Short running title:- Soil variables improve Lapwing habitat model

Soil pH and organic matter content add explanatory power to Northern Lapwing *Vanellus vanellus* distribution models and suggest soil amendment as a conservation measure on upland farmland

HEATHER M. McCALLUM,[1] KIRSTY J. PARK,[1] MARK G. O'BRIEN,[3] ALESSANDRO GIMONA,[4] LAURA POGGIO,[4] & JEREMY D. WILSON,[1,2]*

[1] *Biological and Environmental Sciences, University of Stirling, Stirling, Scotland, FK9 4LA, UK.,*

[2] *RSPB Centre for Conservation Science, 2 Lochside View, Edinburgh Park, Edinburgh, EH12 9DH, UK.,*

[3] *BirdLife International Pacific Programme, GPO Box 1 8332, Suva, Fiji.,*

[4] *The James Hutton Institute, Craigiebuckler, AB15 8QH, UK*

* Corresponding author: Heather McCallum, RSPB, 2 Lochside View, Edinburgh Park, Edinburgh, EH12 9DH, UK. Tel: +44 131 317 4142 Email: heather.mccallum@rspb.org.uk

Habitat associations of farmland birds are well studied yet few have considered relationships between species distribution and soil properties. Charadriiform waders (shorebirds) depend upon penetrable soils, rich in invertebrate prey. Many species including our study species, the Northern Lapwing *Vanellus vanellus* have undergone severe declines across Europe, despite being targeted by agri-environment measures. This study tested whether there were additive effects of soil variables (depth, pH and organic matter content) in explaining Lapwing distribution, after controlling for known habitat relationships, at 89 farmland sites across Scotland. The addition of these soil variables and their association with elevation improved model fit by 55%, in comparison with models containing only previously established habitat relationships. Lapwing density was greatest at sites at higher elevation, but only those with relatively less peaty and less acidic soil. Lapwing distribution is being constrained between intensively managed lowland farmland with favourable soil conditions and upland sites where lower management intensity favours Lapwings but edaphic conditions limit their distribution. Trials of soil amendments such as liming are needed on higher elevation grassland sites to test whether they could contribute to conservation management for breeding Lapwings and other species of conservation concern that depend upon soil-dwelling invertebrates in grassland soils, such as Eurasian Curlew *Numenius arquata*, Common Starling *Sturnus vulgari*s and Ring Ouzel *Turdus torquatus*. Results from such trials could support improvement and targeting of agri-environment schemes and other conservation measures in upland grassland systems.

Key words: agriculture; grassland; lime; shorebird; wader; soil pH; High Nature Value; agri-environment; earthworm; Lumbricidae

Agricultural conversion is a globally dominant land use change and driver of biodiversity loss (Foley *et al*. 2011). Over the past century, the loss of around half of global wetlands, often through agricultural conversion, has been a major cause of population declines of charadriiform waders (shorebirds) (Zedler & Kercher 2005, Stroud *et al*. 2006). Some species persist on agricultural land and, across Europe, Eurasian Oystercatcher *Haematopus ostralegus*, Eurasian Stone-curlew *Burhinus oedicnemus*, Northern Lapwing *Vanellus vanellus*, Common Snipe *Gallinago gallinago*, Black-tailed Godwit *Limosa limosa*, Eurasian Curlew *Numenius arquata* and Common Redshank *Tringa totanus* have all long been regarded as characteristic of bird assemblages of agricultural landscapes. However, since the mid-20th century there have been declines of many species as increasingly intensive cultivation, drainage and grazing regimes have reduced both the availability and security of suitable nesting habitat and the availability of large, soft-bodied soil arthropod prey upon which these birds depend (Newton 2004, Wilson *et al*. 2009).

In countries with a history of rich and diverse farmland wader assemblages such as the UK and the Netherlands which are amongst the three most important EU countries for breeding populations of all except one of the above species (Birdlife International 2004), measures to improve breeding habitat conditions have become central to agri-environment scheme expenditure. To date, agri-environment schemes (AES) targeted at breeding waders have focussed on manipulating the intensity and timing of grazing, mowing or cultivations to reduce the risk of nest destruction by trampling or mechanical operations (Ausden & Hirons 2002, Kleijn & Van Zuijlen 2004, Verhulst *et al*. 2007, O'Brien & Wilson 2011). Measures have also included raising of soil water tables, and reducing agrochemical inputs as means to increase prey availability and nesting habitat quality (Ausden & Hirons 2002, Wilson *et al*. 2007, O'Brien & Wilson 2011, Baker *et al*. 2012). Although these interventions can increase nest success and abundance (e.g. Sheldon *et al*. 2007, Rickenbach *et al*. 2011), successful reversal of national population declines of wader populations on agricultural land remains elusive (Kleijn *et al.* 2010, Baker *et al*. 2012, Smart *et al*. 2013) and continuing declines of breeding wader populations are striking in the latest Atlas of birds published for Britain and Ireland (Balmer *et al*. 2013). Failure of AES to halt population declines may result from poor implementation of habitat measures, high predation rates or simply the fact that high quality agri-environment measures are not deployed over a sufficiently large scale to reverse national population declines (O'Brien & Wilson 2011, Smart *et al*. 2013). This gap between success of agri-environment measures at the scale of the management intervention and failure at the scale of the policy intervention is common (Wilson *et al.* 2010, Kleijn *et al*. 2011). Lastly, and despite the fact that the habitat requirements of breeding waders in agricultural landscapes have been well studied, it is also possible that the suite of measures available remains incomplete. In this study, we test this hypothesis for the Northern Lapwing (from now on referred to as Lapwing).

