lbis (2022)



The effect of conservation interventions on the abundance of breeding waders within nature reserves in the United Kingdom

SEAN JELLESMARK,*^{1,2} D MALCOLM AUSDEN,³ TIM M. BLACKBURN,^{1,2} MIKE HOFFMANN,² LOUISE MCRAE,² PIERO VISCONTI⁴ & RICHARD D. GREGORY*^{1,3}
 ¹Centre for Biodiversity and Environment Research, University College London, London, UK
 ²Institute of Zoology, Zoological Society of London, London, UK
 ³RSPB Centre for Conservation Science, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK
 ⁴International Institute for Applied Systems Analysis (IIASA), Schlossplatz 1, A-2361, Laxenburg, Austria

Breeding populations of many wading birds have declined globally, primarily caused by habitat degradation and loss. In the UK, population declines have been particularly notable on lowland wet grasslands. In response, some areas of lowland wet grassland have been restored and are under ongoing management to improve the breeding conditions of target species. Here, we assess the efficacy of management measures using a Bayesian framework and controlling for confounding factors. We focus on four wader species, Northern Lapwing Vanellus vanellus, Eurasian Curlew Numenius arguata, Common Snipe Gallinago gallinago and Common Redshank Tringa totanus, that breed in numbers on wet grassland reserve sites in the UK. We collated annual site-specific climate variables, management information (e.g. the creation of wet features and predator control measures) and bird counts between 1994 and 2018. We found the effects of conservation actions varied between intervention types and species. For Lapwing and Redshank, excluding predators by predator-exclusion fencing, especially in combination with fox control, was generally associated with higher breeding counts. For all study species, sites with longer histories of management were associated with higher breeding numbers, with the effect of site age being particularly notable for management on former arable land. Our findings support the effectiveness of targeted conservation actions to achieve high numbers of breeding waders on lowland wet grassland reserves, and also highlight the value of consistent and reliable monitoring data.

Wetlands are among the world's most biodiverse ecosystems and play a key role in helping to mitigate climate change, providing essential ecosystem service benefits and contributing to people's livelihoods (Ramsar Convention on Wetlands 2018). However, due to intensification and expansion of agriculture, water extraction and drainage, these habitats and the species that depend on them are disappearing at alarming rates (WWF 2020). In Europe, population declines have been particularly notable for breeding wading birds (order Charadriiformes) on lowland wet grasslands (Franks

*Corresponding authors.

Emails: sean.jellesmark.18@ucl.ac.uk (S.J.), richard.gregory@ rspb.org.uk (R.D.G.) Twitter: @SJellesmark (S.J.), @RichDGregory3 (R.D.G.) *et al.* 2018, Hayhow *et al.* 2019), triggering a range of conservation responses. Here, we present a detailed assessment of different site-based interventions and the number of breeding waders on nature reserves in the United Kingdom (UK).

Considerable resources have been invested into halting these declines. For example, in the UK, the Royal Society for the Protection of Birds (RSPB), the UK's largest wildlife conservation charity, acquired and restored over 7000 ha of land at more than 80 lowland wet grassland nature reserve sites between 1993 and 2018. The RSPB currently manages 159 000 ha of land for conservation in the UK. These reserves are particularly important because recent estimates indicate that although the amount of land under formal protection in the UK stands at nearly 29%, much less than half of this is specifically for nature conservation (Starnes *et al.* 2021). The restoration of land at these sites has required the RSPB to undertake active management to convert them from drained grassland, arable land or former mineral extraction sites, into wet grasslands by raising water levels, excavating pools, scrapes and foot drains (shallow, water-filled ditches) and, in the case of ex-arable sites, establishing a grass sward. Subsequent ongoing management has involved manipulating water levels, grazing and mechanical mowing, and reducing the impacts of generalist predators on nesting birds using predator-exclusion fencing and lethal control (Ausden *et al.* 2019).

The positive effects that these conservation measures have on waders have been well documented (Ausden et al. 2001, Ausden & Hirons 2002, Smart & Coutts 2004, Wilson et al. 2004, Smart et al. 2006, Eglington et al. 2008, Malpas et al. 2013, Franks et al. 2018). For example, Malpas et al. (2013) tested the effectiveness of predator-exclusion fencing on nest survival at 10 lowland wet grassland reserves from 2004 to 2011. They found that nest survival and overall productivity increased within predator-exclusion fenced areas. However, for a variety of reasons, including limited person power and resources, studies have often tested a single intervention type or category of protected area as a uniform treatment, therefore not accounting for potential differences between management across study sites. Studies have furthermore often been limited to a few selected sites that have been monitored over a relatively short period. This increases the risk that observed effects are due to confounding factors. Considerable efforts have recently been made to document and summarize the effectiveness of conservation interventions in various contexts (Sutherland et al. 2019) but large-scale evaluations in general remain rare.

