such as the rapidly declining Eurasian Curlew *Numenius arquata*, is likely to be more challenging. Here, we quantify variation in curlew nest survival in order to explore how management could be targeted to boost this key component of breeding productivity. Up to 80 pairs of Eurasian Curlew were monitored annually between 2019 and 2021 in eight locations across Breckland, eastern England, where nesting densities range from < 1 to ca.7 pairs km^{-2}. For 136 nests across grassland- and arable-dominated sites, the majority of failure (86%) was caused by (primarily nocturnal) predation and the mean probability of surviving incubation (PSI) for all hatched or predated nests (127) was ca. 0.25. Nest survival showed little annual or seasonal variation but did vary slightly between sites, however, this spatial variation was not clearly related to management conditions or nest concealment at these sites. Fencing to exclude mammalian nest predators can be effective for waders, but too few Eurasian Curlews currently nest within fenced areas in Breckland to produce observable effects. Fencing the few sites with high nesting densities could potentially double the number of chicks hatched each year within the study area, but landscape-scale actions to reduce predator impacts on nests and chicks are likely to be needed to maintain breeding numbers in the wider countryside.

Keywords: Conservation, Shorebird, Predator exclusion, Management

Human-driven biodiversity loss is one of the most critical global environmental problems for which mitigation actions are not currently sufficient (Cardinale *et al.* 2012, Tittensor *et al.* 2014, Mace *et al.* 2018). Conservative estimates suggest that the average rate of vertebrate species loss over the last century is up to 100 times higher than background rates (Ceballos *et al.* 2015). Unless slowed, this is likely to threaten ecosystem services and, ultimately, human wellbeing (Dirzo *et al.* 2014). To meet post-2020 targets set by the Convention on Biological Diversity, substantial changes to environmental policy across all levels of government are required (Mace *et al.* 2018, Lim 2021), as well as evidence-based, targeted management to restore and maintain biodiversity (Sutherland *et al.* 2004, Mazor *et al.* 2018).

Targeted management can potentially help to restore threatened populations by implementing specific actions capable of boosting a given demographic rate (usually productivity or survival) in locations and/or at times when those rates are low and could potentially be improved (Morrison *et al.* 2022). To inform this type of management, research is required to identify; 1) the demographic rates influencing population growth, 2) spatial and temporal variation in these demographic rates, 3) the drivers of that variation and, 4) the actions required to boost demographic rates (Johnson *et al.* 2020, Plard *et al.* 2020, Morrison *et al.* 2022).

This evidence-based approach to conservation has been used effectively to conserve several rare and localised species of birds and mammals (e.g. Stanbury *et al.* 2010, Simón *et al.* 2012, Nicoll *et al.* 2021), and is now increasingly required to reverse or stabilise population declines of once abundant and widespread species (McRae *et al.* 2017), including bees *Anthophila spp.* (Drossart & Gérard 2020), butterflies *Rhopalocera spp.* (Van Dyck *et al.* 2009), small mammals (e.g. Pettett *et al.* 2018, Coomber *et al.* 2021) and numerous species of ground-nesting birds (e.g. Silva *et al.* 2018, Assandri *et al.* 2019). However, successful attempts to restore populations occurring sparsely and at low densities have so far been limited (Vickery *et al.* 2004, Butler & Norris 2013, Pe'er *et al.* 2014), particularly in human-modified landscapes where space to restore habitats is constrained by other land-uses (e.g. Xun *et al.* 2017).

A group of species for which targeted management is increasingly required are waders *Charadrii spp.*, one of the world's most threatened but also most comprehensively monitored avian groups (Harrington *et al.* 2002, Amano *et al.* 2010). The relatively large body size and conspicuous behaviour of waders means that their populations are often well-monitored, in both breeding (e.g. Brlík *et al.* 2021, Harris *et al.* 2021) and non-breeding seasons (e.g. Frost *et al.* 2019, Nagy & Langendoen 2020), and individual-level studies of distribution and demography are common (e.g. Gill *et al.* 2019, Méndez *et al.* 2020, Verhoeven *et al.* 2020). Consequently, the multitude of complex, interrelated threats that act on waders (Sutherland *et al.* 2012), and the demographic rates influencing population growth, are often quite well understood (e.g. Macdonald & Bolton 2008, Roos *et al.* 2018, Cook *et al.* 2021).