Lapwings nest on the ground in short grassland. Arable crops may be used if they are close to suitable chick rearing habitat in the form of pasture or damp areas (Berg *et al.* 1993, Galbraith 1988, Sheldon *et al.* 2004). Nest sites with open views are selected often in relatively flat, large fields, and the birds tend to avoid areas with perches for avian predators (e.g. trees) and field boundaries that restrict the area that can be seen (Wallander *et al*. 2006, Shrubb 2007). To ensure access to their soil invertebrate prey, Lapwings are strongly associated with damp habitats (Berg 1993, Rhymer *et al.* 2010). Earthworms are a particularly important prey resource, taken by both adults and chicks (Galbraith 1989, Baines 1990, Beintema *et al*. 1991). During territory establishment the length of the pre-laying period is highly negatively correlated with the abundance of earthworms, indicating that Lapwings can obtain adequate body condition for egg laying faster in areas that are particularly earthworm-rich (Hogstedt 1974). Earthworm abundance in turn is strongly influenced by soil moisture, organic matter and pH (Edwards & Bohlen 1996, Curry 2004). It therefore seems likely that Lapwing distribution may be strongly influenced by soil properties but, with the exception of soil moisture, associations between Lapwing, or indeed any other farmland bird species, and soil properties have been largely overlooked (Table 1). Specifically, there has been little consideration of how manipulation of soil properties (other than wetness) might be used as a means to improve effectiveness of agri-environment or other conservation measures for breeding waders. This is surprising given clear inter-dependence between agricultural processes, soil properties and vegetation and invertebrate communities (Webb *et al*. 2001, Bardgett *et al*. 2005, White 2006). Here we test whether the inclusion of soil properties adds to the explanatory power of a farm-scale species distribution model for Lapwings, based on established habitat relationships, using a data set collected across Scotland in 2005. We use the results to consider the extent to which effectiveness of agri-environment management interventions for Lapwings and other farmland-nesting waders might be enhanced by explicit consideration of manipulation of soil properties

METHODS

Data used in modelling

This study used field-scale data on breeding Lapwing abundance and agricultural habitat collected at 89 farmland sites across mainland Scotland in 2005 for a study of breeding wader response to agri-environment scheme management over the preceding 13 years (O'Brien & Wilson 2011). In that study, O'Brien and Wilson selected 60 "key" and 60 "random" 1 km square sites from a larger sample of sites surveyed in 1992 (O'Brien 1996). Key sites had been identified by ornithologists in 1992 as areas supporting high densities of breeding Lapwing (16.8 km^{-2}), Eurasian Oystercatcher (10.1 km^{-2}), Common Redshank(3.6 km^{-2}) , Eurasian Curlew(7.5 km^{-2}) or Common Snipe(6.1 km^{-2}) and these were paired with randomly selected 1 km squares. Thirty of the "key" and 30 of the "random" sites had come under agri-environment management for breeding waders by 2005 (Supporting Information Appendix S1), and these were paired with the closest "key" or "random" site that was not under agri-environment management. All sites were defined as farmland through being classified as between Land Capability for Agriculture classes 1 and 5.3, as defined by the Macaulay Land Capability for Agricultural (LCU) Classification in Scotland (http://www.macaulay.ac.uk/explorescotland/lca.html, accessed 14 April 2013). Of the 120 sites selected, we used the 89 mainland sites (Figure 1) for our study (one other mainland site had no field data collected in 2005 because surveyors were refused access by the landowner).

From this data set, we used breeding Lapwing abundance as our response variable. Lapwings were counted on a field by field basis following O'Brien and Smith (1992) which uses three survey visits between 15th April and 21st June, at least one week apart. The number of Lapwing pairs was calculated by dividing the number of Lapwings recorded in a field (excluding those in flocks) on one of the first two site visits, selecting the visit where the maximum number of Lapwings was recorded across the whole site (Barrett & Barrett 1984). Explanatory variables obtained from O'Brien and Wilson (2011) were, vegetation height, % soft rush and % flooding which indicate site wetness (Table 2a). For detailed methods used by O'Brien & Wilson see Supporting Information Appendix S2. To these explanatory variables we added measures of field area (ha) and elevation (m) from the UK Ordnance Survey Digital Terrain model, and a measure of field enclosure (Table 2b). Elevation was calculated as the mean of all points within a field (50 m grid) and enclosure was calculated by measuring the length of field boundaries consisting of trees, hedges, buildings or scrub (using Google Earth) and dividing this by the total length of the field perimeter. All Geographical Information System (GIS) manipulations were conducted with ArcGIS 9.2 (Esri inc. 2006).