In this study, we collated and combined breeding counts of wading birds and conservation management information from nature reserves to assess how different site-based conservation interventions relate to the abundance of breeding waders on managed lowland wet grassland reserves across the UK. Specifically, we tested for the effects of interventions that target the manipulation of site hydrology and control of predators. We also tested whether the duration of site management (hereafter referred to as site age) and former land use affected breeding abundance when accounting for other site-specific conservation actions and climatic conditions. Unlike previous studies, this dataset allowed us to estimate the effect of multiple conservation actions while accounting for potential confounding effects from other ongoing management actions and abiotic factors.

METHOD

Datasets

We extracted data from RSPB reserve management reports (building on work done in Jellesmark *et al.* 2021), and online repositories of weather records, to create a national, spatially explicit dataset of annual numbers of breeding bird pairs, wetland conservation interventions and climatic variables, at a spatial resolution of 1 km² (Supporting Information Table S1).

Site selection and count data

We collated breeding bird counts for four wading bird species - Northern Lapwing Vanellus vanellus. Eurasian Curlew Numenius arguata, Common Snipe Gallinago gallinago and Common Redshank Tringa totanus - for the period 1994-2018, from RSPB-managed lowland wet grassland nature reserves in the UK. Lowland wet grassland is defined as grassland that is periodically inundated by freshwater, such as seasonally flooded meadows and grazing marshes, usually below approximately 250 m elevation (Wilson et al. 2005). We chose these four wading bird species because they are all of high conservation concern in the UK and RSPB reserve management actions are designed to benefit their populations (Ausden et al. 2019, Jellesmark et al. 2021). We defined sites as blocks of lowland wet grassland habitat acquired by the RSPB in the same year. A reserve can contain multiple discrete sites if blocks of land are not contiguous and have been managed differently. A small number of sites were excluded from the analysis where it was not possible to differentiate between numbers of breeding waders on blocks of land acquired at different times. These sites made up about 8% of the current total area of lowland wet grassland on RSPB reserves. Our analyses are thus based on annual breeding pair counts from 5781 ha of lowland wet grassland across 79 sites acquired between 1993 and 2018 (mean site area = 73.5 ha \pm 67.9 sd; Fig. 1). Most of these



Figure 1. Study sites. UK lowland wet grassland reserve sites under RSPB management acquired in 1993 or after (n = 79).

© 2022 The Authors. Ibis published by John Wiley & Sons Ltd on behalf of British Ornithologists' Union.

sites were drained grasslands or arable land prior to reserve acquisition, with only a few being either mixed grass and arable land or ex-mineral extraction sites (Jellesmark *et al.* 2021). The number of breeding pairs was estimated using standard lowland wader survey methods described in Gilbert *et al.* (1998). In 2018, the study sites had on average been under reserve management for 16 years.

Conservation interventions

We gathered data on conservation interventions and site management activity from reserve annual reports for the period 1993-2018. Annual reports contain prescribed management information and are submitted annually to the RSPB headquarters. In a small number of cases, older annual reports were missing and the relevant information was instead collated using information from other centralized RSPB sources in liaison with staff. The management and conservation information contained in reserve annual reports usually included: vegetation management (e.g. the type of livestock used for grazing, the period grazed and whether mechanical vegetation removal was used); predator control (e.g. whether nests were protected from predation by Red Fox Vulpes vulpes and Badger Meles meles using predator-exclusion fencing (Malpas et al. 2013), whether Red Foxes or Carrion Crows Corvus corone were killed to protect wader eggs and chicks, whether predator-exclusion fencing was applied in combination with lethal control. or whether neither predator-exclusion fencing nor lethal control was applied); and manipulation of site hydrology (e.g. installation of water control features, or excavation to create pools, scrapes or foot drains). Predator control was recorded as being active when at least one individual of Red Fox or Carrion Crow, or one Carrion Crow nest, was removed within the reporting period (hereafter referred to as foxes and crows) (Table S1). We did not include vegetation management in the analyses as the recorded level of detail was not adequate to model this in any meaningful manner.

Climatic data

We created seasonal climatic variables for each year using temperature and rainfall observations from the HadUK 1-km grid monthly climatic data (Hollis *et al.* 2019). The autumn/winter season temperature variable was created as the mean

monthly temperature between October and March. The autumn/winter season rainfall variable was created by summing monthly precipitation from October to March. These variables provide a measure of, in particular, wetness during the winter before waders settle to breed from March onwards, as well as of the severity of the winter cold prior to the breeding season. The spring/summer variables were created similarly using monthly temperature and precipitation data from April, May and June and provide a measure of climatic conditions during the wader breeding season. We paired the seasonal climatic data to reserve sites by selecting the 1-km climate grid that overlapped with each site's centre point (British National Grid projection).

Other covariates

We recorded the area of each site, the former habitat type and date of land acquisition (used to calculate site age) by the RSPB, all of which are held on a central database.

Pre-analysis

To avoid statistical problems in the primary analysis we explored the data for each species prior to specifying the explanatory models (Zuur *et al.* 2010). We checked for correlation between explanatory variables using Pearson's correlation values (excluding variables if Pearson correlation r > 0.7) and examined for collinearity between variables using generalized variance inflation factor values (excluding the collinear variable when the variance inflation factor exceeded 3; Zuur & Ieno 2018).

