Bird Study

ISSN: 0006-3657 (Print) 1944-6705 (Online) Journal homepage: www.tandfonline.com/journals/tbis20

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To cite this article: Thibaut Powolny, Cyril Eraud, Kévin LeRest & Vincent Bretagnolle (2018) Seed depletion and landscape structure affect aggregative response in two wintering passerine birds, Bird Study, 65:1, 98-107, DOI: 10.1080/00063657.2017.1414144

To link to this article: https://doi.org/10.1080/00063657.2017.1414144

BIRD STUDY, 2018
VOL. 65, NO. 1, 98–107
https://doi.org/10.1080/00063657.2017.1414144

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Seed depletion and landscape structure affect aggregative response in two wintering passerine birds

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ABSTRACT

Capsule: Seed abundance but also seed depletion during winter modifies habitat use and aggregation behaviour of Eurasian Sky Lark *Alauda arvensis* and Meadow Pipit *Anthus pratensis*.
Aims: To investigate the effect of seed abundance on the density of two passerine birds, the Eurasian Sky Larks and the Meadow Pipit, at an agricultural landscape scale during winter.
Methods: Bird counts as well as seed density measurements were carried out in winter to quantify the aggregative response of farmland birds to seed abundance from November to March.
Results: Seed resources varied by a factor of ten between crop types, but declined so sharply over the winter that seed abundance was low and similar among crop types by late winter. Sky Larks selected for higher seed density plots, but only at the end of winter when the resources were the lowest. Conversely, Meadow Pipits did not show any aggregative response to seed abundance.
Conclusion: These results show that an uptake of seed-rich habitats in agricultural landscape would be very beneficial for wintering granivorous birds, by fulfilling the late winter 'hungry gap'. The inclusion of seed mixtures in habitats that attract high densities of birds and retain seeds until late winter is of primary interest.

ARTICLE HISTORY
Received 20 June 2017
Accepted 30 October 2017

Understanding the distribution and abundance of organisms represents a challenge for the development of effective conservation planning (Caughley & Sinclair 1994), particularly when trying to anticipate the consequences of environmental changes on biodiversity (Sutherland 1996). Since the 1970s, populations of many farmland birds suffered rapid declines across Europe (Pain & Pienkowski 1997, Chamberlain *et al.* 2000, Donald *et al.* 2001), as a result of marked changes in agricultural practices (Robinson & Sutherland 2002, Benton *et al.* 2003). An important factor suspected to have negatively impacted farmland wintering bird populations is the decrease of winter stubble fields that have been replaced by the general use of winter crops (Gillings *et al.* 2005). The decrease in winter stubble led to a greatly reduced wild flora, and therefore the associated seed stock strongly declined in arable farmland (Robinson & Sutherland 1999). Indeed, a concomitant decline in the overwintering survival rates of granivorous species (Peach *et al.* 1999, Siriwardena *et al.* 2000a, Newton 2004) suggested that winter food availability could be directly involved (Siriwardena *et al.* 1998, Watkinson 2000, Siriwardena *et al.* 2008). During winter, seed stock of wild plants continuously declines with season, since they will not be renewed until the following spring and are continually depleted during the winter either by predation (birds, small mammals, carabid beetles, etc.) or by physical and chemical degradation (Hulme 1998). If wild seed stock is limiting, bird feeding on them in winter, including most farmland passerines (Moorcroft *et al.* 2002, Robinson & Sutherland 2002), may therefore have their survival negatively impacted (Siriwardena 1998, Robinson & Sutherland 1999, Moorcroft *et al.* 2002).

For centuries, control of unwanted plants within crops has been considered to be a critical issue and a limiting factor in crop production (Oerke 2006), hence the widespread use of herbicides has resulted in strong declines of wild plant species that are regarded as weeds in an agricultural context (Marshall *et al.* 2003). Farmland birds are currently a complete guild of conservation concern (Gibbons *et al.* 2006), but disentangling whether their decline results from farming

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Supplemental data for this article can be accessed http://dx.doi.org/10.1080/00063657.2017.1414144.

practices and habitat structure changes or food availability, is not an easy task. The suitability for farmland birds of arable fields as foraging habitats is determined by vegetation cover (Moorcroft *et al.* 2002), habitat (i.e. crop) types, agricultural practices (Chamberlain *et al.* 1999) or landscape composition and heterogeneity (Benton *et al.* 2003, Wretenberg *et al.* 2010) since adjacent habitats have a strong influence on bird abundance and community composition (Berg *et al.* 2002). The aggregative response, which is the spatial association between predator and food abundance (Sutherland 1996), can provide an indication of how habitat use will change in relation to changes in food availability. Though Stephens *et al.* (2003) argued that the study of aggregative responses is time-consuming since data are difficult to collect, it nevertheless represents the most straight-forward tool available to modellers for studying the consequences of change in resource availability.

