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Concentrating or scattering management in agricultural landscapes: Examining the effectiveness and efficiency of conservation measures



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ABSTRACT

A key issue in conservation is where and how much management should be implemented to obtain optimal biodiversity benefits. Cost-effective conservation requires knowledge on whether biodiversity benefits are higher when management is concentrated in a few core areas or scattered across the landscape, and how these effects vary between species. To address these questions, we examined species-specific behavioural responses of over-wintering farmland birds to enhanced seed availability. In a two-year experiment we first examined the relationship between landscape-scale seed availability and farmland bird density. Then we investigated the relative resource delivery (difference in bird densities between landscapes with and without additional management) and the efficiency (number of individuals supported per unit management) of conservation actions, both at the landscape-scale (*ca* 100 ha) and at the scale of the conservation measures (3.6 ha). The conservation actions were targeted towards ten seed-eating farmland bird species, but we also considered the responses of seven non-targeted and more generalist seed-eating species, seven species that are less dependent on seeds and three species of birds of prey. We found a positive relationship between bird density and landscape-scale seed availability for eleven species and, for four of these species, the slope of this relationship changed before and after a threshold seed density. For two seed-eating specialists, the number of individuals using conservation patches declined with landscape-scale seed availability. In addition, we found that the relative resource delivery declined with landscape scale seed availability for three seed-eating specialists and was independent of landscape-scale seed availability in four other species. Our results suggest that farmland specialists may benefit most from winter food additions if conservation actions result in high landscape-scale seed availability. This may be achieved by concentrating conservation measures or by establishing measures in areas with high baseline seed availability. By contrast, species that can utilize a wider range of habitats and resources may benefit more from scattering measures across larger areas. Therefore, optimal management for the full range of farmland birds in wintertime may require a combination of core areas with concentrated management and more widely distributed smaller patches of conservation measures.

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1. Introduction

A key issue in conservation is where and how much management should be implemented to obtain optimal biodiversity benefits, for example in terms of the number of different species supported (species richness) and abundance of those species. With respect to *where* conservation should be targeted, studies examining the effectiveness of conservation on farmland generally find that biodiversity increases are more pronounced in low-quality landscapes supporting moderate biodiversity levels

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than in high-quality, high-biodiversity landscapes (Tscharrntke et al., 2005; Scheper et al., 2013; but see Kampmann et al., 2008; Batary et al., 2010). The explanation for this is that in high-quality landscapes, biodiversity in intensively managed sites is being subsidised by the continuous colonisation of species from the surrounding landscape, which may mask any biodiversity responses to management. This is not the case in lower-quality landscapes so that conservation-induced differences in biodiversity can be more easily detected, provided that source populations of target species persist that can benefit from conservation. This hypothesis was originally developed by Tscharrntke et al. (2005) using landscape structure as an indicator of landscape quality and species richness as an indicator of biodiversity. However, the theory should apply to any indicator of habitat quality or resource availability and to any indicator of biodiversity (cf. Kleijn et al., 2011). This hypothesis therefore predicts that it is more effective to target conservation actions at medium- to lower-quality areas than at high-quality areas.

A study by Hammers et al. (2015) on a functional group of seed-eating farmland birds supported this prediction. They used winter food availability as an indicator of habitat quality and provided additional winter food to improve habitat quality. They demonstrated experimentally that the relative increase (in experimental versus control areas) in resource use of a group of over-wintering farmland birds decreased with increasing food availability in the wider area surrounding the food patches. Intriguingly, they also showed that the density of individuals per ha of management was independent of the amount of food that was already available in the landscape. This finding has important implications for conservation as it suggests that the conclusions regarding the effectiveness of conservation management may differ depending on whether the *relative effectiveness* or the *conservation efficiency* (i.e. amount of biodiversity supported per ha or per €) of conservation measures is considered. Often, studies evaluating conservation actions only consider relative effectiveness by comparing responses on sites with management relative to sites without management (but see e.g. Aebischer and Ewald, 2004; Smart et al., 2014). However, when the cost-effectiveness of management is considered, conservation efficiency may be a more important indicator than the relative increase in the number of individuals.

Linked to this is the issue of *how* to implement management to obtain optimal biodiversity benefits. Conservation activities can improve the ecological quality of agricultural landscapes, but it is currently unknown how much landscape quality – measured in terms of availability of key resources – should be raised to elicit a response. Since ecological processes are often density-dependent, the effectiveness of conservation actions is likely related to the quantity or density of management. However, few studies have specifically examined the relationship between the quantity of conservation actions and its effectiveness (but see Heard et al., 2007; Hinsley et al., 2010; Carvell et al., 2011). It is particularly relevant to test whether responses are proportional to the amount of conservation, whether conservation actions only trigger a response when habitat quality is raised above a threshold, or whether additional conservation actions do not have any effect when habitat quality exceeds a threshold. Cost-effective use of limited conservation budgets also requires knowledge on whether biodiversity benefits are higher when habitat quality is improved in high-quality patches scattered in low-quality landscapes, or when clustered in larger-scale core areas, and how this varies between species (Siriwardena et al., 2006).

Seed-eating birds are among the farmland animal groups that have suffered greatest population declines in recent decades (Fuller et al., 1995; Donald et al., 2001). One of the main causes of their decline is reduced over-winter survival due to insufficient

seed availability in winter (Newton, 2004). Conservation actions that are regularly implemented to improve winter food availability include set-aside of farmland, stubble fields, managed field margins and wild bird seed mixtures (e.g. Henderson et al., 2004; Vickery et al., 2004; Gillings et al., 2005). Numerous studies have reported positive behavioural (e.g. habitat use) or demographic (e.g. changes in survival, reproduction or population size) responses of farmland bird species in response to such conservation actions (e.g. Newton, 2004; Siriwardena et al., 2007; Baker et al., 2012). However, little is known about how the intensity and spatial configuration of conservation actions affect how farmland birds respond to improved resource availability (but see Siriwardena et al., 2006). Moreover, most conservation programmes are aimed at preventing further declines of rare or target species (Hoffmann et al., 2010), while common or non-target species may show greatest declines in terms of abundance and biomass (Inger et al., 2015). Therefore, investigating the potential side-effects of conservation actions aimed at rare or target species on common or non-target species is important to 'keep the common species common', which is crucial for the continued functioning of ecosystems.