Models

We used zero-inflated negative binomial (ZINB) and Poisson models to explain the effect that sitespecific factors and management actions have on the number of breeding pairs on lowland wet grassland reserve sites. We used a combination of linear and non-linear effects of the covariates and fitted all models in a Bayesian framework with integrated nested Laplace approximation (INLA) (Rue *et al.* 2009). Each model was initially specified using a ZIN distribution and the Watanabe Akaike information criterion (WAIC) value was obtained and used to compare with less complex models, such as Poisson and negative binomial. Based on the WAIC values, we selected the ZINB model for Redshank, Lapwing and Snipe. The breeding pair counts for these three species contain a large proportion of zeros (Fig. 2; Lapwing = 18.7%; Redshank = 19.7%; Snipe = 38.3%) and counts vary substantially between sites. Curlew was fitted using a Poisson distribution, as the more complex models did not improve the WAIC value. Curlew breeding pair counts contained a relatively low proportion of zeros (Fig. 2; 13.8%) and varied less than the other three species.

The zero-inflation part of the models was fitted using an intercept only. For the count (negative binomial and Poisson) part of the models, site was used as a random intercept in all models. We furthermore considered random intercepts for reserve identity. Spatial dependency between proximate sites was included with the stochastic partial differential equation (SPDE) approach (Lindgren *et al.* 2011, Lindgren & Rue 2015). We used default priors for the fixed effects and noninformative priors for the random effects (Carroll *et al.* 2015). The priors for the second-order random walk functions were penalized complexity priors with parameter values U = 1 and a = 0.01(Simpson *et al.* 2017).

A stepwise model selection approach, based on WAIC values, was used to select the best fitting combination of random effects and to determine whether to include the spatial term. We considered a model improved when the WAIC value decreased by at least 3, and selected the most parsimonious model. Sites without observations were excluded from our analysis. We specified a separate model for each species, as we expected different responses to conservation actions between the study species (Franks *et al.* 2018, Ausden *et al.* 2019, Jellesmark *et al.* 2021).

The breeding count for each species for each combination of site and year was modelled as a function of site size, fox and crow control,



Figure 2. The frequency distribution of breeding pair counts between 1994 and 2018 for Lapwing (n = 1132), Redshank (n = 995), Curlew (n = 311) and Snipe (n = 625) across 79 study sites.

predator-exclusion fencing, precipitation and temperature in the winter and spring season, water control features and water surface features. Foot drains, excavation of ponds and scrapes and other fixed structures, such as earth bunds, were aggregated and included as a single water surface features variable, reflecting improvements in a site's ability to retain surface water during the wader breeding season. If improvements were completed within a site prior to the breeding season in any of the three water surface categories (fixed structures, foot drain, or excavation of pools and scrapes), the variable increases by 1 for each improved category. otherwise the value of the previous year carries over, thus representing the relative water feature improvements between the year of site creation and the breeding season in a given year. Water control structures were modelled similarly but were restricted to a maximum annual improvement of 1. Most predator control requires appropriate permission from the relevant statutory conservation agency. Crow control is performed immediately before and during the wader breeding period, and virtually all fox control during January to March. Lethal control of predators can increase the number of breeding pairs by increasing chick survival and thus the number of birds in the following year (Niemczynowicz et al. 2017, Laidlaw et al. 2020). We modelled this as a lagged relationship so that control efforts after the breeding season in year t_{-1} but prior and during the breeding season in year t_0 were assessed relative to the breeding counts in year t_1 . Predator-exclusion fencing was assumed to be associated with higher breeding numbers through reduced predation risk (Fontaine & Martin 2006) and was therefore modelled relative to the current year's breeding numbers. We included interaction terms between fox control and predator-exclusion fencing, between crow control and predator-exclusion fencing, and between adjustable water control structures and surface water features.

To examine how site age relates to the breeding numbers for the four target species, we fitted site age as a smoothed function using a second-order random walk process. The second-order random walk produces a smoothed term based on the second-order differences that allows us to identify whether a pattern exists between site age and the breeding numbers while accounting for the other explanatory variables. If a pattern exists, and thus a changing effect of site age, the random walk trend diverges from a horizontal line of no change. To allow for a different temporal trend between sites of different former habitats (i.e. drained grassland, arable land, former mineral extraction sites, and mixed arable and grassland), site age was specified individually for each former habitat type using a dummy variable. Site age was included to capture the temporal effect of factors such as ceasing conventional agricultural practices, reseeding former arable land, introducing beneficial grazing regimes, and the overall gradual effect that continuous site management through time is expected to have on populations of breeding birds (Ausden & Bolton 2012).