Most examples of aggregative responses for farmland birds focus on a single crops (Robinson & Sutherland 1999, Moorcroft *et al.* 2002 for stubble, Watkinson 2000 for beet), though many species are known to forage on various habitat types in winter (Geiger *et al.* 2014). The main aim of this study was to quantify field use by two bird species in an intensive farmland landscape, in relation to habitat, seed abundance at the field scale and the spatial arrangement of crops at the landscape scale. Farmland birds and seeds were sampled simultaneously on fields belonging to five different habitat types. This sampling design was repeated throughout the winter season. We evaluated how the combined effects of seed abundance and habitat characteristics influenced variation in field use as foraging areas for the two most abundant species in the study area in winter: the Eurasian Sky Lark *Alauda arvensis* (hereafter Sky Lark) which is considered to be strictly granivorous during the winter and the Meadow Pipit *Anthus pratensis* which forages on seeds and invertebrates (Tellería *et al.* 2016). The aggregative response and the variation in its shape were quantified according to habitat type and structure at landscape scale, and date. Here, we predicted that species aggregative responses change during the winter, depending on seed availability and depletion, with higher seed dependence for Sky Larks when seed densities are low in late winter.

Methods

Study site and sampling

The study was carried out from December to March during the winter 2009–10 on an intensive agricultural landscape (450 km^2) located in central-western France (south of the *Département des Deux-Sèvres*, 46°15′N, 0° 30′W), the Long-Term Ecosystem Research in Europe 'Zone Atelier Plaine & Val de Sèvre', mostly dedicated to cereal crop production. Fields were selected randomly across the study site without prior knowledge of their bird populations, and chosen to cover a wide variety of habitats (see below).

Aggregative response was investigated using two complementary approaches: diachronic and synchronic. The latter relied on a first set of 224 fields (wheat stubble: 29, winter cereal: 51, oilseed rape: 36, alfalfa: 50, grassland: 58) that were sampled from 19 January to 11 February 2010. In those fields, both birds and seeds were sampled simultaneously (see below), during a single visit. In addition, a diachronic approach was used to analyse seed depletion during winter. Sixty fields were randomly selected from among the 224 sampled fields, consisting of 12 fields of each crop type. They were monitored between 15 December 2009 and 15 March 2010; Sky Lark and Meadow Pipit occurring on the fields were counted weekly and seed abundance was obtained monthly.

Bird counts

Fields, which were rectangular in shape, were walked along a diagonal transect to flush the birds present and provide an estimate of abundance of the target species. Care was taken to avoid double counting through observation of movements of previously flushed individuals. We assumed that the detectability of birds did not differ between crops since they were counted in flight. Birds were counted under suitable meteorological conditions of good visibility, no rain and wind speeds below 10 m/s. Birds flying over the field but not landing were not counted. All counts began 1 hour after dawn and were completed at least 1 hour before dusk to avoid biases caused by birds moving to roosting sites. The order in which the observers visited fields was randomized.

Seed sampling and food depletion

Seed densities in the upper layer of the soil were estimated using the following methodology. In each field, the sample consisted of 30 soil cores collected at regular distances along the same diagonal transect assigned to birds counts. Since field size varied greatly (from 0.48 to 10.79 ha), the distance between sampling points varied accordingly, so that 1st and 30th samples were always at the two opposite corners of the field, at a distance of 2 m from the border. Each soil cores was 2 cm in diameter and 2 cm in depth, giving a total volume of soil of approximately 6.3 cm^3. Samples were placed in polythene bags and stored at approximately 4°C to prevent germination. The 'seedling emergence method' was used to estimate seed density (ter Heerdt *et al.* 1996, 1999). Within one month after sampling, the soil material was sieved, using a 3-mm mesh width, to reduce the sample by removing plant fragments and stones. Each sample was spread out on a plastic tray on a steam-sterilized sand mix which provided adequate surface area for germination (Price *et al.* 2010). Afterwards, trays were placed in a random arrangement in a greenhouse and kept moist under controlled conditions, with a diurnal cycle of 14 hours light with a temperature ranging from 15°C to 35°C. These light and temperature conditions were close to the optimum for germination. Trays were kept continually moist with an irrigation system. In addition, as a control against contamination, 30 trays containing only the steam-sterilized sand mix were evenly distributed among the sample trays in the greenhouse. The number of emerged seedlings was counted every three days for ten weeks until the new germination rate approached zero. Every new emergence was removed from trays after being counted. After the ten weeks of germination, 40 samples were chosen (two samples for each crop type (alfalfa, winter cereal, oilseed rape, grassland and stubble) and for each month (December, January, February and March), then washed through sieves to control for the presence of non-germinated seeds potentially edible by birds. No statistical differences in mean number of non-germinated seeds were observed between habitat types (two-way analysis of variance $F_{4,20} = 0.21$, $P = 0.935$) or months ($F_{3,20} = 0.44$, $P = 0.728$).