Soil property data were derived from the Scottish Soil Survey (Lilly *et al*. 2010) which records soil profiles on a 10km grid of 700 sites across Scotland, with data collected between 1978 and 1988, and for which an extension of regression kriging had been used to create an interpolated surface (Poggio *et al*. 2010). We extracted interpolated values for soil organic matter content, soil pH and soil depth for our study sites in a GIS framework (Table 2c). A more recently available soil pH data set from the Countryside Survey of 2007 could not be used as its spatial resolution is much lower (200 randomly selected 1 km squares) and thus unsuited to interpolation.

Data analysis

Because soil variables were measured on a 10-km grid, we first pooled field-scale data to the site level by calculating the mean value (for the covariates) and sum (for Lapwing counts) for all fields within a site. Due to strong co-linearity between some covariates (Pearson's $r > 0.5$), preliminary Principal Components Analyses (PCA) were undertaken, and resultant principal components used in subsequent modelling. Specifically, the habitat variables soft rush cover and flooding were positively correlated (Pearson's $r = 0.60$), and both altitude ($r = -0.55$) and soil organic matter ($r = -0.74$) were inversely correlated with soil pH. As the sole aim of the PCA was to remove problems associated with high co-linearity, all principal components were included within the model, thus eliminating the risk of reducing explanatory power by only including principal components with large eigenvalues (Graham 2003).

Data analysis was carried out in two stages; models in the first stage included only habitat variables, or the derived principal components that had been identified by previous research as influencing Lapwing distribution, specifically vegetation height (Shrubb 2007), soft rush and percentage flooding (O'Brien 2001, Rhymer *et al*. 2010), field enclosure and field area (Small 2002). In stage 2 we added soil variables (depth, pH and organic matter) and an associated topographical variable (elevation), or the derived principal components, as the basis for identifying a final model.

Both stages used Generalised Linear Models (GLMs), specifying Lapwing count from the 2005 survey as the response variable, a log link and Poisson error, and fitting $\log_e$ (site area) as an offset so that we were modelling correlates of variation in breeding Lapwing density. In stage 1, a set of models using all possible combinations of predictor variables (totalling 32 models) was implemented and an information-criterion approach to model selection was adopted (Supporting Information Appendix S3). The relative likelihood of each candidate model (Akaike weight) was calculated for each candidate model using QAICc (i.e. correcting for over-dispersed data and small sample size) and variables were ranked by summing Akaike weights across all models in which the variable was included (Burnham & Anderson 2002). Predictor variables with summed Akaike weights >0.9 were retained to form the final stage 1 model. Soil and topographical variables were then added (stage 2) and model selection was carried out as above, again identifying the final model as that containing all explanatory variables with summed Akaike weights of >0.9 (Supplementary Information Appendix S4).

All statistical analyses were implemented in R version 2.15.0 (R Development Core Team 2012) using standardised variables (Schielzeth 2010). Standard errors were corrected for overdispersion using quasi-likelihood (Zuur *et al*. 2009). Model residuals were tested for spatial autocorrelation using Moran's I test within the APE package (Paradis *et al*. 2004) and visualised using correlograms with the ncf package (Bjornstad 2012). Model fit was assessed by comparing QAICc of the final model and null models to give a measure of deviance explained by the model, whilst taking into account the number of parameters within the model (Burnham & Anderson 2002). The dispersion parameter was taken from the global model (i.e. the model with the most parameters in it), and used in all QAICc calculations, and was included as a parameter in calculating K. The deviance explained within the model was then calculated as:- deviance explained = 1 – ($QAIC_c$ maximum model / $QAIC_c$ null model) (Cameron & Trivedi 1998).

RESULTS

Principal components of explanatory variables

The first of the principal components (PCs) derived from the PCA of % flooding and % soft rush ('Wet 1'; Table 3a) accounted for 80% of variation in the data, and represented the gradient from drier sites (negative PC values; little flooding and soft rush cover) to wetter sites (positive PC values; high levels of flooding and soft rush cover). The second principal component ('Wet 2') described sites where there is an inverse correlation between rush cover and flooding, with negative PC values describing low rush cover but high % flooding, and positive values having high rush cover and low flooding. The first of the principal components derived from the PCA of altitude, soil organic matter and soil depth ('Soil 1'; Table 3b) accounted for 72% of variation in the data and describes the typical relationship between elevation and soil conditions in the leached, high rainfall environments of Scotland (Aitkenhead *et al*. 2012), with peaty (higher soil organic matter), more acidic (lower soil pH) soils at higher elevations (negative value of the PC), and sites at lower elevations having, lower soil organic matter and higher soil pH (positive values of the PC). The second principal component ('Soil 2') accounted for 20% of variation in the data and represents a secondary and contrasting gradient from sites at lower elevations with higher organic content and lower pH (negative values of the PC) moving to those sites at higher elevation with lower organic content of soils, and higher soil pH (positive values of the PC), perhaps reflecting impacts of localised agricultural improvement. The third principal component accounted for only the remaining 8% of variation in the data and is not interpreted further here as it played no part in modelling outcomes.