We assessed two different mechanisms by which rainfall during spring/summer can affect the breeding numbers within a site. Large amounts of precipitation during the spring/summer in year t_0 can flood a site, causing pairs to breed in suboptimal habitats outside reserves (Ratcliffe *et al.* 2005). Precipitation in year t_0 thereby affects the number of breeding birds in year t_0 . Additionally, flooded sites cause breeding pairs to nest on adjacent suboptimal land, leading to reduced breeding productivity and therefore a lower number of birds in year t_1 . Each of these potential mechanisms was tested in separate models.

Posterior parameter mean estimates and 95% credible intervals > 0 on the log scale were considered to show a positive effect on breeding counts; estimates < 0 were considered to show a negative effect. All continuous explanatory variables with linear effects were standardized to make regression coefficients comparable.

All analyses were done in R version 4.0.2. We used the tidyverse packages for data manipulation (Wickham *et al.* 2019) and the ncdf4 package (Pierce 2019) for climatic data in nc format. All models were fitted in INLA (Rue *et al.* 2009). All code used is available at github.com/seanjellesmark.

RESULTS

Between 1994 and 2018, a sum total of 31 665 pairs of the four study species were counted breeding on reserve sites acquired within the study period (17 456 Lapwing pairs; 10 578 Redshank pairs; 1095 Curlew pairs; 2536 Snipe pairs). Lapwings were found on 75 sites, Redshank on 65 sites, Snipe on 39 sites and Curlew on 17 sites. Lapwing and Redshank were widely distributed across all the lowland wet grassland reserve sites,

and on average in higher breeding numbers than Snipe and Curlew (Fig. 2). Curlew occurred primarily in Northern Ireland and Scotland, and Snipe were almost entirely absent from reserves located on the southern and south-eastern coast of England (Supporting Information Figs S1–S4).

The models that included site as the only random effect produced the lowest WAIC values for Lapwing, Snipe and Curlew. Reserve identity was included as an additional random effect for Redshank as it reduced the WAIC value below the predefined threshold value. None of the models was improved by including a spatial term. Model validation indicated that the models for Lapwing, Redshank and Curlew were slightly underdispersed, with a small number of outliers (Supporting Information Figs S5–S8).

Larger sites were associated with higher breeding counts for all wader species except Curlew, although the 95% credible interval for Snipe and Curlew overlapped zero (Fig. 3). Sites with predator-exclusion fencing were associated with higher breeding counts of Lapwing, Redshank and Curlew, although the 95% credible intervals of this effect overlapped zero for all species. Snipe were negatively associated with predator-exclusion fencing. Higher breeding counts for Lapwing and Redshank were generally associated with а combination of fox control and predator-exclusion fencing. The breeding abundance of Redshank and Lapwing was higher on sites with more adjustable water control structures and surface water improvements, but the opposite was true for Curlew and Snipe. However, the credible intervals overlapped zero for all species except for water control structures and Curlew. The interaction between water control and water surface features was positive for Curlew and Snipe but negative for Lapwing and Redshank, with the credible intervals overlapping zero for all species except Snipe. Neither fox nor crow control had a clear effect on the breeding abundance of the target species, with all 95% credible intervals overlapping zero (Fig. 3). The interaction of crow control and predator fencing was negatively associated with breeding abundance of Redshank and Lapwing. High amounts of precipitation in the spring and early summer were negatively associated with breeding numbers for Redshank and Lapwing. There was no clear association between spring or winter temperature, winter rainfall and breeding pairs, and similarly no association between the amount of rainfall in year t_0 and the breeding number in year t_1 (mean \pm 95% credible interval; Lapwing -0.003 ± 0.06 ; Redshank -0.003 ± 0.06 ; Snipe 0.06 ± 0.08 ; Curlew -0.007 ± 0.08).

The relationships between site age and breeding pairs were largely similar for all species within each former land type (Fig. 4). The number of breeding pairs on former drained grasslands increased initially for all the study species but decreased slightly thereafter for Lapwing and Curlew (although these subsequent declines are based on a very small number of sites), whereas both Redshank and Snipe displayed a second, slight increase after around 12 years. For Lapwing, Redshank and Snipe, the effect of site age was more prominent on former arable sites.

DISCUSSION

In this study, we carried out a detailed assessment of the impact of different site-based conservation actions on the number of breeding waders on lowland wet grassland nature reserve sites in the UK. Combining information from annual management reports with climatic data and site counts allowed us to evaluate multiple site-based interventions and the effect of site age on a national scale while controlling for potential confounding variables. We found that excluding foxes and badgers using predator fencing is an effective measure associated with high breeding abundance of Lapwing, Redshank and Curlew. The largest relative increases in breeding numbers were observed in the years immediately after site acquisition. The breeding populations generally increased more on former arable land than on former drained grasslands, which is unsurprising, as arable land undergoes larger habitat changes than drained grassland when transformed into wet grassland.

