

Scenarios of habitat management options to reduce predator impacts on nesting waders

Rebecca A. Laidlaw^{*1}, Jennifer Smart², Mark A. Smart³ and Jennifer A. Gill¹

¹School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich NR4 7TJ, UK; ²RSPB Centre for Conservation Science, Royal Society for the Protection of Birds, The Lodge, Sandy SG19 2DL, UK; and

³Royal Society for the Protection of Birds, The Lodge, Sandy SG19 2DL, UK

Summary

1. Wetland ecosystems throughout the world are threatened by drainage and intensification of agriculture. Consequently, many wetland species of conservation concern are now restricted to fewer and smaller sites, and maintaining these species often requires intensive habitat management.

2. In Western Europe, breeding wader populations have declined severely as a result of wetland degradation, but very high levels of predation on eggs and chicks are now preventing population recovery. Wet grassland management for breeding waders has focussed on providing suitable nesting habitats, but the potential for management of landscape features to influence predation rates remains largely unknown.

3. Using a 7-year study of breeding lapwing *Vanellus vanellus* and redshank *Tringa totanus* we first identify features that influence nest predation, and then use this information to compare the magnitude of change in nest predation rates that could potentially result from future landscape management scenarios.

4. As lapwing nest predation rates are higher (i) in fields further from patches of tall vegetation, (ii) close (<50 m) to field edges in wet fields, (iii) further from field edges in dry fields and (iv) in areas of low lapwing nesting density, we modelled a series of realistic scenarios in which the area of tall vegetation and the extent and distribution of surface water were varied across the reserve, to quantify the magnitude of change in nest predation rate that could potentially have been achieved through management.

5. Modelled scenarios of changes in surface water and area of tall vegetation indicated that reduced surface flooding combined with removal of tall vegetation could result in significant increases in lapwing nest predation rates in areas with low nesting densities and nests in field centres. By contrast, a ~20% reduction in nest predation, corresponding to ~100 more chicks hatching per year, is predicted in scenarios with expansion of tall vegetation in areas with high lapwing nest density and nests close to field edges.

6. *Synthesis and applications.* These management scenarios suggest that, for breeding waders in wet grassland landscapes, creating areas of tall vegetation and concentrating surface flooding (to encourage high nesting densities and influence nesting distribution) can potentially help to reduce the unsustainably high levels of nest predation that are preventing population recovery.

Key-words: conservation management, farmland birds, lapwing *Vanellus vanellus*, nesting, predator, predator–prey interactions, redshank *Tringa totanus*, shorebirds, wader, wet grassland

*Correspondence author. E-mail: r.laidlaw@uea.ac.uk

We dedicate this paper to the memory of Ralph Loughlin, warden at Berney Marshes from April 1989 to November 2015.

Introduction

The expansion and intensification of agriculture throughout the developed world has resulted in increasingly homogenous landscapes of cropland and pasture replacing natural grasslands, wetlands and forests (Chamberlain *et al.* 2000; Goldewijk 2001). Consequently, many species of conservation concern are increasingly restricted to areas managed specifically to provide the required environmental conditions (Ausden & Hirons 2002; Smart *et al.* 2008; O'Brien & Wilson 2011; Geldmann *et al.* 2013; Brooks, Fonseca & Rodrigues 2016). However, even within such managed environments, maintaining sustainable populations and facilitating re-establishment of populations beyond protected areas can be very challenging (Roodbergen, van der Werf & Hötter 2012).

A particularly complex conservation issue is managing the influence of predators that can be a major constraint on population sustainability and recovery in species of conservation concern (MacDonald & Bolton 2008a; Redpath *et al.* 2013). In western Europe, the impacts of generalist predators such as foxes and corvids appear to have increased in recent decades, perhaps as a result of declines in predator control associated with land use changes (Tapper 1992; Gregory & Marchant 1996; Reynolds & Tapper 1996). Reducing impacts of predation is rarely straightforward (Bolton *et al.* 2007; Bodey *et al.* 2010; Malpas *et al.* 2013), and several studies have shown that control of one predator species can result in increased impacts of others (Conner, Rutledge & Smith 2010; Brook, Johnson & Ritchie 2012; Ellis-Felege *et al.* 2012). Understanding the influence of landscape and habitat management on predator activity may help to address this issue.

Conservation management tends to focus on providing resources for target species, such as food or nesting sites, but much less attention has been given to management of habitat features that may influence predator impacts. For example, predation rates on ground-nesting birds are often lower in more complex landscapes (Whittingham, Percival & Brown 2001; Lecomte *et al.* 2008; Schekkerman, Teunissen & Oosterveld 2008), but incorporating these relationships within management plans requires identification of the specific habitat features that influence predator activity. The scale at which these relationships operate is also difficult to determine, with local-scale management often aiming to influence the distribution and demography of species distributed over larger spatial scales.

In the UK, over 40% of wet grasslands have been lost to drainage since the early twentieth century, with only 300 000 ha remaining (Benstead *et al.* 1997). Commercially managed wet grasslands typically have intensive drainage and grazing, and support very low levels of biodiversity (Wilson, Ausden & Milsom 2004). Conservation management to reinstate and maintain high water levels and short vegetation in wet grasslands has been very successful at attracting breeding waders (Eglington *et al.* 2008; Fisher *et al.* 2011), particularly on nature reserves (Ausden &

Hirons 2002; Smart *et al.* 2008; O'Brien & Wilson 2011). However, lowland breeding waders have been declining dramatically (Wilson *et al.* 2005), and the impact of predation on the reproductive stage is a key factor limiting population recovery (MacDonald & Bolton 2008a; Schekkerman, Teunissen & Oosterveld 2009; Malpas *et al.* 2013).