In Europe, studies have linked wader population declines to changes in landscape composition (e.g. Wilson *et al.* 2014, Jóhannesdóttir *et al.* 2019), breeding habitat quality (e.g. Wilson *et al.* 2004, Smart *et al.* 2006), vegetation structure (e.g. Kentie *et al.* 2015) and land management practices (e.g. Verhulst *et al.* 2007, Exo *et al.* 2017), caused mainly by agricultural intensification (e.g. Kleijn *et al.* 2010) and afforestation (e.g. Douglas *et al.* 2014, Kaasiku *et al.* 2022, Pálsdóttir *et al.* 2022). These environmental changes have resulted in nests and chicks becoming more vulnerable to predation, which is thought to be the main driver of ongoing wader population declines across the region (Macdonald & Bolton 2008, Roodbergen *et al.* 2012, Roos *et al.* 2018). To compound threats further, human-induced climate change is rapidly altering environmental conditions, reducing habitat suitability (e.g. Smart *et al.* 2006) and the availability of invertebrate prey (e.g. Pearce-Higgins *et al.* 2010), as well as driving changes in wader breeding phenology for which the long-term impacts on demography are yet to be fully understood (Kentie *et al.* 2018, Alves *et al.* 2019, Gill *et al.* 2019). Warmer, drier springs are also advancing mowing and grazing dates such that they can now coincide with incubation and chick-rearing in agricultural landscapes (Schroeder *et al.* 2012), and effective management of grassland breeding habitat is predicted to become more challenging in the face of increasingly severe drought and flood events (Joyce *et al.* 2016).

In response to wader declines across Europe, considerable effort has been made to design, trial and deploy targeted management actions with the aim of boosting wader breeding productivity (Franks *et al.* 2018, Jellesmark *et al.* 2021, Laidlaw *et al.* 2021). These actions include habitat management to increase the suitability of breeding sites by altering conditions such as hydrology (e.g. Eglington *et al.* 2008), vegetation structure (e.g. Laidlaw *et al.* 2017) and timing of grassland management practices (e.g. Verhulst *et al.* 2007), controlling predator activity through targeted culling (e.g. Bolton *et al.* 2007, Smith *et al.* 2010) and/or exclusion fencing (e.g. Smith *et al.* 2011, Malpas *et al.* 2013), and headstarting (raising eggs and chicks in captivity through the early weeks of life) (e.g. Pain *et al.* 2018, Laidlaw *et al*. 2021).

These tools target the nesting, incubation and chick-rearing stages of the breeding cycle and have helped to increase breeding productivity in some threatened wader populations, particularly those restricted to nature reserves or other protected areas (Smart *et al.* 2014, Jellesmark *et al.* 2021). In these areas, land-use and management are usually aimed at biodiversity and conservation goals and, as breeding wader densities tend to be higher in nature reserves (Silva-Monteiro *et al.* 2021), targeted management in these areas can impact relatively large numbers of birds in a relatively small area. However, not all threatened wader species breed in large numbers within nature reserves or protected areas, and some breed at much lower densities across human-modified landscapes (Silva-Monteiro *et al.* 2021). Targeted management for such species is likely to be challenging, particularly as the interventions outlined above have not yet been demonstrated to work effectively and sustainably outwith protected areas.

The globally Near-Threatened Eurasian Curlew *Numenius arquata* (hereafter, Curlew) (IUCN 2022) was once an abundant and widespread species across much of western, northern and eastern Europe. However, in recent decades the number of breeding pairs has declined steeply in these regions (Keller *et al.* 2020) with some populations already on the verge of extirpation (e.g. O'Donoghue 2019). These declines have been attributed to low rates of breeding productivity (Berg 1992, Valkama & Currie 1999, Johnstone 2007, Zielonka *et al.* 2020), likely driven by the same mechanisms influencing productivity in other breeding wader populations across western Europe (Fletcher *et al.* 2010, Douglas *et al.* 2014, Franks *et al.* 2017). These population declines, alongside the recent history of extinction among related species in the Numeniini tribe (Pearce-Higgins *et al.* 2017), mean that conservation interventions are urgently needed to prevent the further extirpation of breeding populations. A greater understanding of how key components of Curlew breeding productivity vary in space and time is required to enable these interventions to be targeted effectively.

Here, we quantify spatial and temporal variation in nest survival, assess potential drivers of this variation, and identify likely nest predators and other causes of nest failure for Curlew breeding at low densities across a human-modified landscape. We use these findings to explore opportunities for targeting management to boost nest survival in such species and landscapes, and the types of actions likely to be required.

METHODS

Study area

The study took place in Breckland, a 1019 km^2 region of eastern England, where breeding Curlew are thought to be stable or possibly increasing in abundance and range (Balmer *et al.* 2013). Traditionally, the region comprised large areas of semi-natural fallow land, disturbed and maintained over time by fluctuating patterns of livestock and rabbit grazing and low intensity, rotational farming methods (Dolman *et al.* 2010). However, wide-scale land-use change has transformed the Breckland landscape into a mosaic of habitats dominated mainly by commercial forestry and arable fields, interspersed with remaining patches of semi-natural grassland (Dolman *et al.* 2010). Landowners and stakeholders in the region include private estates managed for agriculture, livestock farming, shooting and equine breeding, Forestry England, the Ministry of Defence and conservation NGOs.