Modelling outcomes

Lapwing densities were higher at wetter sites with shorter vegetation (Akaike weights = 1), and these variables (vegetation height and 'Wet 1') were retained from stage 1 of the modelling into stage 2, and remained within the final selected model (Table 4). The principal component 'Soil 2' and soil depth were selected from stage 2 for the final model as their summed Akaike weights were also >0.9 (Table 4b). In summary, this final model shows that Lapwing density was highest at higher elevation sites with deeper, less acidic, mineral soils, wetter conditions and shorter vegetation. Whilst short vegetation (<20 cm) was common across study sites, wetter sites were scarce (Figure 2), and it is notable that for all variables, there is considerable scatter in the data, with by no means all sites fitting closely the overall relationship between each variable and residual Lapwing density. Overall, however, inclusion of soil-related variables in addition to habitat variables identified as influential by previous research increased the proportion of deviance explained (after accounting for the increase in number of parameters within the model) by 55% from 0.20 to 0.31. Spatial autocorrelation was not detected in either the final stage 1 or stage 2 model (Stage 1: Moran's I = 0.23, p = 0.62, stage 2: Moran's I = -0.011, p = 0.99).

DISCUSSION

There is a growing literature on the habitat requirements of farmland-breeding waders and the design and evaluation of agri-environment measures to assist their conservation, especially in countries which have a history of high breeding densities of such species but which have experienced severe population declines in recent decades (Verhulst *et al.* 2007, O'Brien & Wilson 2011, Smart *et al*. 2013). However, very few studies have considered soil properties other than moisture content. Here we show that a correlated suite of soil and topographical variables can markedly improve habitat association models of breeding Lapwings, in comparison with models that include only established habitat relationships with wet conditions and short vegetation.. Specifically, higher Lapwing densities were associated with higher elevation and deeper, and less acidic and less peaty soils. The improvement in model fit by adding these variables occurred despite the length of time (17 to 27 years) between national soil survey data collection and this study, and the fact that overall model-fit is relatively low due to averaging over between-field variation in habitat conditions for Lapwings on individual farms (Small 2002). More recent soil pH data collected on a sparse grid of random 1 km square sites across Scotland in 2007 do suggest small mean increases in soil pH (0.2 units) in improved grasslands in Scotland in recent decades, probably due to reductions in acidity of atmospheric deposition (Emmett *et al*. 2010). However, this change is small compared with the range of pH within our sites (difference between lowest and highest pH of 2.8 units), and therefore unlikely to have significantly impacted on our conclusions. Moreover, localised acidification, potentially related to reduction in lime use (Kuylenstierna & Chadwick 1991, Baxter *et al*. 2006) has been detected in higher elevation agricultural grasslands, which are becoming an increasingly important breeding habitat for this species in the UK as a result of the severity of declines in lowland agricultural landscapes (Shrubb 2007, Balmer *et al*. 2013).

Lapwing density was not related to the principal component 'soil 1' which accounted for over 70% of the variation in soil variables and elevation, and described a gradient from low ground sites with higher pH, humic soils, to higher altitude sites with more acidic, peaty soils, where earthworms are found at low densities or are entirely absent. This principal component describes a dominant edaphic trend in the UK from high rainfall upland environments with strong leaching effects and a tendency towards gradual acidification and accumulation of organic matter as peat, to more nutrient- and humus-rich lowland soils of higher pH (Aitkenhead *et al*. 2012). However, sites supporting high Lapwing densities now cut across this landscape grain, and are found at those sites where higher pH, mineral soils occur at higher elevation. Indeed, Lapwing density exceeding 16.8 pairs km^{-2}, the threshold previously identified as defining a key site for this species in Scotland (O'Brien & Bainbridge 2002), occurred at less than 10% of our study sites. At first sight the relative lack of Lapwings in low-elevation sites with rich, humic soils likely to support abundant soil invertebrate prey resources (Edwards & Bohlen 1996) seems counterintuitive. However, these are exactly the environments where, in Scotland as elsewhere across western Europe, drainage, re-seeding and heavy-stocking of grasslands, and autumn-sowing coupled with repeated field operations on arable land have created conditions in which it is very difficult for Lapwings, other farmland waders and a wider suite of ground-nesting birds to rear young (Shrubb 2007; Wilson *et al.* 2009). Our results suggest that, in effect, Lapwings are being squeezed between agricultural intensification of low ground and environmental limits at higher elevation. Similar effects can be seen in the lowlands where wetlands on fen peats of limited agricultural capability (low intensity grassland management) are now a refuge for breeding waders such as Lapwing and Common Snipe on the Somerset Levels in south-west England (Green & Robins 1993). Nonetheless, where appropriate agricultural management is practiced across a range of soil types, then sand and clay loams will typically support higher wader densities, as found by Groen *et al*. (2012) for Black-tailed Godwits in the Netherlands, probably due to higher abundances of soil invertebrate prey.