Previous studies have suggested that breeding wader distribution and success can be influenced by effects of landscape structure on predator distribution and activity (Wilson *et al.* 2014). A key mechanism through which landscape management can potentially influence predator distribution is by altering the relative abundance and distribution of prey resources. Red foxes *Vulpes vulpes* are typically the main predator of wader nests (MacDonald & Bolton 2008a), but the main prey of this generalist predator is small mammals (Forman 2005). In wet grassland landscapes managed for breeding waders, small mammals are largely restricted to areas of tall vegetation in field verges (Laidlaw *et al.* 2013), and lapwing nests closer to tall vegetation have lower predation rates (Laidlaw *et al.* 2015). Maintaining large areas of short vegetation for breeding waders may therefore reduce alternative sources of prey for foxes and increase their impact on breeding waders. In addition, the high water levels and surface flooding that attract breeding waders (Smart *et al.* 2006; Eglington *et al.* 2008; Fisher *et al.* 2011) and provide invertebrate prey for wader chicks (Eglington *et al.* 2010) may also constrain mammalian predators to drier, more accessible locations. As breeding lapwing can show highly effective anti-predator group mobbing behaviour, particularly against avian predators such as crows (Elliot 1985a) and nocturnal predators such as foxes (Seymour *et al.* 2003), the effectiveness of habitat management may also vary in relation to nesting densities.

Management of wet grassland landscapes can potentially be adapted to alter both the availability of alternative prey resources (areas of tall vegetation that support small mammals) for predators and surface water levels to influence the ease with which nests can be accessed by terrestrial predators. However, the consequences of such management actions, in terms of reductions (or unintentional increases) in predation of wader nests remain unclear and thus neither the value of such management nor the relative benefits of targeting management in specific areas can yet be assessed. Targeting of management is likely to be particularly important because of constraints such as water availability and opportunities to enhance vegetation growth in commercially grazed landscapes.

Using a 7-year study of wader breeding demography in east England, we first quantify the landscape and habitat features influencing the probability of nest predation. We then use these models to explore the potential impact on nest predation rates of the separate and interactive effects of enhanced or reduced areas of tall vegetation and surface water levels. This scenario-based approach provides a means of identifying the magnitude of change in nest predation that can potentially be achieved through different management options and spatial targeting of management.

Materials and methods

The study took place at Berney Marshes RSPB reserve (52°35'N 01°35'E), a 500 ha lowland wet grassland site situated within the Halvergate Marshes, a 1430 ha SSSI. This wet grassland landscape has few trees and fields are separated by ditches (~4 to 6 m wide × ~2 m deep), but are connected by gateways. Extensive deployment of nest temperature loggers and nest cameras has shown that nocturnal predation, principally by Red Foxes, is the primary cause of nest loss at this site (Eglington *et al.* 2009; Laidlaw *et al.* 2015). Numbers of Red Foxes in the area remain unknown, but numbers shot during regular predator management in the pre-wader breeding season are relatively constant between years (mean ± SD: 6.9 ± 2.3, range = 2–9 individuals shot per year between 2005 and 2011; Laidlaw *et al.* 2015). Typical of many wet grassland reserves (Fisher *et al.* 2011), short swards and surface water are maintained on this site to provide suitable nesting and chick-rearing conditions for breeding waders (Eglington *et al.* 2008). The site is commercially grazed by cattle which are introduced in April or in mid-May on a few fields managed within the higher-level stewardship scheme. These livestock are regularly moved throughout the reserve, typically at a pressure of ~1 Lu (livestock units) ha⁻¹ (Bodey *et al.* 2010), to create the required conditions of within-field sward heights of ~5–15 cm across most of the reserve. Consequently, the vast majority of the landscape comprises short swards, and taller vegetation is restricted to field verges which comprise only ~5% of the landscape (Laidlaw *et al.* 2013).

WADER NEST SURVIVAL

The nesting success of breeding waders at this site has been monitored intensively since 2003 (Smart *et al.* 2006; Eglington *et al.* 2009; Bodey *et al.* 2010). Each year, regular (every 4–5 days) surveys on between 33 and 52 fields are carried out to locate as many nesting attempts as possible. Redshank nests are located by systematic searching and incidental flushing of adults from concealed nests, whereas lapwing nests are located through observation of incubating adults from a vehicle. All nest locations were spatially referenced between 2007 and 2011 for redshank, and 2005 and 2011 for lapwing.

From the date on which each nest was first located (FIND DAY; capitals indicate variables used in statistical models), the estimated lay date was calculated from egg length, breadth and mass using the following equation derived from successful nests (Smart 2005):

$$\text{Laydate} = \text{FINDDATE} - ((\text{Laying period} + \text{incubation period}) - (\text{Number of days to hatching}))$$

$$\text{Number of days to hatching} = (271\,919 * (\text{egg mass}(\text{g}) / \text{egg volume}(\text{mm}^3))) - 113.88$$

where laying period = 5 days for both species, and incubation period = 26 and 24 days for lapwing and redshank, respectively. Lay dates were calculated for each egg, and then averaged per nest.

The status of nests was assessed (e.g. adults seen sitting on nests, adults flushed off nests by vehicles or walked to check nest contents), at least every 5 days and more regularly near their estimated hatch date to determine their fate. Nests were considered successful if one or more eggs hatched, and predated nests were

defined as those that were empty and without eggshell fragments to indicate hatching (Green, Hawell & Johnson 1987).

To determine the timing of nest failures, iButton dataloggers (Maxim Integrated Products Ltd, CA, USA) have been placed in a random selection of nests (40–85% annually) since 2007. The resulting temperature traces allow the date and time of predation to be identified from the sharp change in nest temperature from incubation temperature to ambient temperature. For nests where the exact date of predation was not known, failure day was taken as the mid-point between the final two visits. Nests that were deserted ($n = 33$), flooded ($n = 11$) or trampled ($n = 54$) without any evidence of prior predation were excluded from analyses of hatched ($n = 594$) and predated ($n = 760$) nests.