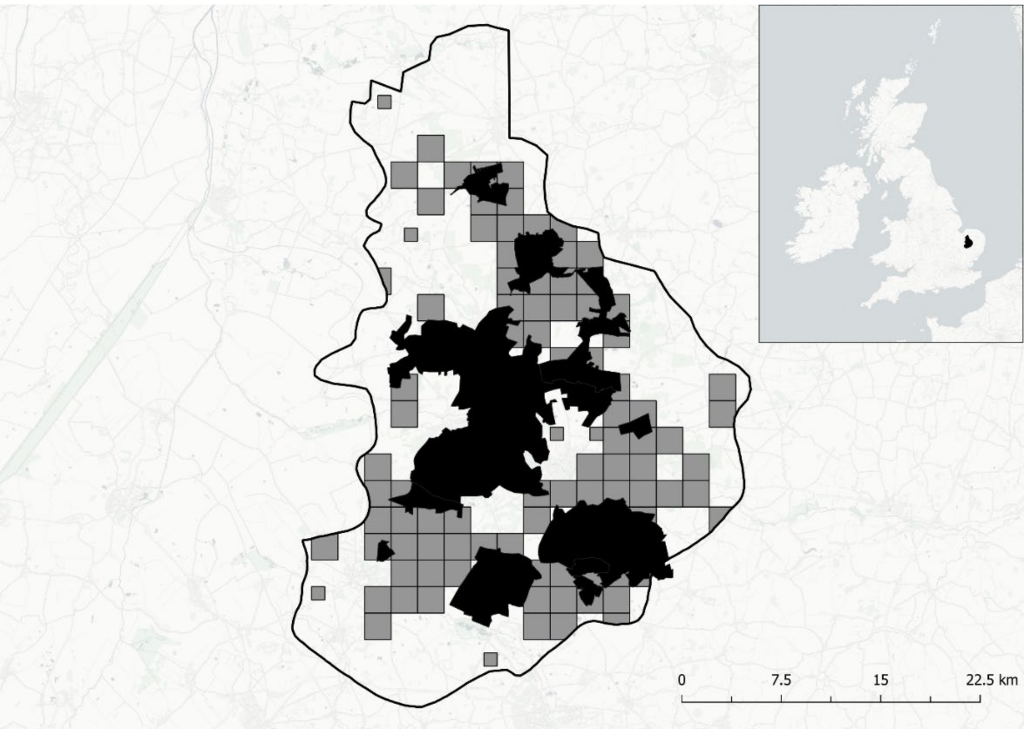

Figure 1: Areas within Breckland (outlined in grey) in which Eurasian Curlew have been reported as possible, probable or confirmed breeding (grey blocks) in national bird monitoring schemes (Balmer et al. 2013, Harris et al. 2021) over the last decade, and the study area (black polygons) within which breeding curlew were monitored between 2019 and 2021. Inset indicates the location of Breckland within the UK.

Permission to monitor breeding Curlew was granted at eight sites across Breckland; the entirety of two private estates, two grassland sites within two other private estates, an arable farm, a military training area, an RAF base and the entire area managed by Forestry England (Fig. 1). All eight sites were monitored during 2019 and 2021, but only four sites were monitored during 2020, when access restrictions were tightened due to the Covid-19 pandemic.

The eight study sites were dominated by arable fields or semi-natural grassland, which were maintained by mowing or livestock grazing. Five sites contained ground-disturbance plots; ca.4 ha areas of semi-natural grassland, recently rotovated to create bare ground to to encourage breeding Stone Curlew *Burhinus oedicnemus* (Hawkes *et al.* 2019, 2021). Public access was restricted at all sites and some areas within grassland sites were enclosed by fencing. Fences were in place to prevent wild mammalian herbivores (e.g. deer spp. *Cervidae* or European Brown Hare *Lepus europaeus*) from penetrating boundaries or to restrict human access to hazardous areas on military sites, and were also likely to act as barriers to mammalian predators (e.g. Red Fox *Vulpes vulpes* and European Badger *Meles meles*). Most grassland sites were either unfenced or partially or fully enclosed by livestock fences (large-mesh or non-electrified stranded fence, mostly less than 2 m high), which were unlikely to act as a barrier to mammalian predators (White & Hirons 2019). Nests were therefore classified as fenced if they were within areas that were fully enclosed by fencing with mesh sufficiently small to prevent access by foxes and badgers, at least 2 m in height, with no obvious access points in or under the fence line.

Nest finding and monitoring

In 2019 and 2021, Curlew pairs were located between late-March and mid-April by approaching all open areas within each site to at least 100 m on foot or by vehicle. All areas in which a curlew pair was located were revisited throughout the season to classify pairs as possible, probable or confirmed breeders, using breeding evidence codes (see Supporting Information Table S1). Nests, including re-lays, were found between mid-April and mid-June by searching study areas for incubating birds and observing incubating birds returning to nests. In 2020, surveys and nest monitoring did not commence until late-May due to the Covid-19 pandemic.

The location of each nest was recorded with a GPS device, and an iButton temperature logger was deployed in the nest lining (Maxim Integrated Products Ltd, San Jose, CA, USA), set to record every 10 minutes and covered with tape to prevent the metallic surface from reflecting. Predicted hatch dates of nests found on a clutch of one or two eggs, and thus likely during laying, were estimated by back-calculating the lay date of first egg (assuming that one egg was laid every 1.5 days (Grant 1996) and adding 34 days (average laying period plus average incubation period (Grant 1996)). All eggs in clutches of three to five were weighed and measured to enable laying and hatching dates to be predicted, following Grant (1996).