Here, we examine the relationship between landscape-scale winter seed availability and densities of over-wintering farmland birds and test species-specific behavioural responses to experimental increases in winter seed availability in landscapes representing a gradient in food availability. Specifically, we explore where and how much seed additions should be made to obtain optimal biodiversity benefits and how this differs between species. This work extends our previous work on the factors determining the effectiveness of conservation measures. Hammers et al. (2015) have previously used data from this experiment to test one of the key hypotheses explaining conservation effectiveness (ecological contrast hypothesis, see Kleijn et al., 2011), using a 'guild approach' (the pooled number of individuals of a functional group of ten farmland bird species). The current study differs considerably from our previous work. First, Hammers et al. (2015) have not tested whether and how different species respond to management, which we do in the current study. Specifically, here we investigate relationships between seed availability and densities of 27 targeted and non-targeted farmland species. Despite being more complex than the combined responses of a functional group, such species-specific responses are more useful from an applied conservation perspective (e.g. for conservation practitioners). Second, in the current study we investigate whether scattering or clustering conservation measures represents a more effective conservation strategy, a question not considered in our previous work. Finally, we consider how the conclusions may differ depending on whether this question is studied in terms of relative effectiveness or efficiency.

Although behavioural responses (i.e. birds moving to areas with food) cannot be used to establish whether the conservation actions elicit responses at the population level, they can be used as measures of how many birds benefit from the resources provided by conservation actions (e.g. Siriwardena et al., 2008). The gradient in food availability in our study was largely the result of pre-existing conservation practices targeted towards farmland birds or European hamster (*Cricetus cricetus*). This conservation-induced gradient in food availability allowed us to explore how much food needs to be available before species start responding to management and at which food densities species stop responding (i.e. reach saturation densities). This also allowed us to test whether wintering farmland birds show greater increases in resource use when measures are being implemented in areas that already contain much food or in areas with lower initial food availability. In addition, we examine the relative effectiveness (difference in numbers using the resource in areas with versus without enhanced

food availability), as well as the efficiency (the number of birds per unit area or food) of increasing winter food availability along the gradient of pre-existing conservation efforts.

Our specific research questions were: (1) Does the density of over-wintering farmland birds increase with increasing landscape-scale seed availability, do these relationships differ between species, and what are the threshold seed densities at which different species start or stop responding to increased seed availability? (2) Does the relative resource delivery (in experimental versus control areas) of wild bird seed mixtures change with increasing seed availability in the landscape? (3) Does the number of birds in fields with enhanced seed availability change with increasing seed availability in the landscape? (4) Does the number of birds per unit food change with increasing seed availability in the landscape?

2. Material and methods

2.1. Study sites

We performed a large-scale field experiment in ten area-pairs (20 areas in total) of about 100 ha of farmland habitat in the south-eastern part of the Netherlands in the winters of 2011–2012 and 2012–2013 (Supplementary Fig. A1; below we provide a detailed summary of the description of the study sites and experimental design, for full details we refer to Kleijn et al. (2014) and Hammers et al. (2015)). The two study areas within each area-pair were chosen because of their apparent similarity with respect to cropping patterns, landscape structure, size and shape. Subsequent analyses showed that the area-pairs did not differ significantly in terms of the area of woody landscape elements, area size and baseline seed availability (Kleijn et al., 2014; Hammers et al., 2015). Seed availability was experimentally enhanced in one area within each area-pair, leaving the other as a control area. In each treatment area, food availability was enhanced by sowing winter bird seed mixtures on a total area of 3.6 ha (3 separate 1.2 ha food plots, each containing three 0.4 ha subplots sown with one of three mixtures, see Supplementary Table A1, Fig. A1 and Hammers et al., 2015) in spring 2011 and 2012, respectively, and leaving them in the field until April of the next year. The ten area-pairs were situated in areas with contrasting levels of existing baseline food availability (Hammers et al., 2015). In wintertime, conventional farmland in the Netherlands is generally devoid of seeds (Bijlsma, 2013). We therefore selected part of our study sites in areas with pre-existing conservation measures targeting farmland birds (one area-pair) or European hamster (three area-pairs). The conservation measures that were implemented in parts of those areas involved not harvesting crops (2.6–23.1 ha with a variety of cereals and oil seed rape (*Brassica napus*)) in order to provide food and/or cover in winter time (Out et al., 2011). The remaining six area-pairs were located in areas having little (three areas with 0.7–1.1 ha of conservation strips) or no over-wintering seed crops or mixtures for farmland birds.

2.2. Sampling seed availability

Seed availability was estimated in November, January and March in both winters. In each study area, seed availability was sampled both in the experimental food plots and in the non-manipulated parts of the ca 100 ha treatment area. Seed availability was also sampled in all control areas.

2.2.1. Seed availability in food plots

Seed availability in the 3.6 ha food plots was estimated by sampling seeds in above-ground biomass of the sown mixtures as well as by sampling seeds lying on the ground. In order to

determine seed density in experimental plots (in each 0.4 ha subplot), all biomass in two 0.5 × 0.5 m sample plots located in a subplot was harvested, after which the number of seeds per plant species was counted in the lab and the seed weight measured. This resulted in 18 sample plots per sampling round in each experimental area. The summed estimated number of seeds and seed weight for each species were then used to estimate the above-ground food availability in food plots (kg seed 3.6 ha⁻¹) per sampling round in each experimental area. The density of seeds lying on the ground was determined by removing a thin layer of soil in a 0.15 × 0.15 m sample plot located in each above-ground sample plot. After sieving, the number of larger-sized (>1 mm) and smaller-sized (0.8–1 mm) seeds were counted and seed weight was determined for a representative selection of 10 samples per size fraction. Using these average weights and the estimated number of seeds per sample the ground-level food availability in food plots (kg seed 3.6 ha⁻¹) was estimated using the same approach as for the above-ground seed samples.

2.2.2. Baseline seed availability

Baseline seed availability in all study areas was estimated by sampling above-ground and ground-level seed density in all dominant land-use types of the non-manipulated parts of the treatment and the control areas. Seed density (i.e. the combination of above-ground and ground-level seed density) was estimated using the same protocols as in the food plots. Samples were randomly taken from fields with different land-use types in different treatment and control areas and in different years and sample periods (see Table A2). We used a single estimate of the average seed density of all samples per land-use type as our proxy for food availability per land-use type. Samples were slightly biased towards the November period and the first winter, but for the purposes of our study this does not pose a problem as food availability in all study areas is calculated using the same estimate for each land-use type. Although this bias may cause a slight overestimation of seed availability in the control plots, we do not believe this causes a problem as, if anything, it makes our analyses more conservative. Baseline food availability per study area and winter period was calculated by multiplying the cover of each land-use type by average seed density and subsequently summing up the total seed availability in all land-use types in each area. Although we have only one estimate of baseline seed availability in each winter available, we believe this measure acts as an accurate predictor of winter food availability for seed-eating farmland birds in the ca 100 ha areas, as it has been shown to be strongly correlated with both density and species richness of a group of ten of these species in both winters (Hammers et al., 2015). Finally, we corrected for small differences in the size of study areas to obtain baseline food availability estimates expressed in kg seed 100 ha⁻¹.