WADER DISTRIBUTION

The GPS locations of nests were used to calculate the minimum DISTANCE TO EDGE of field from each nest to assess the influence of nest location within fields on predation rates (Fig. S1a, Supporting Information). The distribution of all patches of tall (>15 cm) vegetation (hereafter referred to as verges) within the reserve was mapped by digitising outlines from aerial photographs (Millennium Map 2000). To explore the influence on predation rates of terrestrial predators potentially concentrating their activity in areas of close to verge habitats, and taking into account their likely preference for not crossing water-filled ditches, we calculated the DRY DISTANCE from the gateway access point of each field to the nearest verge using a cost–distance analysis in which routes that crossed ditches were excluded by assigning them prohibitively high values of resistance to movement (Fig. S1a). FIELD AREA was also measured for each focal field (Fig. S1a).

For each nest, the number of active lapwing nests within a 100-m radius was calculated (NESTS WITHIN 100 M). Only lapwing nests were considered as lapwing exhibits the strongest mobbing of predators, the likely mechanism by which higher nesting densities reduce predation (MacDonald & Bolton 2008a), and the concealed nature of redshank nests means that lapwing typically respond to predator presence first. Active lapwing nests were defined as those being incubated for at least 1 day during the incubation period of the focal nest. All areas and distance measurements were calculated in ArcGIS v.10 (Environmental Systems Research Institute, Redlands, CA, USA).

ANNUAL AND SEASONAL VARIATION IN EXTENT OF SURFACE WATER

Using GPS locations of all foot drains (shallow channels of varying width designed to hold water within fields), the extent of seasonally varying SURFACE WATER within each field was estimated. High water levels, which result in pools forming around overtopped foot drains, are maintained on the reserve over winter, and the maximum extent of surface water in fields was mapped in March of 2 years (2009 and 2011). From these maps, a five-category surface flooding score that reflected the range of surface flooding across the reserve was developed (maximum extent, ~75%, ~50%, ~25% extent and water in foot drains only) and mapped in ArcGIS v.10 (Fig. S1b).

Monthly surface flooding categories were assigned to each focal field to capture seasonal reductions in surface flooding (Table S1). During March, the surface flooding on the reserve was classified as high, medium or low depending on the cumulative total rainfall from January to March (Table S1). During April to July, surface flooding

was classified according to the rainfall during that month and increasing effects of evapotranspiration as the season progresses (Table S1). The surface flooding category for each month in each year was then applied to each field in which focal nests were active, giving an estimate of surface flooding in each field given rainfall, seasonal evapotranspiration and numbers of foot drains (Fig. 1).

SCENARIO TESTING METHODS

A range of feasible management scenarios in which water levels or verge configuration could be manipulated was identified from discussions with the site manager (Tables 2 and 3). Three water management scenarios were explored; the estimated extent of surface flooding in each field for each month and year (Table S1, Fig. 1) was subject to a 25% increase (wetter scenario) or decrease (drier scenario), and water resources were concentrated in areas identified in the reserve drought plan, in which high water levels would be concentrated in six blocks of fields, through existing sluices, pumps and deep ditches (Fig. 2a, Table 2). Three scenarios manipulating verge configuration (which currently covers 0.28 km² of the reserve) were explored (Table 3, Fig. 2b–d);

verge removal, addition of verge and restructuring to create continuous ‘corridors’ of verge (reducing total verge area to 0.19 km²) along which predators may move. The verge addition option would include converting whole fields within the reserve into areas of tall vegetation with practical and cost-effective management of light cattle grazing and mowing every second or third year to prevent scrubbing over. The verge and water scenarios were modelled separately and in combination, resulting in nine management scenarios (Table 3).

STATISTICAL ANALYSES

Variation in daily nest predation rates (DPR) for lapwing and redshank was explored separately with Generalised Linear Mixed Models (GLMMs), using a formulation of Mayfield’s (1961, 1975) method as a logistic model with a binomial error term, in which success or failure (hatched or predated) was modelled with exposure days as the binomial denominator (Aebischer 2009), with FIND DATE, DRY DISTANCE, FIELD SIZE, DISTANCE TO EDGE, SURFACE WATER and NESTS WITHIN 100 M as fixed factors, and DISTANCE TO EDGE × SURFACE WATER interaction