Nests were visited a minimum of every ten days, and daily from three days prior to the predicted hatch date, to determine their status and outcome. Where possible, nest status was checked remotely to reduce disturbance. Nests were recorded as successful if at least one egg hatched. Hatched eggs were confirmed by the presence of empty eggshells, or at least one newly hatched chick, in or around the nest scrape. Chicks were observed in all successful nests, so hatch date was recorded as the first date on which at least one newly hatched chick was found in the nest. Nests were recorded as failed if there were obvious signs of predation, mowing, trampling or abandonment or, if they were found empty before the estimated hatch date with no eggshell fragments in the nest that would have indicated successful hatching (Green *et al.* 1987). Nests were not visited in cold or wet weather conditions and no obvious tracks were left around the nest during nest visits.

For nests that did not hatch, time and date of nest failure was determined by a sudden and sustained drop in temperature recorded on the iButton temperature logger (44 out of 84 predated nests). For nests that failed prior to full incubation, temperatures in the nest were not stable enough for the loggers to detect a sudden drop at the point of failure and, in some cases, a build-up of nest lining resulted in the logger being too deep in the nest scrape to detect a stable incubation temperature, which also meant that time of failure could not be detected. In these cases, when iButton temperature loggers failed to give reliable results (40 out of 84 predated nests), date of nest failure was calculated as the mid-point between the date that the nest was last observed intact and the date on which the nest was recorded as failed (mean ± sd gap = 5.8 ± 2.3 days).

Nesting conditions

Management conditions for each nest were categorised as arable crop, fenced grassland, unfenced grassland or ground-disturbance plot, as defined above. Nest concealment was recorded on the day on which each nest was located, by measuring the height of the tallest sward at four opposite points directly around the edge of the nest scrape and calculating the mean.

Statistical analyses

Variation in daily nest survival rates (DSR) were explored in Mayfield's logistic exposure models with a binomial error term, in which success (hatched and failed) was modelled with exposure days (number of days from find date to date of hatch or known (from temperature loggers) or estimated (from check midpoints) failure) as the binomial numerator (Shaffer 2004). Nine nests that failed for reasons other than predation were excluded from the analysis so we could focus on predation, the main driver of wader population declines across Europe (Macdonald & Bolton 2008, Roodbergen et al. 2012). Removing these nests made very little difference to our models results (Table S2).

To avoid model overfitting, a two-step approach was taken. The initial model assessed spatial and temporal variation in DSR of all nests monitored during the study period by including site, year and their interaction, lay date, year and their interaction and nest age, as fixed factors in a GLM (Table 1, model i). The subsequent model assessed potential drivers of any spatial variation by including management conditions that varied across these sites (arable, fenced grassland, unfenced grassland or ground-disturbance plot), nest concealment and their interaction and nest age as fixed effects, and site as a random intercept (to account for non-independence of nests from the same site) in a GLMM (Table 1, model ii). Most nests were found soon after laying (mean ± sd nest age on day of finding = 9.9 ± 7.8 days; equivalent to 6 days of egg laying plus 3-4 days of incubation for a clutch of four) (Fig. S1-S3). We ran models excluding older nests (found at 14 days from onset of laying) to explore their influence on model findings, but results did not differ from models including nests of all ages (Table S3).

Continuous variables used in model i and ii (lay date, nest concealment and nest age) were scaled and centred to have a mean of zero and a standard deviation of 1. Non-significant ($P > 0.05$) interaction terms were sequentially removed from models, and inference was made from the maximum model retaining all main effects. All models were run in R (v 4.2.1) using the lme4 package (Bates et al. 2015).

Predicted DSRs were extracted from models and transformed to probability of nest survival over the incubation period (PSI) by raising DSR to the power of 34 (the average Curlew incubation period (days) from the first egg laid, Grant 1996). 95% confidence intervals were calculated using the Delta method (Ver Hoef 2012).

As the proportion of monitored nests within fenced areas was low, a power analysis, using data from Malpas *et al.* (2013) on the difference in wader nest survival in fenced and unfenced areas, was also conducted to assess how many nests would need to be enclosed with predator exclusion fencing to detect a statistically significant effect of fencing and to estimate the effect size required to detect an observable effect of fencing with the number of fenced nests monitored during our study (Table S4; Fig. S4).

To assess whether predation events were more likely during night or day, the frequency of observed night/day predation events was compared to the number of night/day hours summed across all monitored nest-days, to account for variation in day length through the season, using a 2 x 2 Fisher's Exact test.

Table 1: Description of the model variables used to explain variation in daily nest survival rate (DSR) of curlew nests found across Breckland between 2019 and 2021. All variables included in interaction terms are also included as main effects in both models.