In the higher elevation environments of northern Britain, one key limit is the leaching effect of higher rainfall, leading to loss of base cations (calcium, magnesium and sodium ions), gradual acidification of soils, and reduced earthworm densities (Guild 1951, Edwards & Bohlen 1996, White 2006), often exacerbated by the low buffering capacity of upland geologies, where bedrock with infinite pH buffering capacity is restricted to less than 1% of Scotland (Langan & Wilson 1992, Hornung *et al*. 1995). Such leaching effects are also a limit on productive agriculture and, historically, the practice of agricultural liming has been used to counteract poor crop (including grass) growth in leached soils by raising soil pH in association with re-seeding, fertiliser and manure use and drainage (Johnston & Whinham 1980, Gasser 1985). Indeed these practices will have contributed to the combinations of conditions represented by high values of the 'soil 2' principal component which support higher Lapwing densities. However, agricultural lime use in Britain, which was subsidised until 1976 (Church 1985), declined from around seven million tonnes annually in the 1950s and 1960s to just two million tonnes in the late 1990s (Wilkinson 1998). This may have reduced the area of land suitable for breeding Lapwings due to an increase in soil acidity in marginal, grassland areas (Kuylenstierna & Chadwick 1991, Baxter *et al*. 2006), perhaps exacerbated by a continuing reliance on nitrogen and phosphate fertilisers to maintain grassland productivity, a practice known to accelerate leaching of base cations from soils (Gasser 1985, Rowell & Wild 1985).

In addition to the relationship with elevation, soil organic matter and pH, Lapwing density was positively related to soil depth, and this may reflect the requirements both of earthworm prey and of Lapwings to be able to access them. Anecic earthworms, the ecological group that live in deep burrows but feed on the soil surface, require deep soils to persist (Edwards & Bohlen 1996, Curry 2004). Soil depth also influences available water capacity within the soil (Poggio *et al*. 2010) and deeper soils can stay wetter, and thus more accessible to foraging birds, for longer under the same environmental conditions, due to the larger volume of water that is stored (Tromp-van Meerveld & McDonnell 2005).

This study has shown that inclusion of soil variables can markedly improve goodness-of-fit of habitat models explaining breeding Lapwing densities in agricultural landscapes. Critically, it also illustrates that Lapwing populations in the UK are increasingly squeezed between intensive agricultural practices on the edaphically favourable low ground, and edaphic constraints in potentially favourable, lower-intensity agricultural landscapes at higher elevations. This may have important implications for the conservation of breeding Lapwings in the upland grassland systems to which the internationally important populations of breeding Lapwings in the UK (Birdlife International 2004) are increasingly restricted. Trials of soil amendments are needed to test whether historical liming subsidies to reduce soil acidity and increase agricultural potential in leached, upland environments may have had important benefits in supporting breeding Lapwing populations, and whether a limited reinstatement could contribute to conservation management of Lapwings on farmland, and to reversing current, severe population declines. Similar benefits might be predicted for a range of other species which depend upon soil-dwelling invertebrates in grassland soils and which are in decline across upland Britain, including Eurasian Curlew, Common Starling *Sturnus vulgaris* and Ring Ouzel *Turdus torquatus*. Experimental trials for these species should be considered, and results of such trials for Lapwings and other species could inform adaptive improvement to, and targeting of, agri-environment schemes and other conservation measures.

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Supporting Information

Appendix S1 Agri-environment management options implemented for breeding waders at the AES managed sites.

Appendix S2 Survey methods from O’Brien and Wilson (2011).

Appendix S3 Model selection – stage 1 of analysis.

Appendix S4 Model selection – stage 2 of analysis.

Tables

Table 1. Number of papers returned by a Web of Science search using the key words “farmland” and either “bird” or “Vanellus vanellus” then adding “habitat”, “soil moisture”, “soil organic matter”, “soil pH” , “soil depth” or “soil depth” to these terms (published between January 2000 and November 2013).