Data analysis

Count data usually involve a Poisson distribution. However, in our case a Poisson model had a poor fit to count data due to strong over-dispersion, which is not unusual in ecological count data (Richards 2008). We, therefore, used a zero inflated negative binomial (ZINB) model instead of a Poisson model for modelling bird counts. ZINB accounts for both the potential presence of an excess number of zeros (Lambert 1992) and over-dispersion due unexplained heterogeneity (Hinde & Demétrio 1998). In diachronic analyses, field identity was considered as a random effect since the same field was visited weekly. Only 58 fields from the initial 60 were finally used in the analysis because two fields were ploughed early in the winter. Field area was used as an offset, given its large variation, which enabled modelling the density of birds for a unit surface.

Aggregative response analysis aims to link the density of birds with seed density, which was the initial model we built. In our analyses, bird densities are considered as a response variable and explanatory variables are listed in Table 1. We used 500 m circular buffers (followed the outer perimeter of the field) in order to cover the maximum area around fields without overlapping buffers around different pairs of fields. Total boundary lengths between fields, hedge lengths and habitat areas were obtained by geographical information systems analysis using QGIS software. Three interaction terms, including crop types, vegetation height (measured on the field for each count) and date were then explored in addition to single effects. Crop types and vegetation height have been already shown to influence bird feeding ecology (Butler *et al.* 2005). Date was tested because seed depletion was expected and its potential effect on aggregative response was of interest here. Other variables which were also tested included a backward model selection strategy based on the Akaike information criterion was used to identify the most parsimonious models (Burnham & Anderson 2002). Residual spatial autocorrelation was visually checked on the selected models by plotting the variogram of residuals (online Figures S1 and S2). All analyses were performed using R software version 2.14.1 (R Development Core Team 2011) and the package

Table 1. Descriptions of predictors included in statistical models.

Predictors	Variable definition
Boundaries	Measured total boundary structure
Crop type	Stubble; oilseed rape; grassland; winter cereal; alfalfa
Vegetation height	Vegetation height (cm)
Minimum temperature	Temperature minimum (°C) the night before bird counts
Seed density	Measured in number of seed/m^2
Hedges	Total hedge length in a 500 m buffer around field
Permanent area	Total grassland and alfalfa area in a 500 m buffer around field
Oilseed rape area	Total oilseed rape area in a 500 m buffer around field
Annual cereal area	Total winter cereal area in a 500 m buffer around field
Date	Counting date (in Julian calendar)
Field area	Measured in hectares
Seed density × Crop type	Interaction
Seed density × Date	Interaction

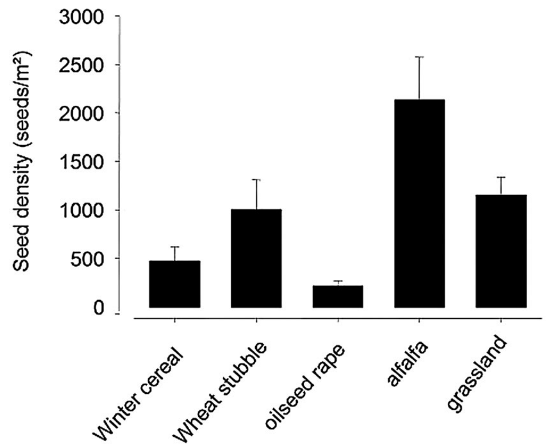

Figure 1. Seed abundance (number of seed/m^2; mean ± se) in five habitat types (winter cereal, wheat stubble, grassland, oilseed rape and alfalfa) from the 19th January to the 11th February 2010. Average and se ($N = 224$ fields).

glmmADMB (glmmadmb.r-forge.r-project.org) for ZINB models.