2.3. Bird surveys

Birds were surveyed during the same periods as the seed sampling: in November, January and March of both winters (i.e. each area was surveyed six times). Surveys were carried out by two or three people walking a standard route covering the whole study area (Kleijn et al., 2014; Hammers et al., 2015). All fields and experimental plots were traversed to flush birds present in the vegetation following standard routes that were generally within 100 m of each point in each study area. Surveys were carried out between 9:00 and 16:00 h and took between two and four hours, depending on how many birds were observed. The treatment area and control area of each area-pair were always counted on the same day but in different order to avoid confounding effects of possible time-related variation in bird numbers. All birds observed were identified to species level and marked on a map. In areas with

food plots, we noted for each observation whether the bird was inside a food plot (i.e. within 10m from its edge) or not (see Hammers et al., 2015).

2.4. Species recorded

In our analyses, we considered 27 bird species that are encountered regularly in farmland in winter in the Netherlands. The conservation measures were targeted towards ten seed-eating farmland species (Table 1). The other species considered included seven more generalist seed-eating species that regularly occur on farmland in winter time and seven species that are less dependent on seeds (Table 1). As the cover and seeds provided by the seed mixtures may attract birds and small seed-eating mammals (e.g. voles), we also considered the responses of three birds of prey (Table 1) that may indirectly benefit through increased prey abundance. Fig. 1 shows the average number of each species in areas with food plots and in control areas. Scientific names of all species are provided in the appendix.

2.5. Statistical analyses

2.5.1. Bird densities in relation to total seed availability and thresholds seed densities (analysis 1)

We investigated whether densities per 100 ha (number of birds in each area divided by area size in ha and multiplied by 100) of each of the 27 species increased with total seed availability

(defined as baseline seed availability plus seed availability in food plots, given in kg seed 100 ha⁻¹). The density of each species and total seed availability were averaged over all months and both years to obtain one value per area (i.e. 20 data points in total) and the significance of the association between these two variables was tested using Spearman rank correlations. Then, in order to estimate threshold seed densities at which farmland birds start or stop responding to increasing seed availability we performed piecewise regressions for all species that showed a significant association with total seed availability. We compared the fit of a model with a single regression slope to the best model with two linear regression slopes around a breakpoint (threshold). For this, we used the 'breakpoints' function in the package strucchange (Zeileis et al., 2002) in R (version 3.1.2). This function uses the Bai and Perron (2003) algorithm for simultaneous estimation of the optimal location of multiple breakpoints. The minimum number of data points required to estimate one segment of the piecewise regression was set to three and we log10 transformed densities and total seed availability to improve model fit.

2.5.2. Relative responses to food provision in relation to baseline seed availability (analysis 2)

We investigated the relative resource delivery (i.e. in number of birds in experimental versus control areas) of experimentally enhancing seed availability, while taking baseline food availability into account. For each species, the density per 100 ha (rounded to the nearest integer) in each survey was the dependent variable (20

Table 1
Bird densities per 100 ha in relation to total seed availability (baseline seed availability plus seeds available in food plots). Significant associations are in bold. In the cases where a significant association was found, we compared a model with a single regression slope with a model containing two separate regression slopes (i.e. before and after a breakpoint) using BIC values (Bayesian Information Criterion; models with a lower value are better supported by the data). For each species the selected model with the lowest BIC value is in bold. Bird densities and total seed availability are averaged over both years and all months (N=20 areas).

Species	Density vs. total seed availability		Breakpoints	
	r_s	P^1	BIC no breakpoints	BIC 1 breakpoint
<i>Targeted species</i>				
tree sparrow	0.52	0.018	61.32	61.53
yellowhammer	0.76	<0.001	44.09	41.85
corn bunting	0.69	<0.001	23.48	-27.47
common reed bunting	0.59	0.007	38.78	24.09
common linnet	0.78	<0.001	49.09	55.12
European greenfinch	0.60	0.005	54.73	41.62
European goldfinch	-0.42	0.065	-	-
common chaffinch	0.48	0.034	-	-
skylark	0.72	<0.001	56.42	62.63
grey partridge	0.48	0.034	-	-
<i>Other seed eating species</i>				
house sparrow	-0.09	0.710	-	-
brambling	0.48	0.031	-	-
meadow pipit	0.04	0.872	-	-
ring-necked pheasant	0.80	<0.001	30.01	34.92
stock dove	0.33	0.160	-	-
wood pigeon	0.36	0.115	-	-
duncock	0.13	0.595	-	-
<i>Species less dependent on seeds</i>				
carrion crow	0.23	0.324	-	-
Eurasian jackdaw	0.27	0.242	-	-
Eurasian magpie	0.29	0.219	-	-
common starling	0.33	0.158	-	-
Eurasian wren	-0.17	0.484	-	-
European robin	-0.33	0.156	-	-
Eurasian blackbird	-0.01	0.967	-	-
<i>Birds of prey</i>				
hen harrier	0.75	<0.001	26.15	27.16
common kestrel	0.82	<0.001	24.28	28.28
common buzzard	0.58	0.008	-3.50	-2.20

1. Benjamini and Hochberg (1995) corrected (False Discovery Rate) significance level is 0.020 instead of 0.05.

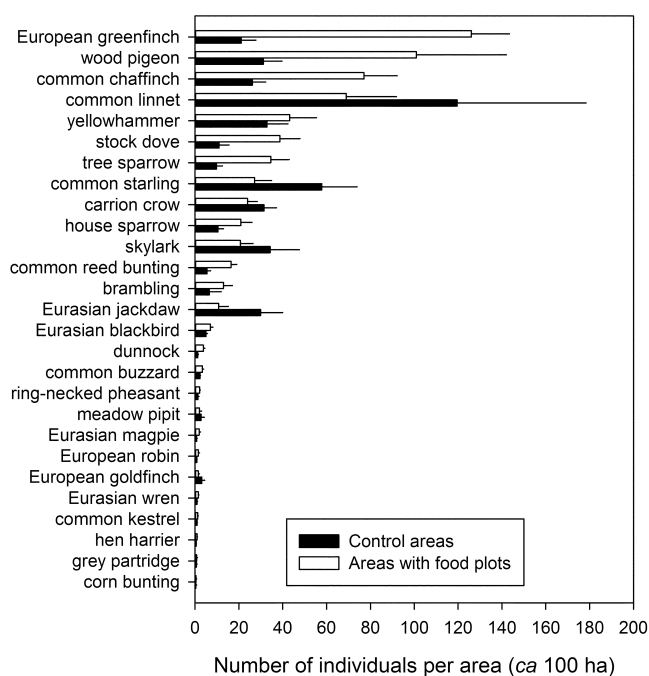


Fig. 1. Number of individuals of 27 bird species in farmland areas with food plots (white bars, $N = 60$ observations in 10 areas) and control areas (black bars, $N = 60$ observations in 10 areas). Data are means and standard errors of raw data. Species are ranked according to their frequency of occurrence in areas with food plots.