	Number of papers	
Search term included with farmland AND bird or Vanellus vanellus in Web of Science Search	**Bird**	**Vanellus vanellus**
Habitat	1093	91
Soil moisture	9	3
Soil organic matter	0	0
Soil pH	3	0
Soil depth	0	0
Soil type	4	0

Table 2. Variables used to explain distribution of breeding Lapwings. a) field data collected in 2005 (O'Brien & Wilson 2011); b) field data extracted using Geographical Information System (GIS) in 2011; c) soil data collected on 10 km grid from 1978 to 1988 (Lilly *et al*. 2010), a and b collected at the field scale and combined by taking the mean across each site to give a site scale variable, c extracted at the site scale. All variables are classified as either habitat (H) or soil/topography (ST) for the purposes of data analyses (see main text).

a)

Variable	**Type**	**Method of data collection**	**Site Range**	**Site Median**
Vegetation height	H	10 measurements made per field, recording height within 8 categories (<5 cm, 5 - 10 cm, 10 - 20 cm, 20 - 30 cm, 30 - 40 cm, 40 - 50 cm, 50 - 60 cm, > 60 cm)	category 1 - 5	category 2
% soft rush	H	Percentage estimated by eye across each field	0 - 23%	1%
% flooding	H	Percentage estimated by eye across each field	0 - 36%	6%

b)

Variable	**Type**	**Method of data collection**	**Site Range**	**Site Median**
Field area	H	Extracted from Ordnance Survey Digital Data layers	1.56 - 14.7 ha	4.9 ha
Field enclosure	H	Proportion of field boundary consisting of trees, hedges, buildings or scrub - assessed using Google Earth imagery	0 - 0.65	0.18
Elevation	ST	Extracted from Ordnance Survey Digital Terrain map using 50 m grid	3 - 402 m	174 m

c)

Variable	Type	Method of data collection	Range	Site
Soil organic matter	ST	Calculated as 1.724 x % elemental carbon content	4.5 - 31%	11.8%
Soil pH	ST	Measured in calcium chloride	pH 4.8 - 7.6	pH 5.4
Soil depth	ST	Depth organic matter	82 - 107 cm	92 cm

Table 3. Principal Components Analysis (Eigenvalues, proportion of variance explained and eigenvectors) for a) habitat variables, and b) soil and topographical variables.

a)

Principal Components	**Wet 1**	**Wet 2**
Eigenvalue	1.6	0.4
Proportion of variance	0.8	0.2
Eigenvectors		
% Flooding	0.71	-0.71
% Soft rush	0.71	0.71

b)

Principal Components	**Soil 1**	**Soil 2**	**Soil 3**
Eigenvalue	2.20	0.60	0.04
Proportion of variance	0.72	0.20	0.08
Eigenvectors			
Elevation	-0.51	0.84	0.19
Soil organic matter	-0.59	-0.51	0.63
Soil pH	0.62	0.21	0.75

Table 4. a) Summed Akaike weights for all models containing the given variable, mean model estimate, mean standard error and mean *t* value for all models containing the given variable for i) stage 1 models (habitat variables only) and ii), stage 2 models adding soil and topography variables to habitat variables with a summed Akaike weight of >0.9, all variables retained within the final model i.e. summed Akaike weight > 0.9 are shown in bold; b) Estimates, standard error and t values obtained from the final stage 2 model retaining only those variables with an Akaike weight of >0.9 in Table 4a (ii).

a)

	Summed Akaike weight	**Estimate**	**Standard error**	***t***
(i) Stage 1				
Wet 1	**1**	**0.46**	**0.09**	**5.2**
Vegetation height	**1**	**-0.57**	**0.16**	**-3.53**
Field area	0.51	0.06	0.12	0.70
Wet 2	0.42	-0.13	0.19	-0.52
Field enclosure	0.42	-0.15	0.16	-0.87
(ii) Stage 2				
Wet 1	**1**	**0.36**	**0.08**	**4.16**
Vegetation height	**1**	**-0.38**	**0.16**	**-2.47**
Soil 2	**0.999**	**0.64**	**0.18**	**3.5**
Soil depth	**0.992**	**0.28**	**0.1**	**2.73**
Soil 1	0.576	0.03	0.1	0.43
Soil 3	0.481	-0.08	0.27	-0.37

b)

	Estimate	**Standard error**	***t***
Wet 1	0.43	0.08	5.5
Vegetation height	-0.72	0.15	-4.7
Soil 2	0.69	0.18	3.8
Soil depth	0.28	0.09	3.16