Results

Seed density during winter

Seedling emergence data suggested that seed densities were highly heterogeneous, with significant differences between habitat types. Alfalfa fields showed ten times more seeds (mean ± se = 2125.6 ± 437.6 seed/m^2) than oilseed rape fields (212.7 ± 54.4 seeds/m^2; Figure 1). However, all habitat types showed seed depletion during winter (Figure 2). For example, the mean seed density of grassland was close to 3000 seeds/m^2 in December and dropped to only 220 seeds/m^2 in March,

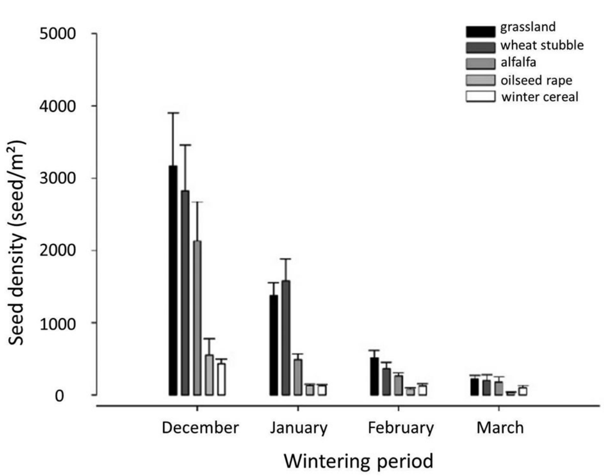

Figure 2. Seed abundance number of (seed/m^2; mean ± se) in five habitat types (winter cereal, wheat stubble, grassland, oilseed rape and alfalfa) over the wintering period at three sampling dates ($N = 58$ fields).

whereas seed density decreased from 430 to 100 seeds/m^2 in winter cereals between the first and last surveys, respectively (Figure 2). By the end of the season, seeds are depleted, but in terms of loss, the change varied substantially between habitat types.

Bird counts in relation to habitats and landscape parameters

Using the synchronic sample design (224 fields, end of January), we found a mean (± se) density of 6.45 ± 1.12 Sky Lark per ha. Sky Lark density varied with crop type and habitat characteristics (all statistics in Table 2): there was a strong positive effect of wheat stubble and oilseed rape, while winter cereal had the lowest densities of Sky Lark. Field use was further influenced by habitat characteristics in a buffer of 500 m, being positively affected by oilseed rape area, permanent crop area and total length of field boundaries (Table 2). Conversely, there was a negative effect of hedges on Sky Lark density. Contrary to expectation, there was no detectable effect of seed densities on Sky Lark abundance (Table 2). During this period, the highest bird densities were observed in oilseed rape, although this crop contained the lowest density of seeds (Figure 3(A)).

Table 2. Fixed effects and interactions terms explaining variation in Sky Lark and Meadow Pipit densities for the synchronic approach ($N = 224$). A backward selection procedure was used, with least significant variables being removed sequentially, until a minimum adequate model was reached in which all variables were retained at $P = 0.05$. Significant results are presented in bold text.

Species	Variables	Estimates	*z*	*P*
Sky Larks	Seed density	−0.14	−1.37	0.17
	Winter cereal	−0.84	−4.05	**<0.0001**
	Wheat stubble	0.49	2.87	**0.0042**
	Oilseed rape	0.47	2.65	**0.008**
	Alfalfa	0.35	1.97	**0.05**
	Grassland	−0.47	−1.96	**0.05**
	Oilseed rape area	0.81	4.64	**<0.0001**
	Minimum temperature	0.17	1.86	0.06
	Hedges	−0.52	−2.92	**0.003**
	Permanent area	1.25	4.75	**<0.0001**
	Annual cereal area	0.76	3.37	**0.0007**
	Boundaries	0.25	2.55	**0.01**
Meadow Pipit	Winter cereal	−0.73	−1.32	0.19
	Wheat stubble	−0.01	−0.03	0.97
	Oilseed rape	−1.15	−1.41	0.16
	Alfalfa	0.089	0.2	0.84
	Grassland	1.81	5.31	**<0.0001**
	Minimum temperature	0.3	2.27	**0.02**
	Seed density	−0.16	−0.64	0.52
	Hedges	−0.43	−2.15	**0.03**
	Seed density × Winter cereal	−0.37	−0.72	0.47
	Seed density × Wheat stubble	0.31	0.64	0.52
	Seed density × Oilseed rape	−0.71	−0.92	0.34
	Seed density × Alfalfa	1.2	3.72	<0.0001
	Seed density × Grassland	−0.44	−1.22	0.22