Type	**Variable**	**Distribution (link)/variable range of values**	**Explanation**
Response	Daily nest survival rate (DSR)	Binomial (logit)	Nest outcome (hatched/failed) accounting for exposure days.
Explanatory	Site	8 sites	Nest site identity
	Year	2019, 2020, 2021	Years in which nests were monitored
	Lay Date (scaled and centred)	Day 1 – 101	Lay date in March days (no. of days from 1st March)
	Management condition	4 management conditions	Arable, fenced grassland, unfenced grassland or ground-disturbance plot

	Nest concealment (scaled and centred)	0 – 57 cm	Mean of four sward height measurements (in cm) taken around the nest scrape.
	Nest age (scaled and centred)	1 – 33 days	Day of the incubation period on which a nest was found.

Model	**Response**		
i	DSR		Site*Year + Lay Date*Year + Nest Age
ii	DSR		Sward Height*Management condition + Nest Age + (1|Site)

RESULTS

In 2019 and 2021, 67 and 80 pairs of Curlew, respectively, were found and monitored across the Breckland study area. The density of pairs classified as probable or confirmed breeders within six of the eight study sites (which comprised 95% of the surveyed area) ranged between 0.17 and 0.72 pairs per km^2, while two other sites which comprised only 5% of the surveyed area hosted densities of between 3.3 and 7.4 pairs per km^2 (at least 47% of the probable or confirmed breeding pairs monitored annually; Fig. 2). Only 21 pairs of Curlew were classified as probable or confirmed breeders in 2020 as fieldwork was limited to late in the breeding season, due to restrictions imposed as a result of the Covid-19 pandemic.

A total of 136 Curlew nests, comprising 471 eggs, were monitored across Breckland during the study period, with the majority being found in unfenced grassland areas. From these 136 nests, 185 chicks hatched from 52 nests and 84 nests failed (Fig. S5). Only one site out of eight failed to hatch any chicks during the study period (Fig. S5a) and chicks hatched in all four management conditions (Fig. S5b). Predation accounted for 86% of nest failures and other nests failed due to abandonment during laying (*n* = 3), trampling by cattle (*n* = 1) and destruction through mowing or other mechanised farming activities (*n* = 5).

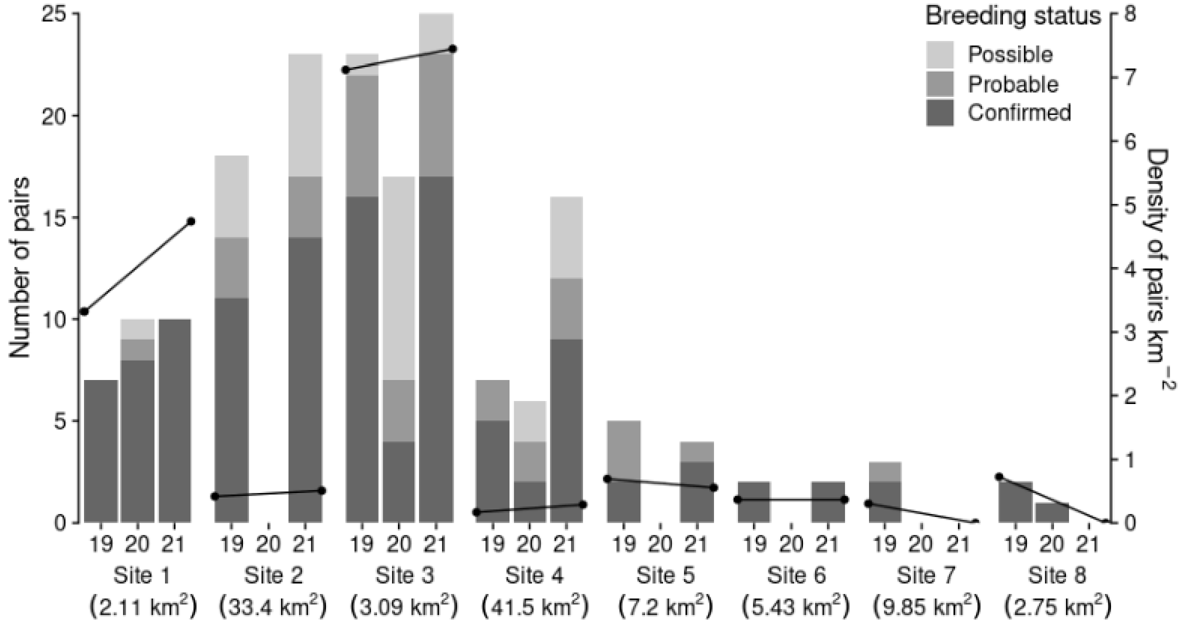

Figure 2: The abundance (bars) and density (points) of possible, probable and confirmed breeding pairs of Eurasian Curlew recorded annually across surveyed areas within eight Breckland study sites, between 2019 and 2021. Density figures for 2020 are excluded due to reduced survey effort. Breeding status categories defined using BTO breeding codes (Table S1)).