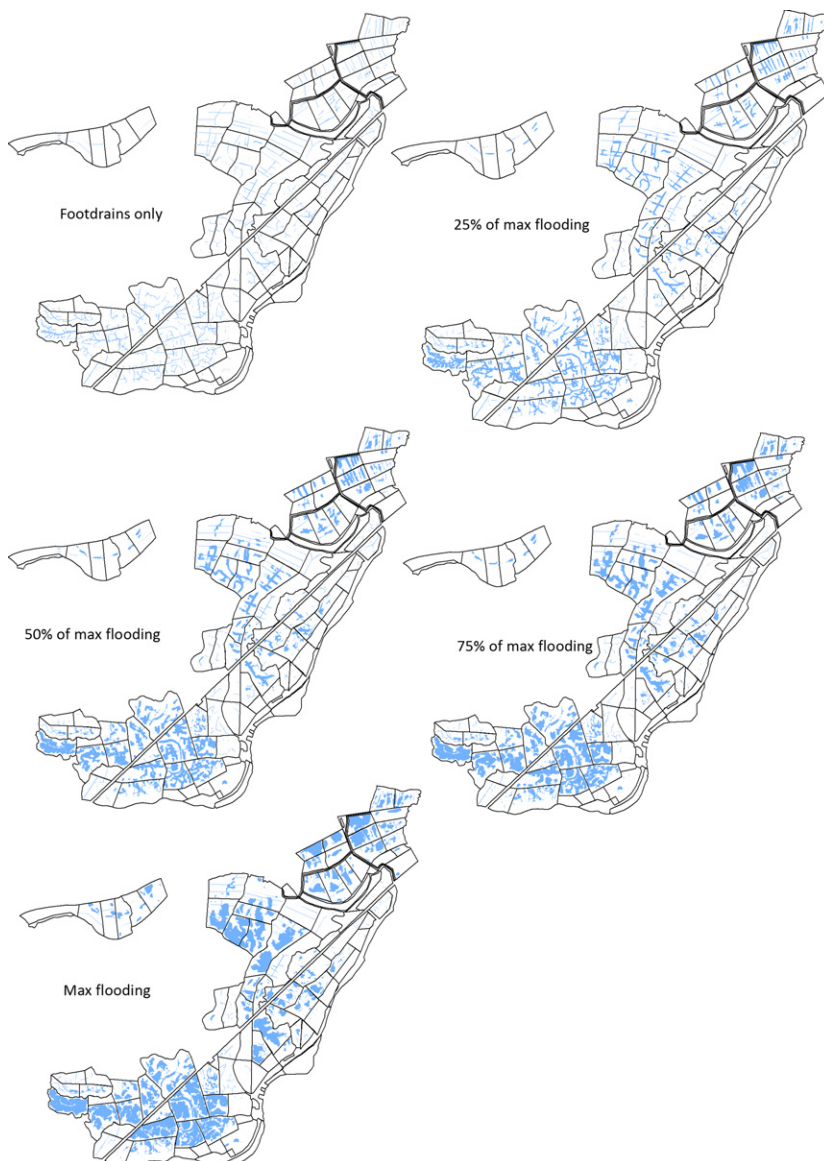


Fig. 1. Representation of the extent of surface flooding across Berney Marshes in each of the five surface flooding categories, from foot drain only to the maximum extent of flooding that was mapped in March 2009 and 2011.

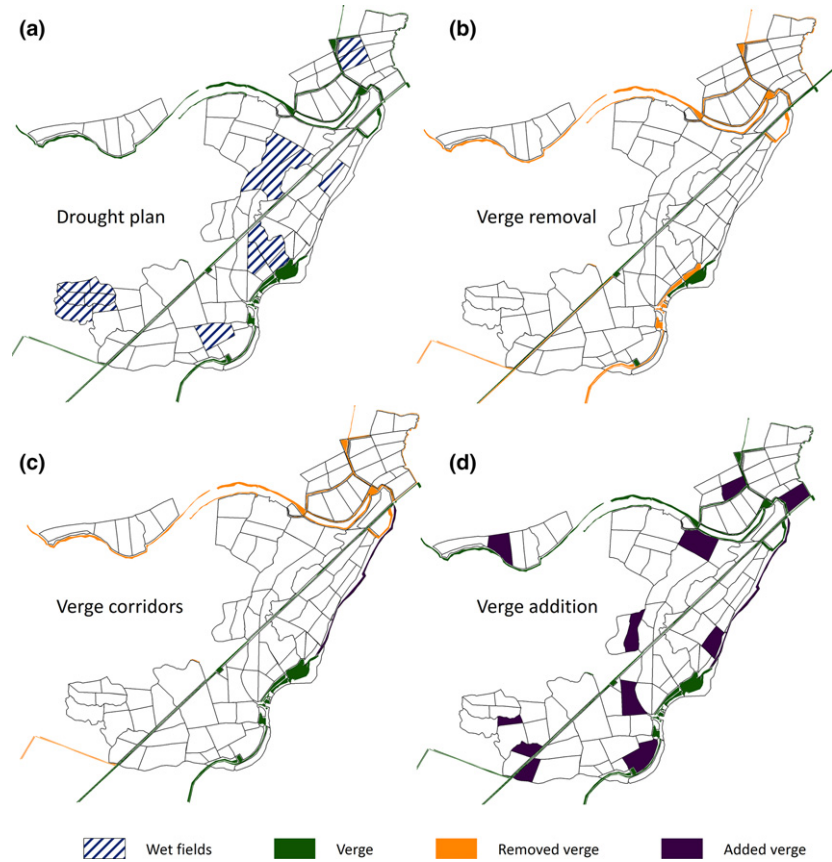


Fig. 2. The location of (a) fields on which high water levels would be maintained in the drought plan scenario, and the verge distribution in scenarios of verge (b) removal, (c) creation of corridors and (d) addition (note this map also shows the current verge distribution). For levels of site wetness see Fig. 1.

(see Figs S2 and S3). YEAR was included as a random effect to account for factors such as annual variation in the abundance of predators and alternative prey, which could influence wader nest predation rates (Table 1). Field was initially considered as a random factor, however, as it explained only 0.028 of the variance (likely reflecting the consistent management of fields and the landscape scale at which predators operate), it was subsequently excluded.

Predicted DPRs from these models were transformed to nest survival over the incubation period (S) by raising the daily survival rate (1–DPR) to the power of the species incubation periods (from first egg laid: Redshank = 30 days; Lapwing = 32

days; Crick, Baillie & Leech 2003; Kragten & de Snoo 2007), and this was used to calculate nest predation probability over the incubation period (1–S).

Non-significant ($P < 0.05$) variables were sequentially removed from these models (although their estimates and associated probabilities in maximal models are reported, for completeness). All models were carried out in R (v 2.13.1) using the lme4 package, and collinearity of model terms was tested. Predictor variables were scaled (mean subtracted and divided by standard deviation) before being included within the models, to facilitate comparison of model predictions under different conditions.