Figure legends

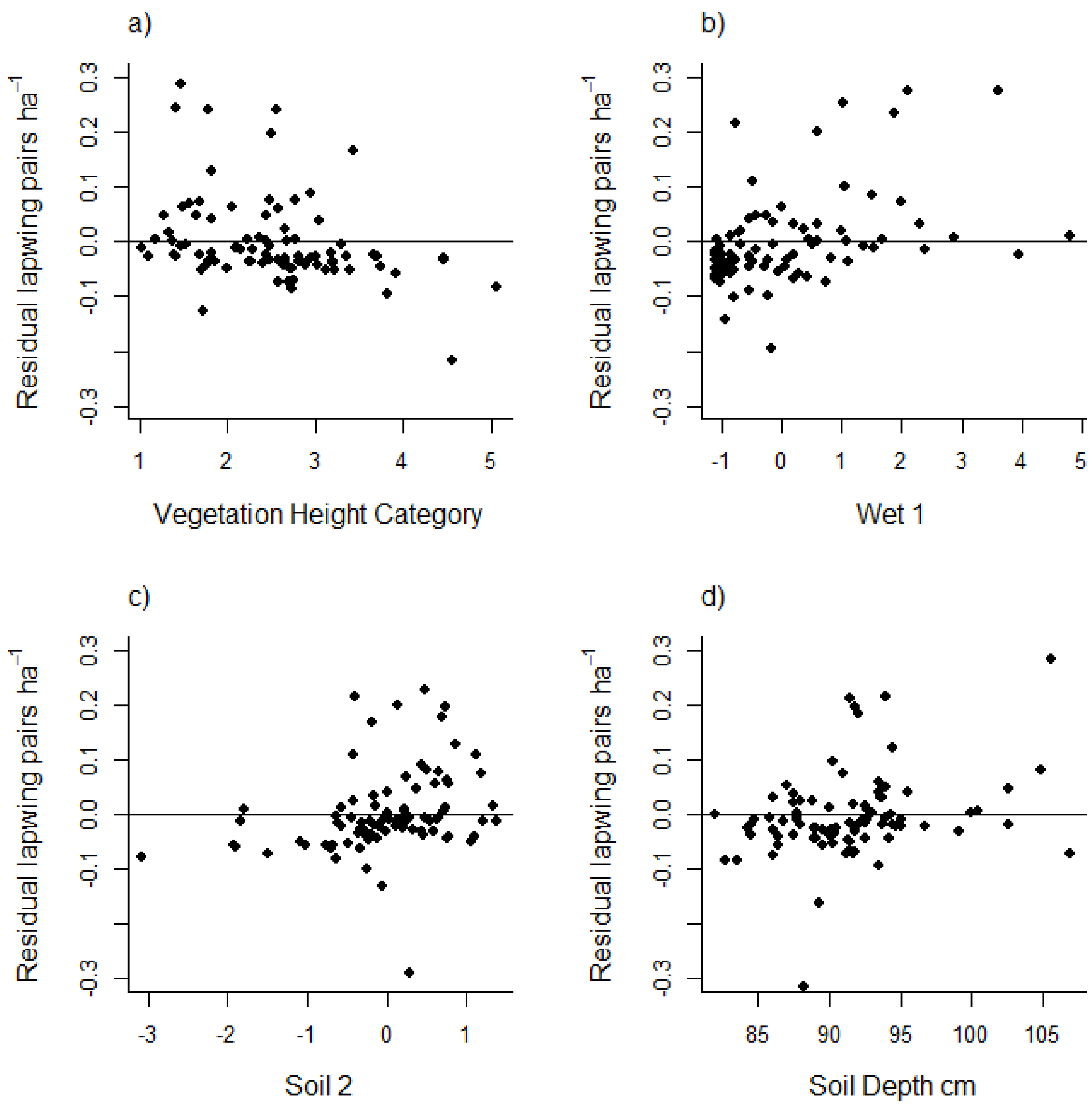
Figure 1. Geographical distribution of 89 farmland sites included within this study.

Figure 2. Model residuals (lapwing pairs per ha) for the final model – the variable plotted on the x-axis (a) vegetation height, b) wet 1, representing a gradient from drier (negative values), to wetter (positive values) sites, c) soil 2 representing a gradient from soils at higher elevations, with low organic matter and high pH (negative values) to sites at lower elevations having, lower soil organic matter and higher soil pH (positive values) and d) soil depth) , thereby depicting the relationship between the x variable and lapwing pairs per ha as described by the model. A horizontal line has been added to each graph where observed and expected lapwing pairs are equal (i.e. residual = zero) to make it easier to see the patterns in the residuals.

Figures

Figure 1

Figure 2


a)
Residual lapwing pairs ha⁻¹
-0.3
-0.1
0.0
0.1
0.2
0.3
1
2
3
4
5
Vegetation Height Category
b)
Residual lapwing pairs ha⁻¹
-1
0
1
2
3
4
5
Wet 1
c)
Residual lapwing pairs ha⁻¹
-3
-2
-1
0
1
Soil 2
d)
Residual lapwing pairs ha⁻¹
85
90
95
100
105
Soil Depth cm

Supplementary Information

Appendix S1

Agri-environment management options implemented for breeding waders at the AES managed sites (O'Brien & Wilson 2011).

Scheme	Years which scheme available	Option description
ESA	1993 - 2000	Water margin grazing control
ESA	1993 - 2000	Wetland grazing control
CPS	1997 - 2000	Flood plain management
CPS	1997 - 2000	"Grassland for birds" management
CPS	1997 - 2000	Wetland creation and management
RSS	2001 - 2006	Flood plain management
RSS	2001 - 2006	Grazed grassland for birds
RSS	2001 - 2006	Mown grassland for waders
RSS	2001 - 2006	Wet grassland for waders
RSS	2001 - 2006	Wetland creation and management

ESA, Environmentally Sensitive Areas; CPS, Countryside Premium Scheme; RSS, Rural Stewardship Scheme

Appendix S2

Lapwing surveys were conducted following O'Brien and Smith (1992), and involved three survey visits between 15th April and 21st of June 2005, with all visits to the same site separated by at least one week. Surveys were carried out within three hours of dawn or dusk on a field by field basis covering all fields within a site on each visit. These were conducted on foot walking to within 100 m of all points of the site and scanning ahead up to 400 m, with binoculars, for waders. The number of Lapwing pairs was calculated by dividing the number of Lapwings recorded in a field (excluding those in flocks) on one of the first two visits, selecting the visit where the maximum number of Lapwings was recorded across the whole site (Barrett & Barrett 1984).