The mean ± 95% CI probability of surviving incubation (PSI) of the 127 hatched or predated Curlew nests monitored across Breckland was 0.2488 (± 0.1786 - 0.3372). There was evidence of variation among sites (Table 2), with PSI being greater at site 1 (15/30 nests predated) than site 2 (24/30 nests predated) (Fig. 3) and being particularly low at site 5, where none of the six nests monitored during the study period hatched successfully (Fig. 3). Mean PSI did not vary significantly through the season, between years or with nest age (Table 2).

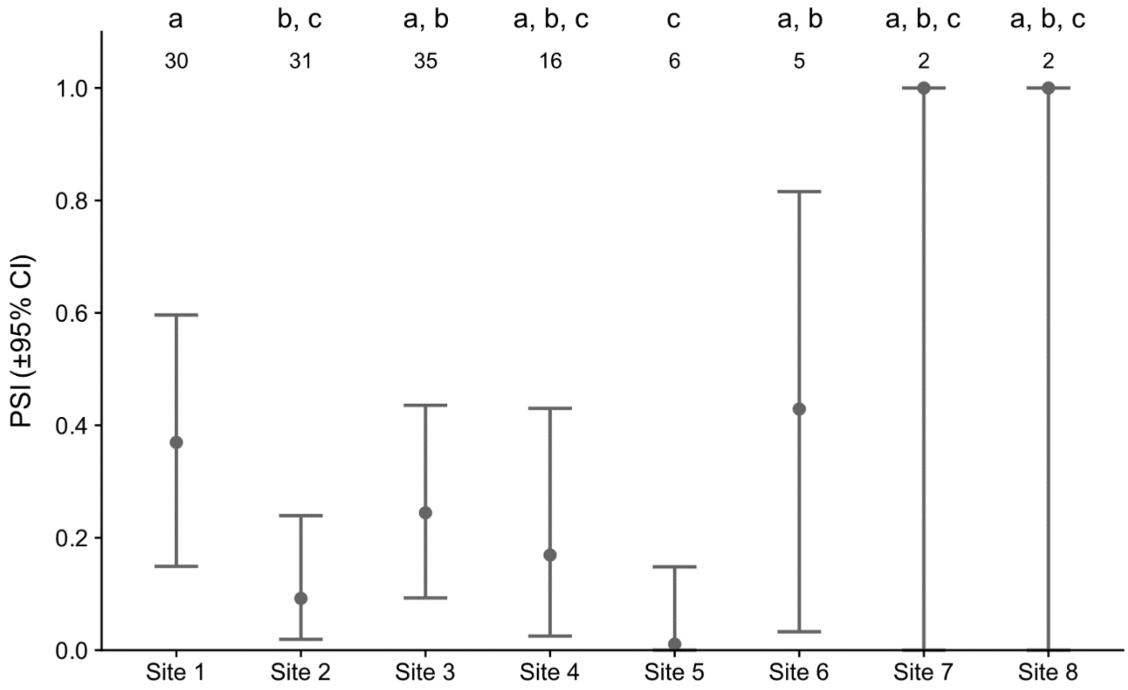

Figure 3: Mean predicted probability of a Eurasian Curlew nest surviving incubation (PSI), and the number of nests monitored (numbers above bars), at eight Breckland study sites, between 2019 and 2021. Sites that do not share a common letter differed significantly (Table 2).

Nest survival was similar in unfenced grassland, fenced grassland, arable fields or ground-disturbance plots, and across levels of nest concealment (Table 2), so the spatial variation in nest survival was not the result of variation in management conditions or nest concealment between sites. Power analysis suggest that 25 nests of the 102 nests found within grassland (fenced and unfenced) would need to have been enclosed by fencing to detect an effect of fencing on nest survival comparable to Malpas *et al*. (2013) (Table S4; Fig. S4). With our sample of nine fenced nests, an effect of fencing would have only been observed had the effect size been > 0.9 (Fig. S4).

Table 2: Results of Mayfield's logistic exposure models of spatial and temporal variation in daily nest survival rates (DSR) (model i) and potential drivers of variation in DSR (model ii) of Curlew nests monitored in Breckland between 2019 and 2021 (see Table 1 for model details). Significant predictors of DSR ($P < 0.05$) are highlighted in bold.

Model	Fixed effect	Chi sq.	Df	*p*
i (Spatial and temporal)	Year	4.037	2	0.132
	Lay date	0.039	1	0.842
	Nest age	0.644	1	0.422
	Site	**17.665**	**7**	**0.014**
	Pseudo R^2 = 0.17			
ii (Drivers)	Nest concealment	0.141	1	0.707
	Management condition	5.597	3	0.133
	Nest age	0.569	1	0.450
	Pseudo R2 = 0.09			

Time of nest failure was extracted from temperature loggers for 44 of the 84 predated nests; 36 nests were predated during the night and eight during the day (Fig. 4). Relative to the ratio of night/day hours monitored (summed across each nest-day monitored; ratio 0.50) predation occurred significantly more often at night than expected by chance (Fisher's Exact test, *P* < 0.01).