areas \times 3 months \times 2 years = 120 data points in total). The presence of food plots (Y/N), \log_{10} baseline seed availability (seed availability in the wider area surrounding the food plots), year (2011–2012, 2012–2013), month (November, January, March) and area of woody landscape features (ha) were included as predictors. Study area nested in area-pair identity was included as a random effect to account for the paired design of our experimental study and the non-independence of observations in the same area. For these analyses we used GLMMs (generalized linear mixed models) with a negative binomial error structure and a log link function. Visual examination of the count data revealed excess zero counts (zero-inflation) in several species. Therefore, for each species a model accounting for zero-inflation was compared with a model without zero-inflation and the model with the lowest AIC value (Akaike Information Criterion, a measure of model fit) was chosen as best model. Subsequently, the interaction between presence of food plots (Y/N) and baseline food availability was tested by adding this term to the model, and was reported separately. A significant interaction with a negative sign would suggest that the relative effect of enhancing food availability declines with increasing baseline seed availability, thus that the relative resource delivery is smaller in areas with high seed availability. We performed the GLMMs with the package `glmmADMB` (version 0.7.7; Fournier et al., 2012). Final models included all fixed effects, irrespective of their significance (cf. Whittingham et al., 2006).

2.5.3. Efficiency: densities in food plots in relation to baseline seed availability (analysis 3)

We investigated whether the number of birds in the 3.6 ha food plots depended on the amount of seed that was available within the food plots and the amount of seed in the surrounding landscape (baseline seed availability). We included only those seed-eating (i.e. the species from the ‘targeted’ and the ‘other seed-eating species’ groups) species that were observed on at least 10 occasions in the food plots (Fig. A2). These GLMMs included a random effect for area to account for multiple observations in each

food plot, and used \log_{10} seed availability within food plots (in kg seed per 3.6 ha), baseline seed availability, year, month, and area of woody landscape features in the 100 ha area as predictors.

2.5.4. Efficiency: the number of birds per unit seed in relation to total seed availability (analysis 4)

To explore whether it is more efficient to concentrate the available resources in a few landscapes or to spread them out over more landscapes that are less resource-rich, we examined whether the number of birds per unit food (number of individuals $100 \text{ ha}^{-1} 10^3 \text{ kg seed}^{-1}$) changes with total food availability. We selected only those species that showed a positive response to increasing total food availability (see Table 1), and those species that significantly increased in areas with food plots, but showed no increase with total seed availability (dunnock and stock dove, see Tables 1 and 2). An increasing number of birds per unit seed with total seed availability in the 100 ha study plots would suggest that birds occur in greater densities in landscapes with large concentrations of seed resources. As seed availability in our study areas is largely determined by conservation measures, this would indicate that concentration of conservation measures is most efficient in attracting birds. Conversely, if the association between the number of birds per unit seed and total seed availability is negative, birds occur in higher densities in areas with scattered conservation measures. The absence of an association between the number of birds per unit seed and total seed availability would suggest that the efficiency is independent of the spatial arrangement of conservation measures. To test this association we followed similar methodology as outlined in Section 2.5.1; for each species we averaged the densities over all months and both years to obtain one average per area, and divided these by total average seed availability per area. Then we used Spearman rank correlations to test the direction and significance of the associations between bird density per kg seed and total seed availability.

In each set of analyses, we corrected the family-wise significance level (initial P value = 0.05) for multiple testing using the Benjamini and Hochberg (1995) false discovery rate (FDR) procedure.

3. Results

3.1. Bird densities in relation to total seed availability (analysis 1)

Densities of seven out of the ten targeted species (tree sparrow, yellowhammer, corn bunting common reed bunting, common linnet, European greenfinch and skylark) showed a significant positive association with total seed availability (Table 1, Fig. 2). Densities of the non-targeted ring-necked pheasant and the three species of birds of prey also showed a significant positive relationship with total seed availability (Table 1, Figs. A3–A5).

For three out of the seven targeted species that showed a significant positive association with total seed availability (tree sparrow, common linnet and skylark), and for ring-necked pheasant and the three birds of prey, the relationship between density and total seed availability was best explained by a model containing a single regression slope (Table 1, Fig. 2). Conversely, for the remaining four targeted species (yellowhammer, corn bunting, common reed bunting and European greenfinch) that showed a significant positive association with total seed availability this association was better explained by two separate regression slopes around a threshold seed density (Table 1, Fig. 2). For yellowhammer, we found a threshold seed density of $\text{ca } 2200 \text{ kg seeds } 100 \text{ ha}^{-1}$, which means that yellowhammer did not occur in our study areas when the seed density was lower than this threshold, but increased sharply with seed availability when seed availability exceeded this threshold (Fig. 2). Corn buntings were absent in all

Table 2

Bird densities per 100 ha in relation to baseline and experimentally enhanced seed availability. Baseline seed availability is the amount of seed which was already present in the landscape; supplementary food is a binary variable stating whether there were food plots (wild bird seed mixtures) in the area or not; NB means that a negative binomial error structure was used and ZINB means that zero-inflated negative binomial error structure was used. Significant variables are in bold.