Our analyses concur with previous studies (Smith *et al.* 2011, Malpas *et al.* 2013) that predator fencing is effective and strongly associated with higher numbers of breeding waders, especially for Lapwing, Redshank and Curlew, though for Curlew, responses to predator control have been mixed (Tharme *et al.* 2001, Fletcher *et al.* 2010). However, fencing a site for predator exclusion is costly and resource-intensive and requires ongoing maintenance. For organizations with a limited budget, such as the RSPB, this means that fences are most often installed on sites that already support high numbers of target species or have the



Figure 3. Posterior parameter estimates and 95% credible intervals for log mean effects of conservation interventions, temperature, rainfall and site size. See Supporting Information Figure S9 for parameter estimates including an offset for site size.

potential to do so. The negative association between predator fencing and breeding populations of Snipe probably reflects the fact that most breeding Snipe on RSPB wet grassland reserves occur on a small number of sites where it has not been practical to instal predator-exclusion fencing, or on an island where there are no foxes or badgers, and not that Snipe prefer to breed outside fenced areas. Hence, we would not necessarily expect a positive relationship between the abundance of breeding Snipe pairs and predatorexclusion fencing.

We did not find a positive association between lethal control of foxes or crows and breeding abundance in the following year. These results are in accordance with Bolton *et al.* (2007), who found



Figure 4. Estimated effect of site age on breeding pairs. The *x*-axis shows years since acquisition on former grassland (left) and former arable (right) sites. The number of sites for each species \times former land type are shown in 5-year intervals. The estimated relationships are presented as smoothed functions with 95% credible intervals. Curlew on former arable land is not included, as the data only contain a single site. Former mineral extraction and mixed arable and grassland sites are not included, as they were too scarce to produce reliable estimates.

no overall effect of predator control on Lapwing population trends. Similarly, Franks *et al.* (2018) found no increase in the likelihood of conservation success for populations of Curlew and Lapwing targeted by predator control. However, our analysis shows that predator fencing leads to higher numbers of Redshank and Lapwing, and that this effect is further increased by additional lethal control of foxes, i.e. carrying out fox control on its own did not appear to increase wader productivity to a high enough level to allow their population to increase. A possible explanation for this is that individual animals removed by lethal control locally may be replaced rapidly from a regional pool, such as removal of territorial crows leading to an influx of other non-breeding crows (Smart al. 2006, Bolton et al. 2007, Eglington et et al. 2008, Fletcher et al. 2010). The initial predator density on sites and on surrounding land therefore influences local effectiveness of predator control. Furthermore, the method and intensity of lethal control also influence its effectiveness. For example, Fletcher et al. (2010) found a positive effect of intensive predator control on breeding numbers and breeding success for Lapwing and Curlew, and Bolton et al. (2007) found that fox control increased nest survival for Lapwing on sites with high initial fox densities. We did not account for initial predator densities, predator densities on land surrounding sites or intensity of predator control, which could have led to different estimates of predator control effectiveness.

Sites with more surface water features were positively associated with breeding abundance for Lapwing and Redshank and negatively associated for Curlew and Snipe. However, none of the associations was strong, with the credible intervals overlapping zero. Other breeding wader studies have demonstrated clear positive responses to management that increases wet conditions within the breeding habitat (Smart et al. 2006, Eglington et al. 2008, Franks et al. 2018). The opportunistic data collection process potentially explains why water control structures, water surface features and local predator control did not show a clear positive effect on breeding abundance. Data were collected from annual management reports written by site managers to describe and monitor local management progress and effectiveness, but did not necessarily use similar terminology or level of detail. We accounted for this lack of detail in our data by creating variables of a more general nature. For example, predator control was modelled as a binary variable, either active or inactive relative to the breeding number in a given year, and the water control variable was essentially modelled as a counter that reflects the number of years a site had improvements made. A more accurate representation of the variables, such as the proportion of shallow water area relative to site size, or other more fine-grained measures of habitat improvements, may have demonstrated the efficacy of the conservation actions. We strongly recommend investment in the greater monitoring of conservation interventions using consistent, standardized and fine-grain methods, recognizing that for many conservation non-governmental organizations (working on limited budgets) this is a challenge and might divert resources away from delivering conservation on the ground.

Estimates of conservation effectiveness from non-experimental data will not have the same level of confidence as estimates from randomized experimental interventions. In particular, estimates will potentially be biased if important variables are systematically different between unobserved treatment levels, or otherwise not accounted for. For example, if larger sites are more likely continuously to receive water control improvements, then site size must be accounted for, as it moderates the likelihood of receiving water control improvements but also breeding abundance. Randomization ensures that such bias is not a concern, as the selection process is unconfounded. However, the primary concern of conservation organizations is to maximize the impact of conservation expenditures, not to undertake evaluations following the highest scientific standards. Such expenditures are constrained by the resources available and are therefore rarely randomized.