Table 1. Descriptions of components and structure of models of wader nest predation rates

Type	Variable	Distribution (link/offset)	Description
Response	Wader predation rate	Binomial (logit)	For lapwing and redshank separately, nest outcome (predated (P)/hatched (H)) accounting for the no. of days the nest was active
		Units	
Explanatory	Year (random factor)		Lapwing: 2005–2011; Redshank 2007–2011
	Find day		Days after March 1 when nest was first located
	Distance to edge	m	Distance from nest to the field edge
	Dry distance	m	Total distance of route from field entrance (gateway) to nearest verge without crossing ditches between fields
	Nests within 100 m		Number of active lapwing nests within 100 m of the nest
	Field area	m ²	Area of field in which focal nest was located
	Surface water		Estimated proportion of field covered by surface water (measured monthly)
Response	Model structure		
Wader predation rate	(1 Year) + Find day + Distance to edge + Dry distance + Nests within 100 m + Field area + Surface water + Distance to edge × Surface water (variables scaled in model)		

Table 2. Descriptions of the three scenarios in which water levels are manipulated from the long-term average, and the resulting extent of surface water (FD = foot drain only, 25%, 50%, 75% or 100% of maximum mapped surface flooding extent in each field) in months with high (H), medium (M) or low (L) rainfall (see Table S1)

Scenario	Change in surface flooding	March			April			May			June			July		
		H	M	L	H	M	L	H	M	L	H	M	L	H	M	L
Current situation	No change	100	75	50	100	75	50	75	50	25	50	25	FD	25	FD	FD
Wetter	Increased by 25%	100	100	75	100	100	75	100	75	50	75	50	25	50	25	25
Drier	Decreased by 25%	75	50	25	75	50	25	50	25	FD	25	FD	FD	FD	FD	FD
Drought plan	Maintained on 15 fields (through pumping).	Dry fields	100	75	50	50	50	25	25	25	FD	FD	FD	FD	FD	FD
	Water levels on all other fields decreases by 25% each month, until water is only present in foot drains)	Wet fields	100	75	50	75	75	50	50	50	25	25	25	25	25	FD

To explore the potential magnitude of change in lapwing nest predation rates under different management scenarios, the DRY DISTANCE and SURFACE WATER (Table 1) estimates for each scenario were recalculated for all lapwing nests and the mean values (Tables 2 and 3) incorporated within the lapwing nest predation model. The predicted nest predation rate for lapwing and redshank was then calculated for each of the 15 scenarios, for conditions of high lapwing density (6 nests within 100 m), low lapwing density (1 nest within 100 m) and when nesting near (20 m) and far (100 m) from field edges. Significant differences were signified by non-overlapping 95% CIs of scenario predictions and observed predation rates (calculated using an intercept-only model).

Results

Between ~50–200 lapwing and ~25–70 redshank nests were monitored each year, and 38–68% of lapwing and 22–87% of redshank nests were predated each year, with nest predation occurring throughout the season and across all environmental conditions and nesting densities in both species (Figs S2 and S3).

Lapwing nest predation probability increased from ~60% to 90% with increased distance to verge, up to 1 km (Fig. 3a, Table 4a). Lapwings nesting at higher densities and in larger fields had significantly reduced predation rates (Fig. 3b,e, Table 4a). Although there was no main effect of surface water on predation probability, a

significant interaction term showed that lapwings nesting within dry fields (<30% surface water) had a higher probability of being predated if they were further from the field edge (Fig. 3c, Table 4a). Conversely, in wet fields (>~30% surface water) nests near the edge were more likely to be predated (Fig. 3d, Table 4a). Redshank nest predation probability decreased significantly with increasing lapwing nest density but was unrelated to any other environmental variables (Fig. 3f, Table 4b).

EFFECTS OF MANAGEMENT SCENARIOS ON PREDATION RATES

Addition of verges, in combination with any of the changes in water management, is predicted to result in significant reductions in lapwing nest predation rates (by ~22%, from the current ~70% per year), but only when nests are close to field edges and in areas of high nesting densities (Fig. 4a, see Fig. S4 for site-wide scenario predation rate estimates). Given average clutch size (3.7) and numbers of nesting pairs on the site (132) between 2005 and 2011, this could potentially result in an increase in numbers of hatched chicks of ~100 (Fig. S5). Lapwing nests that were distant from field edges were at significantly higher risk of predation (by ~22%) under scenarios that combined reductions in field wetness and verges in areas of low lapwing nest densities (Fig. 4d). None of the

Table 3. Descriptions of the three verge manipulation scenarios, and the nine combinations of verge and water manipulation that were modelled (see Table 2 for descriptions of water manipulations)

Verge manipulation	Description	Combination of scenarios
Removal	Removal of all RSPB managed verges to leave the minimum amount of verge (0.12 km ²)	Verge removal + Wetter Verge removal + Drier Verge removal + Drought plan
Corridor	Verge removal and creation to create two continuous 'corridors' of verge through the reserve along the railway and the sea wall (totalling 0.19 km ²)	Verge corridor + Wetter Verge corridor + Drier Verge corridor + Drought plan
Addition	Verge creation at all suitable locations across the reserve (totalling 0.79 km ²). Including within-field changes in management to encourage taller, denser swards (e.g. reduced or rotational grazing, application of fertilisers, hay cropping) in selected dry fields to create areas with tall grass swards	Verge addition + Wetter Verge addition + Drier Verge addition + Drought plan