Species	Baseline seed availability				Supplementary food				Interaction baseline*supplementary food				Type
	Estimate	SE	z	P ¹	Estimate	SE	z	P ²	Estimate	SE	z	P ³	
<i>Targeted species</i>													
tree sparrow	3.07	1.65	1.85	0.064	1.70	0.85	2.01	0.044	-0.13	1.63	-0.08	0.935	NB
yellowhammer	3.23	0.77	4.22	<0.001	1.49	0.62	2.39	0.017	-3.41	1.07	-3.19	0.001	ZINB
corn bunting	27.64	21.09	1.31	0.190	0.63	0.76	0.82	0.411	51.27	48.74	1.05	0.293	ZINB
common reed bunting	2.06	0.62	3.34	<0.001	2.07	0.50	4.14	<0.001	-1.91	1.03	-1.85	0.065	NB
common linnet	5.34	1.32	4.05	<0.001	0.87	0.69	1.27	0.206	-4.19	1.05	-3.99	<0.001	ZINB
European greenfinch	1.77	0.67	2.62	0.009	3.12	0.57	5.49	<0.001	-2.84	0.96	-2.97	0.003	NB
European goldfinch	-1.48	1.09	-1.36	0.175	1.57	1.11	1.42	0.155	3.98	2.35	1.69	0.091	NB
common chaffinch	0.46	0.35	1.33	0.184	1.07	0.31	3.44	<0.001	-0.62	0.65	-0.96	0.339	NB
skylark	2.91	1.24	2.36	0.018	0.70	0.47	1.48	0.139	-0.31	1.01	-0.31	0.759	NB
grey partridge	0.68	0.55	1.24	0.215	0.39	0.69	0.56	0.576	-0.33	1.17	-0.28	0.779	ZINB
<i>Other seed eating species</i>													
house sparrow	-1.12	0.71	-1.57	0.115	1.19	0.62	1.91	0.056	0.25	1.24	0.20	0.842	ZINB
brambling	1.15	0.82	1.40	0.160	0.24	0.80	0.30	0.760	-5.20	2.10	-2.48	0.013	ZINB
meadow pipit	-1.44	0.91	-1.58	0.114	-0.55	0.73	-0.76	0.449	-1.34	1.59	-0.84	0.399	NB
ring-necked pheasant	2.57	0.65	3.95	<0.001	1.28	0.54	2.37	0.018	-1.44	1.07	-1.35	0.177	NB
stock dove	1.18	0.80	1.47	0.141	1.36	0.38	3.54	<0.001	-0.38	0.84	-0.45	0.653	ZINB
wood pigeon	0.84	0.56	1.51	0.131	0.48	0.43	1.11	0.267	1.05	0.78	1.33	0.183	NB
dunnock	-0.02	0.37	-0.04	0.967	1.01	0.28	3.55	<0.001	0.03	0.61	0.05	0.960	NB
<i>Species less dependent on seeds</i>													
carrion crow	0.37	0.47	0.78	0.435	-0.07	0.39	-0.18	0.856	-0.65	0.77	-0.84	0.398	NB
Eurasian jackdaw	-0.79	1.70	-0.46	0.642	0.30	0.61	0.50	0.617	-2.82	1.98	-1.43	0.154	ZINB
Eurasian magpie	2.41	1.41	1.70	0.088	0.55	0.34	1.59	0.111	-0.72	0.66	-1.08	0.278	NB
common starling	0.60	0.40	1.50	0.133	-0.23	0.32	-0.71	0.479	0.36	0.59	0.61	0.542	ZINB
Eurasian wren	0.15	0.39	0.38	0.710	0.20	0.30	0.69	0.490	-0.49	0.61	-0.80	0.420	NB
European robin	-0.43	0.48	-0.91	0.365	0.31	0.32	0.96	0.338	-0.92	0.69	-1.34	0.181	NB
Eurasian blackbird	0.31	0.46	0.67	0.500	0.06	0.19	0.31	0.760	0.11	0.37	0.30	0.760	NB
<i>Birds of prey</i>													
hen harrier	3.21	0.85	3.77	<0.001	0.74	0.48	1.55	0.122	0.04	1.07	0.03	0.973	NB
common kestrel	2.10	0.55	3.81	<0.001	0.41	0.35	1.19	0.233	-0.23	0.76	-0.31	0.757	NB
common buzzard	0.97	0.23	4.19	<0.001	0.22	0.19	1.16	0.246	0.70	0.35	1.98	0.048	NB

1. Benjamini and Hochberg (1995) corrected (False Discovery Rate) significance level is 0.015 instead of 0.05. 2. Corrected significance level is 0.009 instead of 0.05. 3. Corrected significance level is 0.006 instead of 0.05.

areas containing less than *ca* 14000 kg seeds 100 ha⁻¹, but increased with seed availability after this threshold (although densities of this species were always low, Fig. 2). Densities of common reed bunting and European greenfinch increased with seed availability until a *ca* 3300 kg seeds 100 ha⁻¹ before reaching a plateau (Fig. 2).

3.2. Relative responses to food provision in relation to baseline seed availability (analysis 2)

For three targeted species (yellowhammer, common linnet, European greenfinch), the magnitude of the response to experimentally enhanced seed availability depended on baseline seed availability (Table 2, Fig. 3). The sign of the interaction between supplementary food (Y/N) and baseline seed availability was negative (Table 1), which indicates that in these species the increase in resource use in experimental areas relative to control areas declined with baseline seed availability. In other words, the relative use of food provision declines with increasing baseline seed availability in these species.

The densities of four species (common reed bunting, common chaffinch, stock dove and dunnock) were significantly higher in areas with experimentally increased seed availability relative to control areas, independent of baseline seed availability (Table 2).

3.3. Efficiency: densities in food plots in relation to baseline seed availability (analysis 3)

Yellowhammer and tree sparrow showed declining densities in the 3.6 ha food plots with increasing baseline food availability (Table 3). The number of individuals in food plots was unrelated to baseline seed availability in the seven other species considered in this analysis (Table 3).

3.4. Efficiency: the number of birds per unit seed in relation to total seed availability (analysis 4)

Among the 14 species that increased with total seed availability and/or increased in areas with food plots (Tables 1 and 2), we found significant positive associations (FDR corrected $P=0.021$) between bird densities per 100 ha per kg seed and total seed availability for common linnet ($r_s=0.67$, $P=0.001$), corn bunting ($r_s=0.69$, $P<0.001$) and hen harrier ($r_s=0.55$, $P=0.012$) (Fig. 4). Marginally non-significant positive associations were found in yellowhammer ($r_s=0.46$, $P=0.041$) and ring-necked pheasant ($r_s=0.47$, $P=0.035$). We found negative associations for dunnock ($r_s=-0.60$, $P=0.006$), common chaffinch ($r_s=-0.55$, $P=0.012$) and common buzzard ($r_s=-0.80$, $P<0.001$). We found no significant associations for the other six species (all $P>0.109$).