We found evidence that management duration (herein our site age variable) is an important factor affecting the number of breeding pairs on reserve sites, and that the effect is different between former land types and species. As a site is acquired and restoration is initiated, breeding populations increase until a local carrying capacity is reached. It should be noted that the decrease we show here after year 20 for Lapwing and Redshank is driven by a limited number of observations, which is reflected in the larger credible intervals and limited number of sites (Fig. 4). Nonetheless, the results support other findings showing that the number of years since land has been transformed into a reserve, and management initiated, are important factors to consider when designing studies and testing site-based conservation measures (Ausden et al. 2019). Considering the impact of interventions through time is important not only for conservation practitioners aiming to understand how to maximize the impact of new conservation measures and land acquisition, but also for scientists evaluating other conservation actions on sites that are being managed to protect species. Likewise, our results show the importance of considering the former management history of reserve sites. If the aim is strictly to increase the breeding abundance of wetland bird species on a national scale, converting arable land may be a better option than converting drained grasslands, as the latter habitat type already serves as breeding habitat for some waders, albeit being suboptimal for most. Other conservation priorities such as preserving populations of invertebrates or plants on existing areas of wet grassland can justify acquisition and restoration of grasslands over arable land. The costs of those two options differ considerably and for conservation organizations that operate under a constrained budget, the cost-benefits of each intervention and potential land acquisition and subsequent management would need to be evaluated.

Site age was the only variable modelled as a non-linear effect. We took this approach because we did not expect a linear effect to adequately capture how suitable habitat develops at a site upon acquisition and subsequent restoration. Rather, we expected an initial strong effect of time, as the effects of ceasing former management manifest themselves, followed by a smaller increase between later years as populations reach carrying capacity. Our results support these assumptions.

Our results demonstrate more generally how breeding abundances of targeted wading bird species associate with site-level conditions and conservation management. The large number of sites ensures that estimates are derived from an array of different conditions and therefore represent the potential range of responses to particular managements. This is illustrated by the large 95% credible intervals (Fig. 3). The large variation in responses reflect the large variation observed in highly stochastic systems such as wetlands. It also means that, by virtue of the large sample, the results should translate to lowland wet grassland managed by other organizations and individuals both within and outside of the UK.

Our results confirm the importance of excluding foxes and badgers using predator-exclusion fencing while ideally also controlling foxes outside these fences for breeding populations of Lapwing and Redshank. Additionally, our results indicate the importance of installing and maintaining wet features, but also demonstrate that more, better data are required accurately to estimate these effects. Despite reserve management for Snipe and Curlew being successful (Jellesmark *et al.* 2021), the effects of specific interventions appear more subtle. Suitability for Snipe is more influenced by soil softness, which is affected by soil type and field water levels (Smart et al. 2008) and is therefore not well represented by the measures of hydrology used in this study. In the case of Curlew, these generally occur on a small number of sites, which limits the type of analyses possible and the power to pick up any significant effects of management. For example, Curlew breed at 2-3 years of age. A longer lag between interventions such as predator control and breeding abundance could therefore have been appropriate (Fletcher et al. 2010). However, as numbers were low, we were not able to model such a lag appropriately, as increasing the number of years between predator control and breeding abundance reduced the sample size to a point where analysis was not possible. Breeding success is the primary cause of population declines for Curlew (Roodbergen et al. 2012). Future research could therefore assess the impact of conservation on Curlew using a measure of breeding success as the outcome of interest instead of abundance of breeding pairs.

We thank the reviewers for insightful comments and suggestions which have improved the manuscript. We are thankful to the RSPB for providing the data and in particular Will George for providing site-specific information in the early stages of this research. This project has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement number 766417. This communication reflects only the authors' view, and the Research Executive Agency of the European Union is not responsible for any use that may be made of the information it contains.

AUTHOR CONTRIBUTIONS

Sean Jellesmark: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead); resources (lead); software (lead); supervision (equal); validation (equal); visualization (lead); writing – original draft (lead); writing – review and editing (lead). Malcolm Ausden: Conceptualization (equal); data curation (lead); formal analysis (supporting); investigation (equal); validation (equal); writing – review and editing (equal). Tim M. Blackburn: Conceptualization (equal); formal analysis (supporting); investigation (equal); methodology (equal); project administration (equal); supervision (equal); validation (supporting); writing - original draft (equal); writing - review and editing (equal). Mike Hoffmann: Conceptualization (equal); formal analysis (supporting); investigation (equal); methodology (supporting); project administration (supporting); supervision (equal); writing - review and editing (equal). Louise McRae: Conceptualization (equal); formal analysis (supporting); investigation (equal); methodology (supporting); project administration (supporting); supervision (equal); writing - review and editing (equal). Piero Visconti: Conceptualization (equal); formal analysis (supporting); funding acquisition (equal); investigation (supporting); methodology (supporting); project administration (supporting); supervision (equal); validation (supporting); writing - review and editing (equal). Richard D. Gregory: Conceptualization (equal); data curation (supporting); formal analysis (supporting); investigation (equal); methodology (equal); project administration (equal); validation (equal); writing - original draft (equal); writing - review and editing (equal).

FUNDING

H2020 Marie Skłodowska-Curie Actions (Grant/ Award Number: '766417').

ETHICAL NOTE

None.

Data Availability Statement

Not applicable.