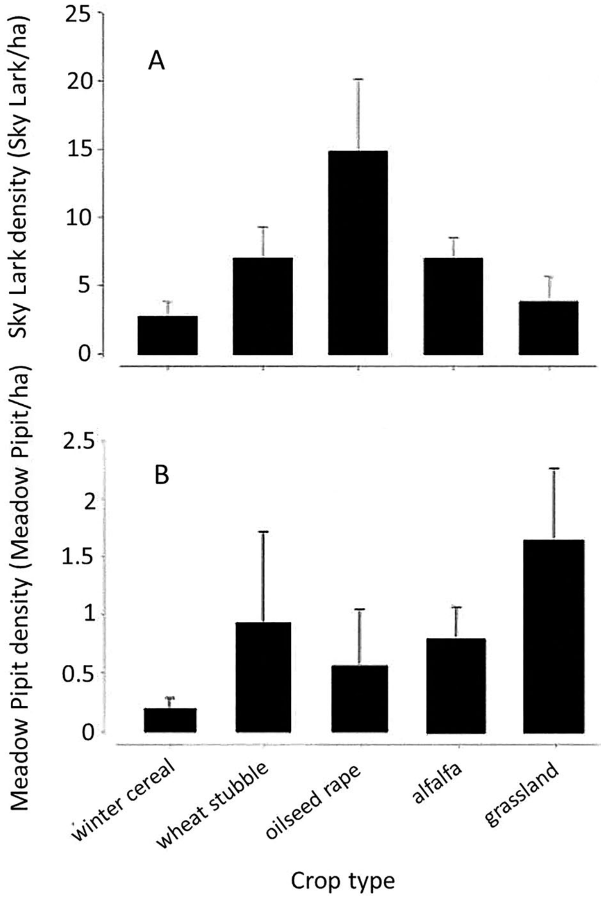

Figure 3. (A) Mean Sky Lark (number of Sky Lark/ha; mean ± se) and (B) Meadow Pipit abundances (number of Meadow Pipit/ha; mean ± se) in five habitat types (winter cereal, wheat stubble, grassland, oilseed rape and alfalfa) from the 19th January to the 11th February 2010 on 224 fields.

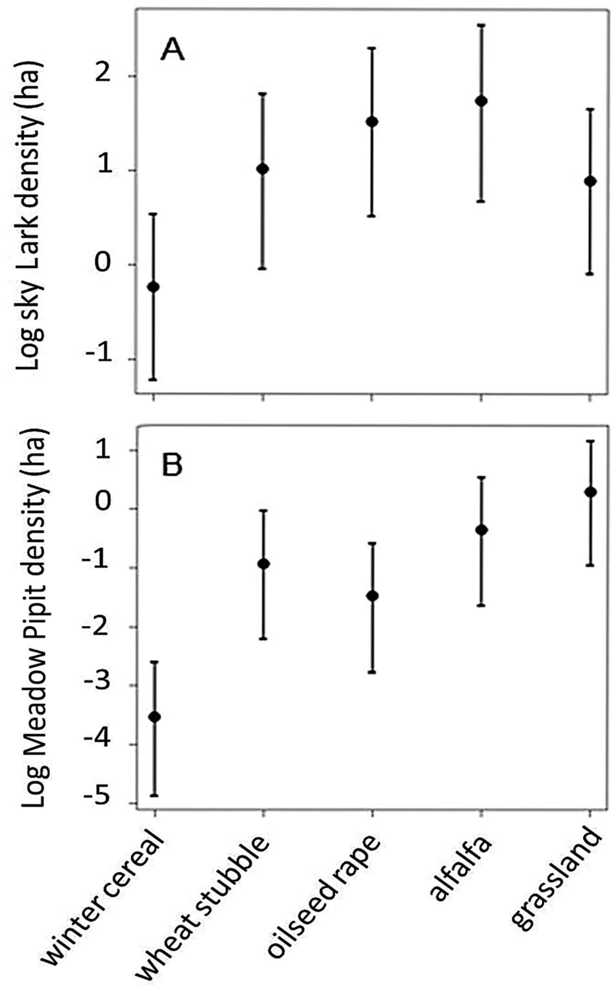

Figure 4. Mean bird abundance of Sky Lark (number of Sky Lark; mean ± se) (A) and Meadow Pipit (number of Meadow Pipit; mean ± se) (B) for each habitat types (winter cereal, wheat stubble, grassland, oilseed rape and alfalfa) across winter (*N* = 58 fields).