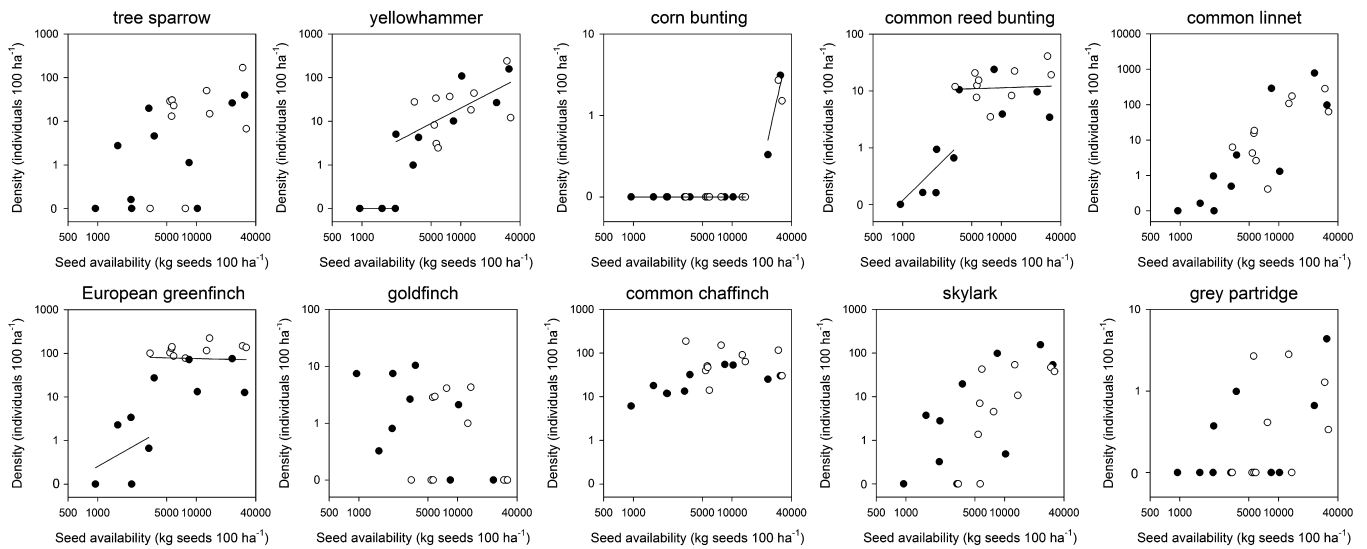


Fig. 2. Bird densities per 100 ha of the ten targeted species in relation to total seed availability (baseline seed availability plus seeds available in food plots). Data are averaged over both years and all months, and presented on a log10 scale for graphical purposes. Closed dots are control areas and open dots are areas with food plots (wild bird seed mixtures). Model predicted regression slopes are provided for the four species where the relationship between bird density and seed density differed before and after a threshold seed density. See Table 1 for the regression information of the association between bird density and seed availability.

4. Discussion

Our results indicate that it is of key importance to consider both the *relative effectiveness* (relative resource delivery) and the *efficiency* of conservation actions when evaluating which conservation strategies best support biodiversity. We found that both types of analyses may lead to different conclusions. Taking both the relative resource delivery and the efficiency into account suggests that scattering measures across an agricultural landscape is more effective than concentrating measures in a few large core areas for European greenfinch (analysis 1 and 2), common reed bunting (analysis 1), common chaffinch (analysis 4), tree sparrow (analysis 3), dunnoek (analysis 4) and common buzzard (analysis 4). For corn bunting (analysis 1 and 4) and hen harrier (analysis 4), concentrating measures in large core areas may offer more value for money than scattering measures. For two targeted species, the conclusions as to whether scattering or concentrating management is a better strategy depended on whether relative effectiveness or efficiency was considered. The relative responses of common linnet and yellowhammer suggest better performance of scattered conservation measures (analysis 2), whereas analyzing the efficiency (analysis 4) suggests that concentration of conservation measures outperforms scattering. This indicates that for these species, winter food provision results in relatively more

concentrated resource use in agricultural landscapes with few conservation actions, but also that bird densities per unit food are nevertheless higher in high-quality landscapes.

A potential limitation of our study is that it addresses behavioural responses to management. It is therefore unknown whether the results can be extrapolated to demographic responses. Although it is probably a reasonable assumption that improved over-winter food availability leads to improved over-winter survival in seed-eating farmland birds (see Newton 2004; Siriwardena et al., 2007), this is not necessarily the case. For example, areas with high food availability may act as an ‘ecological trap’ because they also attract high numbers of predators (De Boer et al., 2013), or demographic effects may only occur during periods of adverse weather. Another potential limitation of our study is that the number of individuals of a species in the landscape at a given time may be influenced by presence of individuals of other species with overlapping diets. Establishing the level of intraspecific competition falls outside the scope of the paper, but may be considered in future studies. Finally, the progressive depletion of seeds during the winter may, at least for some species, lead to a late-winter food shortage. The need for supplementary food could therefore increase towards the end of the winter (Siriwardena et al., 2008). This late-winter food shortage might also affect species-specific responses to food provision in landscapes with

Table 3

Bird counts in the 3.6 ha food plots in relation to the amount of seed which is available in the surrounding landscape (baseline seed availability) and amount of seed which is available inside the food plots (wild bird seed mixtures). NB means negative binomial error structure, ZINB means zero-inflated negative binomial error structure. Significant parameters are in bold.

Species	Baseline seed availability				Food availability inside food plot				Type
	Estimate	SE	z	P ¹	Estimate	SE	z	P ²	
tree sparrow	-3.37	1.18	-2.87	0.004	11.82	4.44	2.66	0.008	NB
yellowhammer	-1.72	0.55	-3.14	0.002	-0.11	1.55	-0.07	0.943	ZINB
common reed Bunting	-0.33	0.36	-0.90	0.369	-0.35	0.84	-0.41	0.679	ZINB
common linnet	-0.16	0.65	-0.25	0.803	-0.16	1.41	-0.11	0.911	ZINB
European greenfinch	-0.53	0.43	-1.23	0.218	0.42	1.00	0.42	0.676	ZINB
common chaffinch	0.68	0.78	0.88	0.378	-2.40	1.67	-1.43	0.151	NB
ring-necked Pheasant	0.81	0.46	1.78	0.076	1.60	1.50	1.06	0.288	ZINB
stock dove	0.52	2.53	0.20	0.839	0.79	4.72	0.17	0.867	NB
dunnoek	-0.76	0.55	-1.39	0.164	-0.96	1.04	-0.93	0.354	NB

1. Benjamini and Hochberg (1995) corrected (False Discovery Rate) significance level is 0.011 instead of 0.05. 2. Corrected significance level is 0.006 instead of 0.05.