At the time of the Lapwing surveys, vegetation height, percentage flooding and percentage soft rush *Juncus effusus* cover were recorded for each field. Vegetation height was recorded on the first two visits taking 10 measurements per field per visit, with heights divided into eight categories. For each field the mean vegetation height category was calculated from all measurements taken on the first two visits. Percentage flooding and soft rush cover were estimated by eye on all three visits and the mean of these was taken for each field.

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O'Brien, M.G. & Smith, K.W. 1992. Changes in the status of waders breeding on wet lowland grasslands in England and Wales between 1982 and 1989. *Bird Study*, **89**: 165-176.

Appendix S3

Candidate models ranked by Akaike weight (highest to lowest) for stage 1 of data analysis modelling lapwing density as a function of habitat variables identified by previous research as influencing Lapwing distribution. Variables / derived principal components included within the candidate models were wet 1 (W1), wet 2 (W2), vegetation height (VH), field area (FA) and field enclosure (FE). For each model K (number of parameters within the model), QAICc (accounting for small sample size and overdispersion), delta QAICc (i.e. difference between candidate model and the “best model”) and the Akaike weight are presented.

Model	K	QAICc	DeltaQAICc	Akaike Weight
W1, VH, FA	6	145.06	0	0.17
W1, VH	5	145.17	0.11	0.16
W1, VH, FA, W2	7	145.63	0.57	0.13
W1, VH, FE	6	145.74	0.68	0.12
W1, VH, W2	6	145.8	0.74	0.12
W1, VH, FA, FE	7	145.74	0.68	0.12
W1, VH, FA, W2, FE	8	146.43	1.37	0.09
W1, VH, W2, FE	7	146.37	1.31	0.09
W1, W2, FE	6	162.96	17.90	0.00
W1, FE	5	163.3	18.24	0.00
W1, FA, W2, FE	7	163.58	18.52	0.00
W1, FA, FE	6	163.93	18.87	0.00
W1, W2	5	164.23	19.17	0.00
W1	4	164.78	19.72	0.00
W1, W2, FA	6	164.8	19.74	0.00
W1, FA	5	165.07	20.01	0.00
W2, VH, FE	6	172.47	27.41	0.00
VH, FA, W2, FE	7	172.58	27.52	0.00
VH, FA, W2	6	173.3	28.24	0.00
VH, FA, W2	6	173.79	28.73	0.00
W2, FE	5	174.11	29.05	0.00
VH, W2	5	174.19	29.13	0.00
VH, FA	5	174.24	29.18	0.00
FA, W2, FE	6	174.66	29.60	0.00
VH, W2	5	175.23	30.17	0.00
FE, FA	5	176.1	31.04	0.00
FE	4	176.22	31.16	0.00
VH	4	177.27	32.21	0.00
W2, FA	5	177.56	32.50	0.00
W2	4	178.21	33.15	0.00
FA	4	178.75	33.69	0.00

Appendix S4

Candidate models ranked by Akaike weight (highest to lowest) for stage 2 of data analysis adding soil and topography variables to variables retained from stage 1 of the analysis (Appendix S3). Wet 1 and vegetation height were retained from stage 1 and included in all models presented. Additional soil and topography variables / derived principal components that were included were: Soil 1 (S1), Soil2 (S2), Soil3 (S3) and soil depth (SD). For each model K (number of parameters within the model), QAICc (accounting for small sample size and overdispersion), delta QAICc (i.e. difference between candidate model and the "best model") and the Akaike weight are presented.

Model	K	QAICc	Delta QAICc	Akaike Weight
S1, S2, SD	8	123.97	0	0.30
S1, S2, S3, SD	9	124.15	0.18	0.27
S2, S3	7	124.63	0.66	0.21
S2, S3, SD	8	124.73	0.76	0.20
S2	6	133.32	9.35	0.00
S1, S2	7	134	10.03	0.00
S2, S3	7	134.08	10.11	0.00
S1, S2, S3	8	134.74	10.77	0.00
S3, SD	7	140.43	16.46	0.00
SD	6	140.59	16.62	0.00
S1, SD	7	140.79	16.82	0.00
S1, S3, SD	8	140.86	16.89	0.00
S1	6	145.77	21.8	0.00
S3	6	145.79	21.82	0.00
S1, S3	7	146.43	22.46	0.00