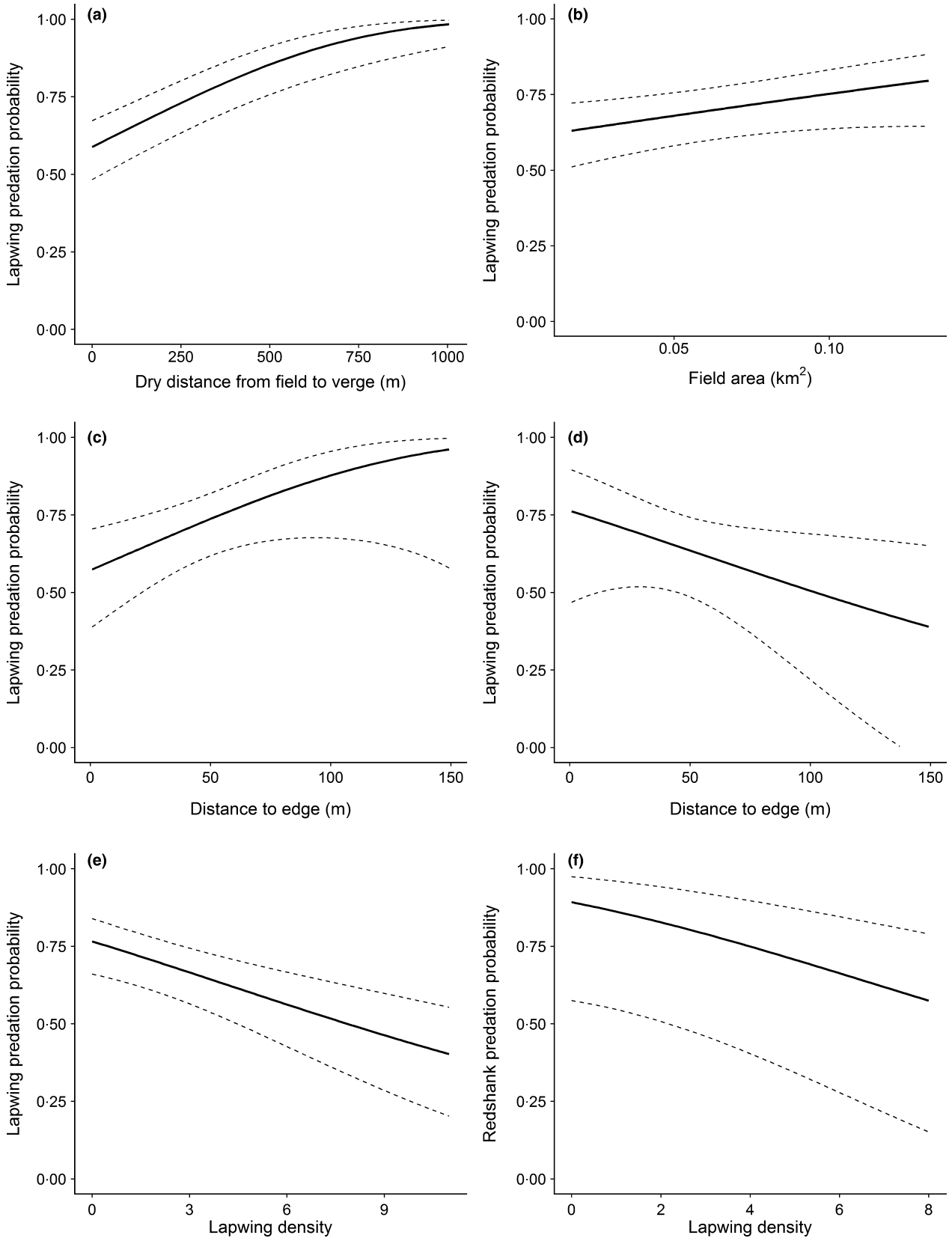


Fig. 3. Predicted nest predation probability over the incubation period for lapwing with (a) increasing distance to verge, (b) increasing field area, increasing distance to edge in (c) dry fields and (d) wet fields, (e) increasing number of active lapwing nests within 100 m and for redshank with (f) increasing number of active lapwing nests within 100 m. Predictions and 95% confidence intervals (shown by dashed lines) are from models in Table 4.

Table 4. Results of Generalised Linear Mixed Models GLMMs (with binomial errors) of nest predation probability for (a) lapwing and (b) redshank. Minimum models are shown above the dashed lines, and non-significant variables excluded from the minimum model (with estimates from the full model; see Table 1) are shown below the dashed lines. Estimates and SE are in logits

Variable	Estimate	Std. error	<i>z</i> value	<i>P</i>
(a)				
(Intercept)	-3.275	0.122	-26.826	<0.001
Distance to edge	0.081	0.053	1.528	0.126
Dry distance	0.304	0.048	6.366	<0.001
Nests within 100 m	-0.165	0.050	-3.297	<0.001
Field area	0.116	0.053	2.184	0.029
Surface water	-0.053	0.048	-1.097	0.273
Dist to edge × surface water	-0.105	0.051	-2.053	0.040

Find day	-0.001	0.051	-0.022	0.983
(b)				
(Intercept)	-2.917	0.318	-9.164	<0.001
Nests within 100 m	-0.223	0.085	-2.618	0.009

Find day	-0.070	0.110	-0.637	0.524
Distance to edge	0.074	0.172	0.428	0.669
Dry distance	0.031	0.091	0.335	0.737
Field area	-0.044	0.091	-0.480	0.631
Surface water	-0.137	0.145	-0.948	0.343
Dry distance × surface water	-0.143	0.221	-0.646	0.518

management scenarios is predicted to significantly alter predation rates of nests far from field edges (Fig. 4b,c), and changes in surface wetness (wetter, drier or concentrated in blocks of fields) were not predicted to significantly alter nest predation rates in any conditions of nesting density or location (Fig. 4).

As redshank nest predation was not significantly related to any of the landscape features, management scenarios could not be explored for this species. However, redshank

benefit from nesting among high densities of lapwing (Fig. 3f) and the current nest predation probability (81.9%, 95% CIs = 74.4–88.3) are predicted to decrease to 66.3% (27.8–84.5) at high lapwing densities (6 active nests within 100 m) and increase to 86.2% (54.6–96.0) at low (1 nest within 100 m) densities.

Discussion

Targeted conservation actions that focus on the specific requirements of single species can inadvertently influence other food web components, including species that may interact directly with the target species. For example, management may influence predators of target species, and thus indirectly influence the effectiveness of conservation management. Identifying factors influencing predator activity can potentially help to reduce impacts on species of conservation concern, but opportunities to explore predator activity in relation to conservation management are rare (Amar & Redpath 2005). In this study, the collation of 7 years of intensive monitoring of breeding waders has allowed the identification of environmental conditions associated with differing levels of nest predation. Lapwing nests were significantly more likely to be predated when far from verges, far from field edges in dry fields, close to field edges in wet fields and when there were fewer other lapwing nesting in the surrounding area. Modelling of the potential impact of realistic management scenarios that altered surface wetness and verge distribution indicated that substantial changes in nest predation rates (up to ~20%) could occur in response to particular management scenarios, but only for nests close to field edges in areas with high nesting densities.