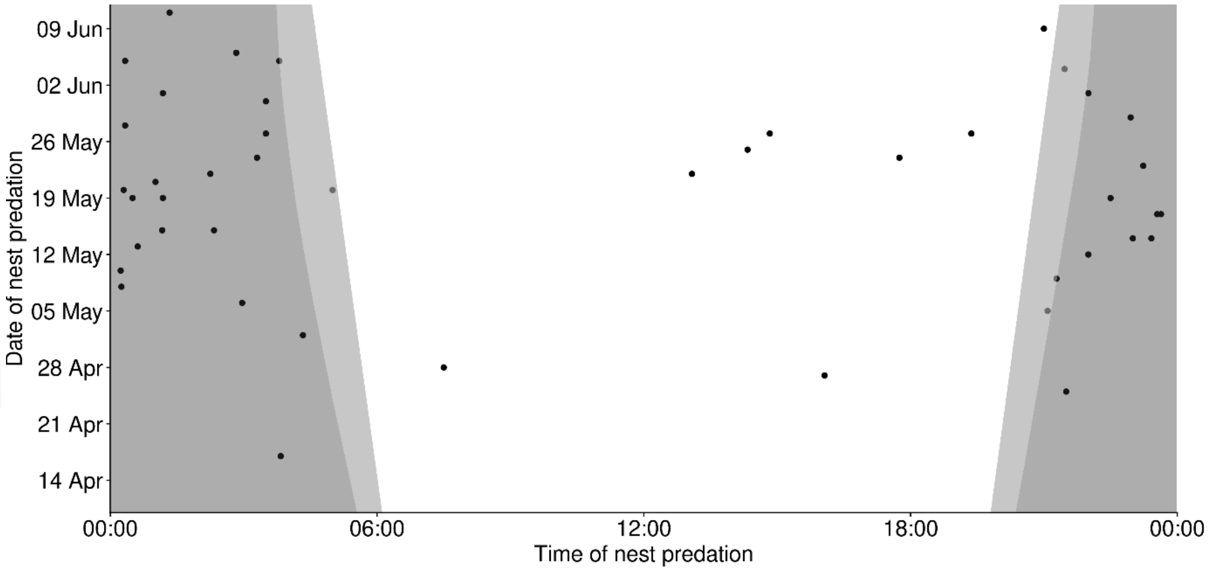

Figure 4: Date and time of 44 Eurasian Curlew nest predation events between 2019 and 2021 in Breckland, eastern England. Shaded area indicates nocturnal (dark grey) and crepuscular (light grey) periods.

DISCUSSION

Breeding Curlew were sparsely distributed across the majority of the Breckland study area, with densities at over 95% of the study area being below one pair per km^2. Nests were found in conditions ranging from bare ground on arable fields to tall (ca. 50 cm) grass in silage fields, but the probability of a Curlew nest surviving to hatch was consistently low (ca. 0.25). A small amount of variation in nest survival was observed between sites (Fig. 3), but this could not be explained by management conditions or levels of nest concealment. As the great majority (86%) of nests failed because of predation, which primarily occurred at night (indicative of mammalian predation), boosting hatching rates of Curlew nests is likely to require actions to reduce mammalian predator impact across the Breckland landscape.

A conservation tool that is commonly deployed to reduce predation on ground-nesting birds' nests is predator-exclusion fencing (Smith *et al.* 2011). Fences have the potential to result in ca. two-fold increases in wader hatching rates (Malpas et al. 2013) and, as they have already been used to boost hatching rates of some threatened wader populations in western Europe, including Black-tailed Godwit *Limosa limosa* (Verhoeven *et al.* 2022) and Northern Lapwing *Vanellus vanellus* (hereafter Lapwing) (Malpas *et al.* 2013, Verhoeven *et al.* 2022), it seems likely that they could also be effective at boosting Curlew nest survival.

In Breckland, fences were not deployed to protect Curlew nests, but a small number of pairs nested within fenced areas (too few to detect an observable effect of fencing on nest survival). Increasing the number of nests enclosed by predator fencing in Breckland could potentially be achieved by deploying temporary electric fencing to protect individual nests, but the substantial efforts required to locate nests and erect and maintain fencing (throughout the season and across years due to the lack of temporal variation in nest survival), means that this is unlikely to be a feasible approach, especially in areas where Curlews breed at very low densities.

One way in which targeted deployment of fencing could potentially be effective might be to enclose ground-disturbance plots. These areas are often used by nesting Curlew (Zielonka *et al.* 2020) and, although we found curlew nest survival to be just as low under these management conditions as elsewhere, they are generally located in areas in which land-use is sympathetic to ground-nesting birds (e.g., areas under higher tier agri-environment schemes; Evans & Green 2007, Chamberlain *et al.* 2009), potentially making fencing more feasible. Plot-level fencing could also be deployed at the start of the season, without the need to locate nests, and may benefit other ground-nesting species such as Stone Curlew (Hawkes *et al.* 2021) and Lapwing (Chamberlain *et al.* 2009, Rickenbach *et al.* 2011). However, these plots currently only support ca. 4-7 breeding pairs of Curlew in our study area, and thus the impact of such measures for Curlew is likely to be quite modest.