REFERENCES

- Ausden, M. & Bolton, M. 2012. Breeding waders on wet grassland: factors influencing habitat suitability. In Fuller, R.J. (ed) *Birds and Habitat*: 278–306. Cambridge: Cambridge University Press.
- Ausden, M. & Hirons, G.J.M. 2002. Grassland nature reserves for breeding wading birds in England and the implications for the ESA agri-environment scheme. *Biol. Conserv.* **106**: 279–291.
- Ausden, M., Hirons, G. & White, G. 2019. Wetland restoration by the RSPB what has it achieved for birds? *Br. Birds* **112**: 315–336.

- Ausden, M., Sutherland, W.J. & James, R. 2001. The effects of flooding lowland wet grassland on soil macroinvertebrate prey of breeding wading birds. J. Appl. Ecol. 38: 320–338.
- Bolton, M., Tyler, G., Smith, K. & Bamford, R. 2007. The impact of predator control on lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves. *J. Appl. Ecol.* 44: 534–544.
- Carroll, R., Lawson, A.B., Faes, C., Kirby, R.S., Aregay, M.
 & Watjou, K. 2015. Comparing INLA and OpenBUGS for hierarchical poisson modeling in disease mapping. *Spat. Spatiotemporal Epidemiol.* 14–15: 45–54.
- Eglington, S.M., Gill, J.A., Bolton, M., Smart, M.A., Sutherland, W.J. & Watkinson, A.R. 2008. Restoration of wet features for breeding waders on lowland grassland. *J. Appl. Ecol.* **45**: 305–314.
- Fletcher, K., Aebischer, N.J., Baines, D., Foster, R. & Hoodless, A.N. 2010. Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. *J. Appl. Ecol.* **47**: 263–272.
- Fontaine, J.J. & Martin, T.E. 2006. Habitat selection responses of parents to offspring predation risk: an experimental test. *Am. Nat.* **168**: 811–818.
- Franks, S.E., Roodbergen, M., Teunissen, W., Carrington Cotton, A. & Pearce-Higgins, J.W. 2018. Evaluating the effectiveness of conservation measures for European grassland-breeding waders. *Ecol. Evol.* 8: 568.
- Gilbert, G., Gibbons, D.W. & Evans, J. 1998. Bird Monitoring Methods. Sandy: RSPB.
- Hayhow, D., Eaton, M., Stanbury, A., Burns, F., Kirby, W., Bailey, N., Beckmann, B., Bedford, J., Boersch-Supan, P., Coomber, F., Dennis, E., Dolman, S., Dunn, E., Hall, J., Harrower, C., Hatfield, J., Hawley, J., Haysom, K., Hughes, J., Johns, D., Mathews, F., McQuatters-Gollop, A., Noble, D., Outhwaite, C., Pearce-Higgins, J., Pescott, O. & Powney, G. 2019. State of Nature 2019.
- Hollis, D., McCarthy, M., Kendon, M., Legg, T. & Simpson,
 I. 2019. HadUK-grid—a new UKdataset of gridded climate observations. *Geosci. Data J.* 6: 151–159.
- Jellesmark, S., Ausden, M., Blackburn, T.M., Gregory, R.D., Hoffmann, M., Massimino, D., McRae, L. & Visconti, P. 2021. A counterfactual approach to measure the impact of wet grassland conservation on UK breeding bird populations. *Conserv. Biol.* **35**: 1575–1585.
- Laidlaw, R.A., Smart, J., Ewing, H., Franks, S.E., Belting, H., Donaldson, L., Hilton, G.M., Hiscock, N., Hoodless, A., Hughes, B., Jarrett, N.S., Kentie, R., Kleyheeg, E., Lee, R., Roodbergen, M., Scott, D.M., Short, M.J., Syroechovskiy, E.E., Teunissen, W., Ward, H., White, G. & Gill, J.A. 2020. Predator management for breeding waders: a review of current evidence and priority knowledge gaps. Wader Study 128: 1–12.
- Lindgren, F. & Rue, H. 2015. Bayesian spatial modelling with R-INLA. J. Stat. Soft. 63: 1–25.
- Lindgren, F., Rue, H. & Lindström, J. 2011. An explicit link between Gaussian fields and Gaussian Markov random fields: the stochastic partial differential equation approach. *J. R. Stat. Soc. B Stat. Methodol.* **73**: 423–498.
- Malpas, L.R., Kennerley, R.J., Hirons, G.J.M., Sheldon, R.D., Ausden, M., Gilbert, J.C. & Smart, J. 2013. The use of predator-exclusion fencing as a management tool

improves the breeding success of waders on lowland wet grassland. J. Nat. Conserv. 21: 37-47.