Lapwing nests in close proximity to areas of tall vegetation have a reduced likelihood of being predated, perhaps as a result of predators concentrating their foraging activities on small mammals within these areas (Laidlaw *et al.* 2013). The increase in lapwing nest predation rates further

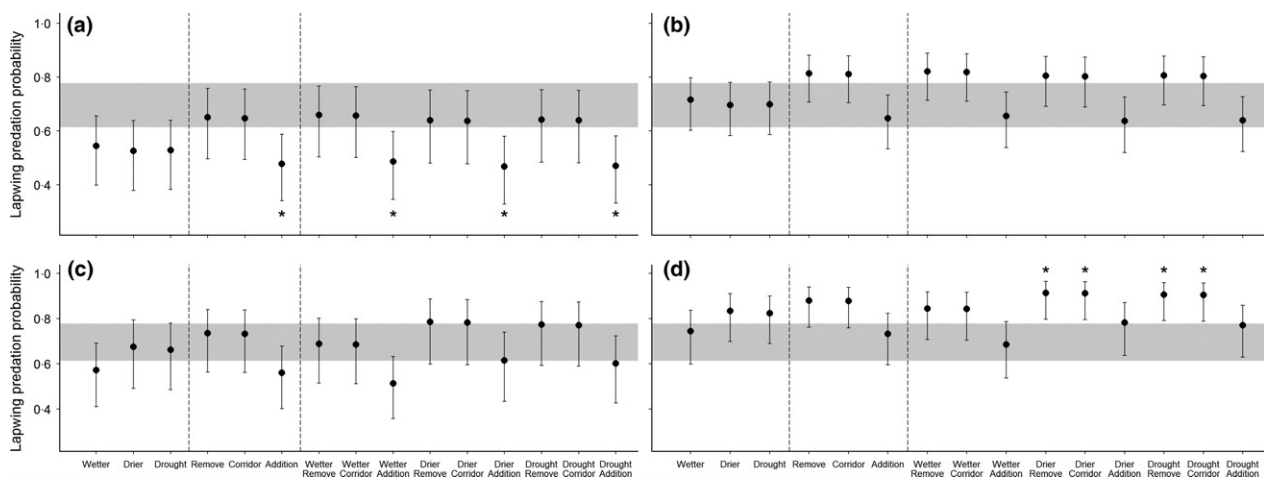


Fig. 4. Predicted nest predation probability (mean \pm 95% CIs) over the incubation period for lapwing under different scenarios of surface wetness and verge vegetation configuration (see Table 2 for descriptions). Model predictions are shown for nests near (20 m; a, b) and far (100 m; c, d) from field edges when the number of active lapwing nests within 100 m is high (6 pairs; a, c) or low (1 pair; b, d). Scenarios for which 95% CIs do not overlap the current 95% CIs (intercept-only model, grey bar) are denoted by '*'. *

from tall vegetation may also suggest that predators may concentrate more on wader nests when small mammals are not available. Agri-environment options for the creation of grass margins are common in arable landscapes, but less so in grazed wetland landscapes in which fields are typically bounded by ditches to which grazing animals may need access. Increasing the area of tall vegetation around wet grasslands may therefore require either targeted deployment of wader management in areas with existing verges, or where tall vegetation can be created along verges or within fields, through reduced grazing pressure.

Within lowland wet grasslands, the configuration of wet features can create complex within-field structures which mammalian predators may find difficult to navigate. Wet features are generally more frequent in the centre of fields (Bodey *et al.* 2010) and, in wet fields, lapwing nests further from the edge had lower predation rates. This suggests that surface flooding may create barriers to predator movement within fields (Harri, Mononen & Sepponen 1999; Berger-Tal *et al.* 2009). In addition, in very wet fields, lapwing may nest closer to field edges to avoid flooding of nests, and predator hunting behaviour may be more efficient along narrow field edges (e.g. Mukherjee, Zelcer & Kotler 2009), whereas dry fields may have few barriers to predator movement, and consequently predators may be more likely to encounter nests in these areas.

The well-documented predator-mobbing behaviour of breeding lapwing (Elliot 1985b) may contribute to the reduced level of nest predation in areas of high lapwing nesting density. Similar protective effects of high wader nesting densities have been found previously (MacDonald & Bolton 2008b) and demonstrated experimentally using artificial nests (e.g. Larsen & Grundetjern 1997). Redshank nest predation probabilities were also lower in areas with high densities of nesting lapwing, suggesting that neighbouring species may also benefit from this defensive behaviour, or from dilution of predation risk in areas of high prey density (Hamilton 1971).

SCENARIO TESTING OF THE POTENTIAL IMPACT OF ALTERING MANAGEMENT

Scenario testing can be a useful means of exploring the potential magnitude of responses to changing management actions, to help inform the development of effective conservation policies (Peterson, Cumming & Carpenter 2003). Although the scenarios explored in this study all related to nature reserve management, they can potentially also inform land management decisions in the wider countryside, for example, through the ongoing development of agri-environment scheme options and spatial targeting of AES deployment. As the consequences of these management options may vary depending on local predator communities and densities (e.g. Bolton *et al.* 2007), similar scenario modelling at other sites managed for breeding waders would help to identify the applicability of these findings in other wetland landscapes.

As climate change is likely to influence rainfall and associated water availability, a site-specific reserve drought plan has been developed in which limited water resources would be concentrated in a small number of fields with suitable hydrology and topography for water retention. Encouragingly, the overall level of nest predation predicted in this scenario does not differ significantly from current levels, and the increase in nesting density that might result from concentrating water resources may provide further protection for nests. However, it is possible that predator distribution and activity could also alter and the availability of prey resources for chicks could potentially be more limited in these circumstances.