Alternatively, permanent barrier fences could be deployed along the boundary of sites supporting high densities of nesting curlew. Fencing the combined boundary length of the eight Breckland study sites that support ca. 80 Curlew pairs annually would require ca.185 km of fencing, but we found ca. 45% of those Curlew to breed in just two of those sites, with a combined boundary length of only 14 km. Assuming such fences would be as effective as described elsewhere (Malpas *et al.* 2013), enclosing these two high-density sites with permanent barrier fencing could potentially boost the total number of chicks hatched in our Breckland study area by ca. 44-67% (ca. 88 – 94 additional chicks hatched) per year.

Targeting actions to reduce predator impacts, such as fencing high density breeding sites and ground-disturbance plots has the potential to provide a relatively efficient solution to boosting Curlew nest survival. However, high-density Curlew breeding sites are becoming very rare, particularly in the English southern lowlands (Colwell *et al.* 2020), and so opportunities to target sites with potential to contribute substantial improvements in nest survival are increasingly limited. Failure to identify and protect remaining Curlew populations effectively will likely increase the need for intensive and expensive actions such as headstarting (raising eggs and chicks in captivity through the pre-fledging period), which is already being deployed to boost Curlew productivity in southern England (Colwell *et al.* 2020).

To sustainably maintain and recover Curlew populations in the wider landscape, in Breckland and elsewhere across the breeding range, actions outwith fenced areas are also likely to be required. Lethal control of foxes, the main mammalian nest predator in the region (Zielonka *et al.* 2020), occurs across much of the Breckland study area, and it is possible that variation in the intensity of lethal control between study sites could contribute to the (small amount of) spatial variation in Curlew nest survival. The impact of lethal control on breeding success of ground-nesting birds can vary substantially between sites (Bolton *et al.* 2007, Porteus *et al.* 2019), and may be influenced by the predator communities present at those locations and times (Bolton *et al.* 2007, Mason *et al.* 2018). Consequently, the contribution of lethal control to maintaining and recovering breeding Curlew populations is currently unknown, and the need for improved understanding of predator behaviour and population dynamics remains urgent (Laidlaw *et al.* 2021).

A greater understanding of the factors influencing nest survival and the causes of nest failure elsewhere across the species' range will also be important so that actions can be targeted across broader spatial scales. For example, nest concealment is a poor predictor of Curlew nest survival in Breckland but vegetation in this region is generally short due to the relatively dry conditions (Dolman *et al.* 2010). Elsewhere, vegetation may be considerably taller due to higher spring rainfall and more intensively managed grasslands, potentially resulting in increased nest concealment and a subsequent boost to nest survival. Landscapes are also likely to differ between (and within) regions in which Curlews breed, so exploring how factors such as landscape composition and configuration (e.g. Jóhannesdóttir *et al.* 2019) influence Curlew distribution and success is likely to help inform effective targeting of actions to boost hatching success in the wider landscape.

Finally, establishment of collaborative stakeholder networks, and integration of evidence-based, Curlew-friendly policies into agri-environment schemes are likely to be of particular importance in maintaining breeding populations, given their generally sparse, low-density distribution. Working with stakeholders to trial management actions for Curlew (e.g., fencing, headstarting, lethal control) will clearly be important part of this, but any actions to boost nest survival should be targeted in areas likely to support chick growth and survival, and further research is required to understand the land management actions that can create and maintain such conditions at different scales.

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Data Availability Statement

The raw data used in this study are available here: osf.io/5ckjm

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SUPPORTING INFORMATION

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

Table S1: Breeding evidence categories used to classify curlews detected on surveys as non-breeding, or possible, probably or confirmed breeding.

Table S2: Results of Mayfield's logistic exposure models of daily nest survival rates (DSR) of all curlew nests (including those mown, trampled and abandoned) monitored in Breckland between 2019 and 2021.

Table S3: Results of Mayfield's logistic exposure models of daily nest survival rates (DSR) of curlew nests (< 14 days old) monitored in Breckland between 2019 and 2021.

Table S4: Sample sizes and standard deviations extracted from Malpas et al. (2013), used to calculate the effect size between the nest survival rates inside and outside of predator exclusion fencing.

Figure S1: Age structure of curlew nests found in each of the four management conditions in Breckland.

Figure S2: Age structure of curlew nests found in each of the eight sites in Breckland.

Figure S3: Age structure of curlew nests found in each of the three study years.

Figure S4: The number of nests required to be enclosed by predator exclusion fencing to detect different effect sizes of fencing on nest survival.

Figure S5: The number of curlew nests that were hatched, predated, destroyed, trampled or abandoned and the number of hatched chicks at each site and in different management conditions in Breckland, between 2019 and 2021.