- Niemczynowicz, A., Świętochowski, P., Brzeziński, M. & Zalewski, A. 2017. Non-native predator control increases the nesting success of birds: American mink preying on wader nests. *Biol. Conserv.* 212: 86–95.
- Pierce, D. 2019. ncdf4: Interface to Unidata netCDF (Version 4 or Earlier) Format Data Files. R package version 1.17. Available at: https://CRAN.R-project.org/package=ncdf4 (accessed 20 May 2020).
- Ramsar Convention on Wetlands. 2018. Global Wetland Outlook: State of the World's Wetlands and their Services to People. Gland, Switzerland: Ramsar Convention Secretariat.
- Ratcliffe, N., Schmitt, S. & Whiffin, M. 2005. Sink or swim? Viability of a black-tailed godwit population in relation to flooding. J. Appl. Ecol. 42: 834–843.
- Roodbergen, M., van der Werf, B. & Hötker, H. 2012. Revealing the contributions of reproduction and survival to the Europe-wide decline in meadow birds: review and metaanalysis. *J. Ornithol.* **153**: 53–74.
- Rue, H., Martino, S. & Chopin, N. 2009. Approximate Bayesian inference for latent gaussian models by using integrated nested laplace approximations. J. R. Stat. Soc. B Stat. Methodol. 71: 319–392.
- Simpson, D., Rue, H., Riebler, A., Martins, T.G. & Sørbye, S.H. 2017. Penalising model component complexity: a principled, practical approach to constructing priors. *Stat. Sci.* 32: 1–28.
- Smart, J., Amar, A., O'Brien, M., Grice, P. & Smith, K. 2008. Changing land management of lowland wet grasslands of the UK: impacts on snipe abundance and habitat quality. *Anim. Conserv.* **11**: 339–351.
- Smart, M. & Coutts, K. 2004. Footdrain management to enhance habitat for breeding waders on lowland wet grassland at Buckenham and Cantley marshes, Mid-Yare RSPB Reserve. *Conserv. Evid.* 1: 16–19.
- Smart, J., Gill, J.A., Sutherland, W.J. & Watkinson, A.R. 2006. Grassland-breeding waders: identifying key habitat requirements for management. J. Appl. Ecol. 43: 454–463.
- Smith, R.K., Pullin, A.S., Stewart, G.B. & Sutherland, W.J. 2011. Is nest predator exclusion an effective strategy for enhancing bird populations? *Biol. Conserv.* 144: 1–10.
- Starnes, T., Beresford, A.E., Buchanan, G.M., Lewis, M., Hughes, A. & Gregory, R.D. 2021. The extent and effectiveness of protected areas in the UK. *Glob. Ecol. Conserv.* **30**: e01745.
- Sutherland, W.J., Dicks, L.V., Ockendon, N., Petrovan, S.O. & Smith, R.K. (eds) 2019. What Works in Conservation 2019. Cambridge, UK: Open Book Publishers. https://doi. org/10.11647/OBP.0179
- Tharme, A.P., Green, R.E., Baines, D., Bainbridge, I.P. & O'Brien, M. 2001. The effect of management for red grouse shooting on the population density of breeding birds on heather-dominated moorland. J. Appl. Ecol. 38: 439–457.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S.,

Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V. ... Yutani, H. 2019. Welcome to the Tidyverse. J. Open Source Soft. 4: 1686. https://doi.org/10.21105/joss.01686

- Wilson, A.M., Ausden, M. & Milsom, T.P. 2004. Changes in breeding wader populations on lowland wet grasslands in England and Wales: causes and potential solutions. *Ibis* 146: 32–40.
- Wilson, A.M., Vickery, J.A., Brown, A., Langston, R.H.W., Smallshire, D., Wotton, S. & Vanhinsbergh, D. 2005. Changes in the numbers of breeding waders on lowland wet grasslands in England and Wales between 1982 and 2002. *Bird Study* 52: 55–69.
- WWF. 2020. Living Planet Report 2020. Bending the Curve of Biodiversity Loss: A Deep Dive into Freshwater. Gland, Switzerland: WWF.
- Zuur, A.F. & Ieno, E.N. 2018. GAM and Zero-Inflated Models. Newburgh: Highland Statistics Ltd.
- Zuur, A.F., leno, E.N. & Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1: 3–14.

Received 29 July 2021; revision accepted 3 July 2022. Associate Editor: Ruedi Nager.

SUPPORTING INFORMATION

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

- Figure S1. Mean annual number of breeding Lapwing pairs.
- **Figure S2**. Mean annual number of breeding Redshank pairs.
- Figure S3. Mean annual number of breeding Curlew pairs.

Figure S4. Mean annual number of breeding Snipe pairs.

Figure S5. Lapwing validation. Observed vs fitted (left) and Pearson residuals vs fitted (right).

Figure S6. Redshank validation. Observed vs fitted (left) and Pearson residuals vs fitted (right).

Figure S7. Snipe validation. Observed vs fitted (left) and Pearson residuals vs fitted (right).

Figure S8. Curlew validation. Observed vs fitted (left) and standardized residuals vs fitted (right).

Figure S9. Mean log posterior parameter estimates and 95% credible intervals for conservation interventions, temperature, rainfall and site size.

 Table S1. Variables used in the analysis.