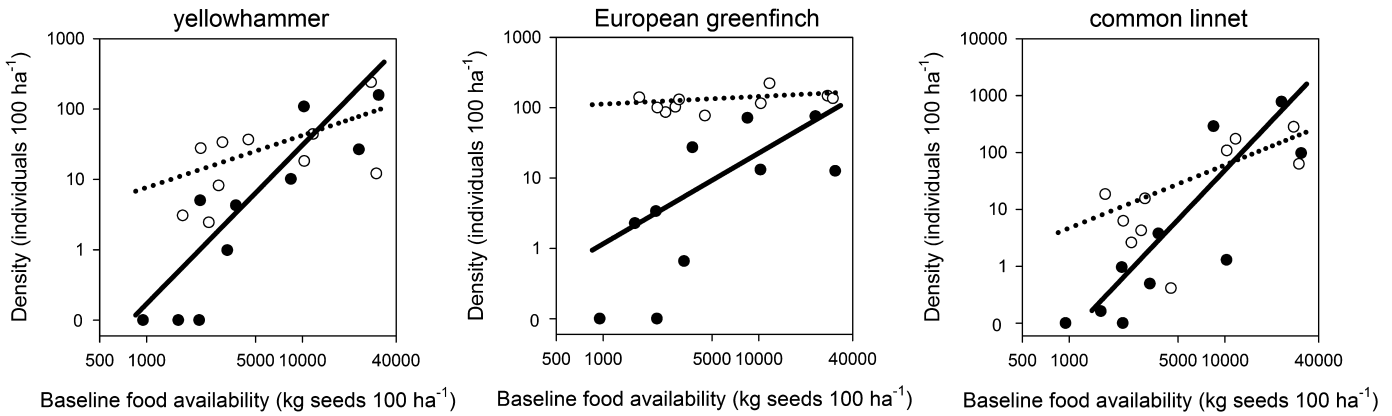


Fig. 3. Bird densities per 100 ha in relation to the amount of seed which is already available in the landscape (baseline seed availability) in 10 control areas (closed dots) and in 10 areas with food plots (3.6 ha experimental winter food provision; open dots). Data are averaged over both years and all months, and presented on a log10 scale for graphical purposes. Lines are model predicted regression slopes of the interaction between food provision and baseline seed availability performed on the full dataset (120 data points, see Materials and methods and Table 2).

different seed availability. For the purpose of this study we considered only one measure of seed availability and bird density for the entire winter, but future studies may investigate whether responses at different time points during winter (e.g. early, mid, late) differ with respect to landscape quality.

For four species we found support for threshold seed densities influencing the response. The fact that yellowhammer and corn bunting (both cereal grain specialists in wintertime, Perkins et al.,

2007) only occurred in our study areas when seed availability exceeds a threshold, and reached highest densities per unit food in areas with high food availability, may help explain their relatively strong population declines in the past decades in north-west Europe following the steady decrease of seed (and especially cereal grain) availability in agricultural areas in wintertime (Bijlsma 2013). By contrast, the two species that did not increase when seed availability exceeded a threshold are species that are able to utilize

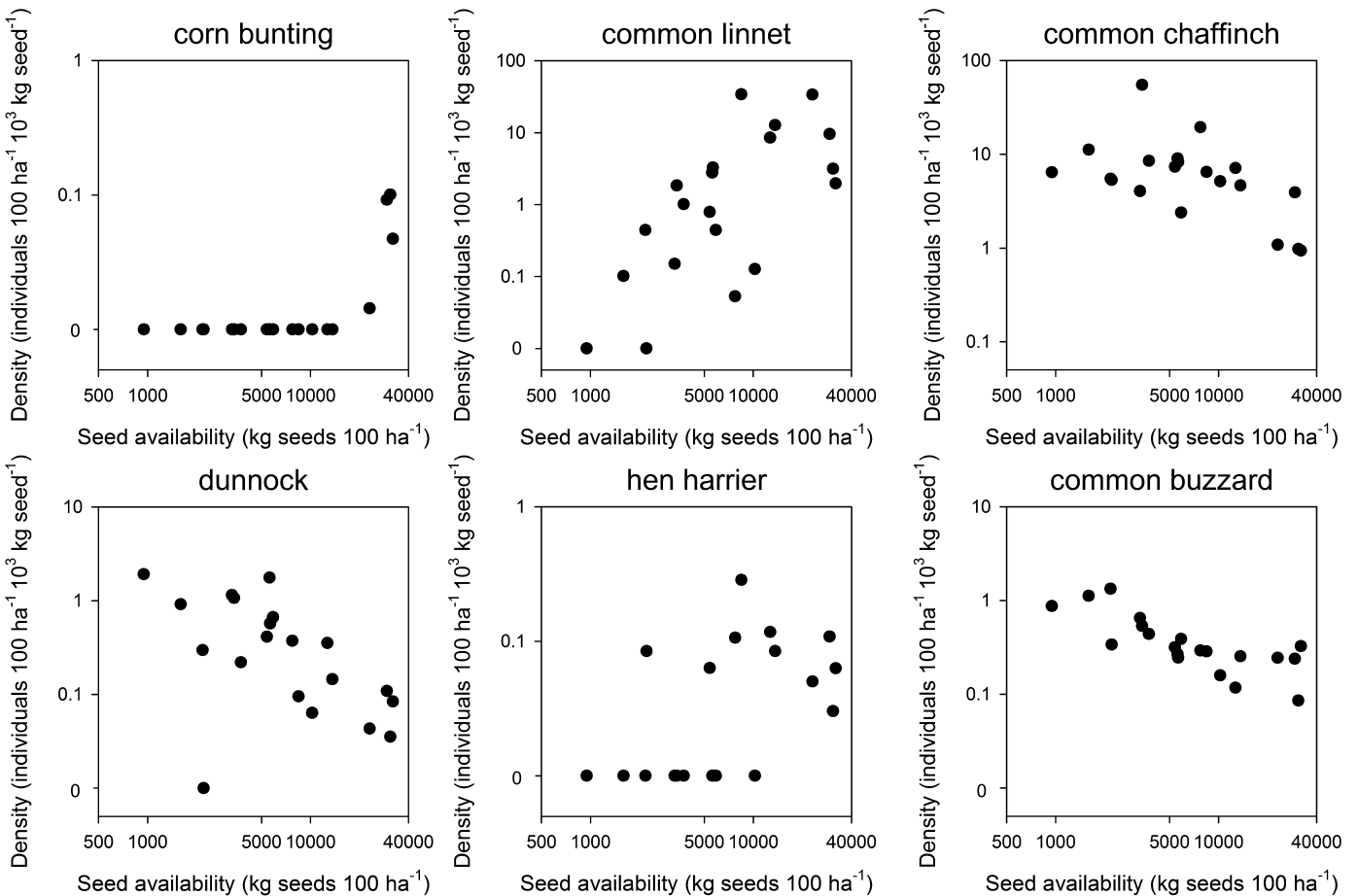


Fig. 4. Bird densities per unit food (number of individuals $100\text{ ha}^{-1} 10^3\text{ kg seed}^{-1}$) in relation to total seed availability in each area ($N=20$). Data are averaged over both years and all months, and presented on a log10 scale for graphical purposes.

a wider range of habitats (greenfinch is common in gardens) and/or food sources (e.g. contrary to the other buntings, reed buntings also forage on maize (Perkins et al., 2007) and consume a range of weed seeds (Orłowski & Czarnecka 2007)). These species, and the other two seed-eating species that showed declining densities per unit food with increasing seed availability (common chaffinch and dunnoek, which both occur in a variety of habitats) most likely have lower demands for high seed availability and appear to benefit more from scattering conservation measures.