Scenarios in which surface water levels were increased or decreased by 25% had little effect on overall nest predation rates. Eglington *et al.* (2008) showed that higher lapwing nesting densities occur close (within 50 m) to areas with surface flooding. Consequently, changes to surface water levels could alter wader nesting distribution, which could influence their predation probability. Despite the high predation rates of lapwing nests in the centre of dry fields and the edges of wet fields (Fig. 3c,d), changes in surface flooding are not predicted to significantly alter predation rates on nests close to or far from field edges (Fig. 4), suggesting that the influence of surface flooding on predator activity is relatively weak. However, increasing the area of surface water within these landscapes could attract higher densities of lapwing which may result in lower levels of nest predation (Fig. 3e). Similarly, reducing the area of surface flooding could attract fewer waders, which could then lead to increases in nest predation, and could also impact chick growth rates and survival, given the dependence of wader chicks on the invertebrate prey resources in wet features (Eglington *et al.* 2010). Such changes would be likely to have similar effects on redshank, given that their breeding densities are also higher in wetter fields (Smart *et al.* 2006), and that redshank nest predation rates are lower when lapwing densities are high (Fig. 3f).

The scenarios of verge removal and creation within the reserve were constrained because not all verges are under the ownership or management of the RSPB, and there are relatively few roads and tracks suitable for verge creation (as most fields are separated by deep ditches). Despite these limitations, both verge removal and creation of continuous verge corridors (which resulted in a decrease in the total verge area) were predicted to significantly increase predation rates of nests far from field edges in areas of low lapwing densities, while verge addition has the potential to significantly reduce predation rates (Fig. 4). This indicates the likely importance of locating verges close to fields that are attractive to breeding waders, as the associated reduction in nest predation is primarily apparent within ~250 m (Fig. 3a).

The scenarios represented here assume that predator behaviour does not change in response to the different management scenarios. Given the ability of foxes to adapt to new situations, as exemplified by their impact as an invasive species (Harding, Doak & Albertson 2001;

Saunders, Gentle & Dickman 2010), they may well respond to landscape alterations, particularly if food resources are scarce. In particular, the effectiveness of creating verge corridors would depend upon the scale over which foxes are attracted to verges. Given the high levels of nest predation that currently occur far from verges (Fig. 3a), and the strong evidence that foxes are the main nest predator (MacDonald & Bolton 2008a), it seems likely that the effect of verge proximity on fox distribution is very local (e.g. adjacent fields), and has little impact on fox abundance and distribution at larger, landscape scales (e.g. across and beyond the study area).

IMPLICATIONS FOR MANAGING PREDATOR IMPACTS ON WET GRASSLANDS

The impact of generalist predators has been widely shown to be a major factor constraining population recovery of declining wader populations across Europe (Bolton *et al.* 2007). Previous studies have shown that the effectiveness of predator control as a tool to reduce predator impacts on breeding waders is inconsistent and varies with the local predator community (Bolton *et al.* 2007). Exclusion of mammalian predators with fencing can be effective (reductions in nest predation from ~66% to ~16% have been recorded), but is expensive and requires constant management (Malpas *et al.* 2013). Our analyses suggest that the best management scenario (wetter + verge addition in areas of high lapwing nest density) has the potential to reduce nest predation rates from the long-term average of ~70% to ~50%. Given the important role of nest predation in limiting recovery of declining wader populations, and the prohibitive costs and the practicalities of excluding predators from large areas of breeding habitat, such relatively easy management approaches could be extremely attractive, but would clearly need to be targeted in appropriate areas of high lapwing density around which verges could be established. Verge creation could also influence the avian and mammalian predators of wader chicks that also have small mammals as their main prey, and predator impacts on chick survival are likely to also contribute to ongoing wader population declines (Sharpe, Clark & Leech 2008). Chick survival rates are far more difficult to measure than nest survival, but the available evidence suggests that survival rates are often higher in areas with greater densities of broods (Eglington *et al.* 2010), and thus targeted deployment of these management strategies in high density areas might offer the best hope for improving overall productivity. However, further work to evaluate the effects of verge addition on chick survival would be valuable, as this may depend on factors such as the extent to which avian and mammalian predators are attracted to verge habitats and the relative profitability of wader chicks and small mammal prey in these landscapes. If management of landscape and habitat structure on wet grasslands can substantially influence nest predation rates, these techniques may also be applicable in wider countryside

management, for example, through the development and targeting of agri-environment schemes.

Authors' contributions

R.A.L., J.S., M.S. and J.A.G. conceived the ideas and designed methodology; R.A.L. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

This project was funded by a UEA Dean of Science Studentship, with additional funding provided by the John and Pamela Salter Charitable Trust and the Royal Society for the Protection of Birds and NERC (NER/J/S/2002/00612 and two NERC-funded PhD studentships). Thanks to the landowners for access to their grazing marshes and to the staff and students working at Berney Marshes for their assistance in the field. We thank Andrew Hoodless, Simon Gillings and Richard Fuller who provided helpful comments that greatly improved this manuscript.

Data accessibility

The data used in this manuscript are all presented in the manuscript and its Supporting Information (Figs S2 and S3).

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Received 3 May 2016; accepted 4 November 2016

Handling Editor: Richard Fuller

Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Illustration of the environmental metrics.

Fig. S2. Numbers of lapwing nests that were predated.

Fig. S3. Numbers of redshank nests that were predated.

Fig. S4. Predicted nest predation probability over the incubation period for lapwing under different scenarios of surface wetness and verge vegetation configuration.

Fig. S5. Predicted numbers of lapwing chicks hatched on the site under different scenarios of surface wetness and verge vegetation configuration.

Table S1. Surface flooding scores.