We can only speculate about other causes of the contrasting behavioural responses of different farmland bird species with respect to scattering or concentrating conservation measures. A likely cause is a difference in wintering ecology between species. For example, Dutch breeding populations of greenfinch winter locally and are joined by large numbers of Scandinavian birds which show wintering site fidelity (Koopman, 1996). For this species, enhancing food availability may therefore mainly concentrate the local breeding and wintering populations and larger quantities of food may not attract more birds. Scattering conservation measures across the landscape is thus expected to produce the largest benefits for this species. Conversely, Dutch yellowhammer populations winter regionally and distances of more than 10 km between breeding and wintering sites have been recorded (Van Noorden, 2013), which may explain why concentrating conservation measures in high quality landscapes appears more efficient than scattering efforts for this species (based on analysis 1 and 4; see next paragraph for a discussion of the contrasting results from analysis 2 and 3 for this species). Also, the level of competition experienced might explain differences in responses between species. For example, a lower density of a focal species may not only be explained by less food being available, but also by individuals moving to different areas in order to reduce the amount of competition. This effect may be dependent on the relative abundance of a focal species. Rare species (e.g. corn bunting) may move to the highest quality areas because they generally occur in low densities and may therefore face low levels of intra-specific competition at these locations. Conversely, commoner species (e.g. European greenfinch, common chaffinch) occur in higher densities and may need to scatter across the landscape to reduce the level of intra-specific competition in high-quality areas. However, a detailed analysis of the causes of the different responses between species requires detailed data on the scales of spatial aggregation, and regional variation in winter dispersal and migration patterns, which are currently unavailable for most species.

The finding that the relative increase in resource use in areas with food plots compared with control areas decreased with baseline seed availability in common linnet, yellowhammer and European greenfinch (three out of the four most frequently observed specialist seed-eating farmland bird species in our study areas) seems to have driven the response observed by Hammers et al. (2015) of farmland birds as a group. Two species (yellowhammer and tree sparrow) occurred in greatest densities in food plots in the areas with lowest baseline seed availability, whereas the number of individuals in food plots was independent of baseline seed availability in the other seven species. An explanation for this is perhaps that in low-quality landscapes tree sparrow and yellowhammer migrate larger distances to the high-quality food patches, while in areas with overall higher food availability these species remain more scattered throughout the landscape. Indeed, tree sparrow is mainly found in areas with very high seed densities (see Field and Anderson, 2004) and yellowhammers cover relatively large areas relative to other species (e.g. common chaffinch and European greenfinch, Siriwardena et al., 2006).

Although the seed mixtures were targeted at a wide range of seed-eating birds, and therefore contained a variety of crop species providing both larger cereal grains (e.g. for buntings) and smaller (oily) seeds (e.g. for finches), a potential limitation of our measure of seed availability is that the response to winter food provision might differ between species, depending on their food preferences and the availability of that type of seed in the seed mixtures. For example, the lack of a response in goldfinch is probably explained by the scarcity of their preferred food (e.g. thistle and teal seeds, Newton, 1967) in the food plots (D. Kleijn pers. obs.). We found that some non-targeted species (e.g. ring-necked pheasant, dunnoek) also benefitted, despite being less dependent on, or less able to use, seeds from wild bird seed mixtures. From a conservation perspective this is relevant as local populations of many widespread farmland species have recently shown strong declines (Inger et al., 2015).

The greater numbers of birds of prey observed in areas with highest food availability is perhaps explained by a higher abundance of voles (their preferred prey) or passerines in this type of habitat. The absence of significant responses of birds of prey to the establishment of the 3.6 ha areas with wild bird seed mixtures is probably explained by the scale at which these conservation measures were implemented: as these species have large foraging ranges, landscape-scale food availability may be more important than food availability at the plot level.

5. Conclusions

As this study clearly shows, examining the relative effects of management or its efficiency may lead to different conclusions when qualitatively contrasting landscapes are being compared. For conservation managers and policy makers, conservation efficiency may be more relevant than relative effectiveness, whereas conservation scientists may be more interested in the relative effectiveness. The use of both indicators facilitates meaningful comparisons between the effects of conservation actions in intensively farmed areas and those in agriculturally marginal areas (e.g. Batary et al., 2010). There is a great need for such comparisons because agriculturally marginal areas currently host the bulk of the populations of rarer farmland species. Most knowledge, however, is available from the small and declining populations in intensively farmed regions and only few studies have examined the benefits of conservation in high-value farmland areas (Sutcliffe et al., 2015).

Our study suggests that the bird species that are most dependent on farmland (generally species of specific conservation concern because of their strong declines following agricultural intensification) will benefit most if seed availability is high in large areas, which may be achieved by concentrating conservation measures in specific areas or by establishing measures in areas with high inherent seed availability. Providing the high seed availability needed by some of these species (e.g. more than 14000 kg seeds or ca 15 ha conservation measures per 100 ha in early winter for corn bunting) most likely requires the cooperative management by groups of neighbouring farmers (and nature conservation organizations). In our study areas this was generally achieved by spatially targeting management in nature reserves and agri-environment schemes on adjoining farmland.

By contrast, species that are able to utilize a wider range of habitats and/or resources (generally more common and widespread species) may benefit more from scattering measures across as large an area as possible. Scattering conservation measures across large areas of countryside has the added benefit of being more effective in terms of awareness raising, as was obvious from the responses from the general public to the current experiment. The large groups of passerines using the isolated seed-rich fields in

otherwise barren landscapes were noticed and appreciated by many local people. Concentrating measures in a few core areas would expose a much smaller group of people to such clear illustrations of the plight of these species in winter time. Although we have not investigated the effectiveness of concentrated and scattered measures when applied together it seems likely that, when the whole range of farmland birds and support for nature conservation from the general public are considered, the most widespread benefits may be obtained by a combination of a few core areas with large concentrations of measures and more widely distributed smaller patches of conservation measures.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2016.10.005>.

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