The mean (±se) density for Meadow Pipit was 0.82 ± 0.03 individuals per ha. There was a positive effect of the minimum temperature the night before counting on Meadow Pipit densities (all statistics in Table 2). As for Sky Lark, Meadow Pipit density was mainly determined by habitat types, being positively influenced by grassland (Figure 3(B)), and negatively affected by hedges. We only found a significant positive effect of seed density in alfalfa crop, which underlined that finding that crop type drove the aggregative response of Meadow Pipit.

Aggregative response and its seasonal variation

The diachronic sample totalled 720 visits over 58 fields monitored. The mean (±se) densities of Sky Lark and Meadow Pipit were 4.02 ± 0.87 and 0.92 ± 0.09 individuals per ha, respectively. As with the synchronic analysis, we found that Sky Lark densities varied significantly with crop types (Figure 4(A)), and had the highest densities in alfalfa, oilseed rape and wheat stubble. Sky Lark density decreased through the winter (Figure 4(A); all statistics in Table 3). There were additional significant negative effects of field vegetation height and presence of hedges in a buffer of 500 m around the field. The diachronic approach revealed a significant positive interaction between seed density and date on Sky Lark density (Table 3; Figure 5), outlining that the number of Sky Lark was higher where seeds were the most abundant in late winter. This suggested that Sky Larks, as a likely consequence of seed depletion, were increasingly prone to select fields with high seed density as the winter progressed (Figure 5).

For Meadow Pipits, higher densities were found in permanent habitats such as alfalfa and grassland, whereas winter cereals showed the lowest densities (Figure 4(B); Table 3). The analysis of Meadow Pipit

Table 3. Fixed effects terms explaining variation in Sky Lark and Meadow Pipit densities for the diachronic approach ($N = 58$). Models were fitted with field identity as a random factor. A backward selection procedure was used, with least significant variables being removed sequentially, until a minimum adequate model was reached in which all variables were retained at $P = 0.05$. Significant results are presented in bold text.

Species	Variables	Estimates	*z*	*P*
Sky Lark	Winter cereal	−1.21	−3.47	**<0.001**
	Wheat stubble	0.02	0.05	0.96
	Oilseed rape	0.54	1.51	0.13
	Alfalfa	0.74	1.91	**0.05**
	Grassland	−0.08	−0.25	0.80
	Seed density	0.08	0.42	0.67
	Hedges	−0.59	−3.12	**0.002**
	Vegetation height	−0.39	−2.01	**0.04**
	Date	−0.41	−2.26	**0.02**
	Seed density × Date	0.51	3.05	**0.002**
Meadow Pipit	Winter cereal	−2.35	−5.52	**<0.0001**
	Wheat stubble	0.27	0.69	0.49
	Oilseed rape	−0.28	−0.71	0.48
	Alfalfa	0.85	2.21	**0.03**
	Grassland	1.50	4.10	**<0.0001**
	Seed density	−0.05	−0.25	0.80
	Vegetation height	0.44	1.90	0.06
	Rape	0.63	2.49	**0.01**
	Date	−1.36	−5.52	**<0.0001**
	Seed density × Winter cereal	−0.27	−0.57	0.57
	Seed density × Wheat stubble	0.25	0.75	0.45
	Seed density × Oilseed rape	1.11	2.76	**0.006**
	Seed density × Alfalfa	−0.87	−2.26	**0.02**
	Seed density × Grassland	−0.22	−0.78	0.44

densities revealed a negative effect of date (Table 3) and significant interactions between seed density and crop type were observed (Figure 6), positive for oilseed rape and negative for alfalfa (Table 3).

Discussion

We investigated aggregative response of birds feeding mainly on seeds during winter (Sky Larks) or with a mixed diet (seed/insects for Meadow Pipits) according to habitat type, season and seed density. By quantifying seed abundance, field characteristics and landscape variables, our analyses provide strong support for the idea that farmland passerine birds are sensitive to seed abundance, but its effect depends on habitat type, date and diet. Over the winter, the total number of wild plant seeds declined substantially. A similar decline was found by Robinson & Sutherland (1999) and Moorcroft *et al.* (2002) in conventionally farmed cereal stubbles and by Holland *et al.* (2008) in various crop types. Our results indicate that depletion of wild plant seeds between December and March was very sharp (on average, and all crops included, 89.7% depletion). In addition, we detected large variation in seed density among habitats, with higher densities in grasslands

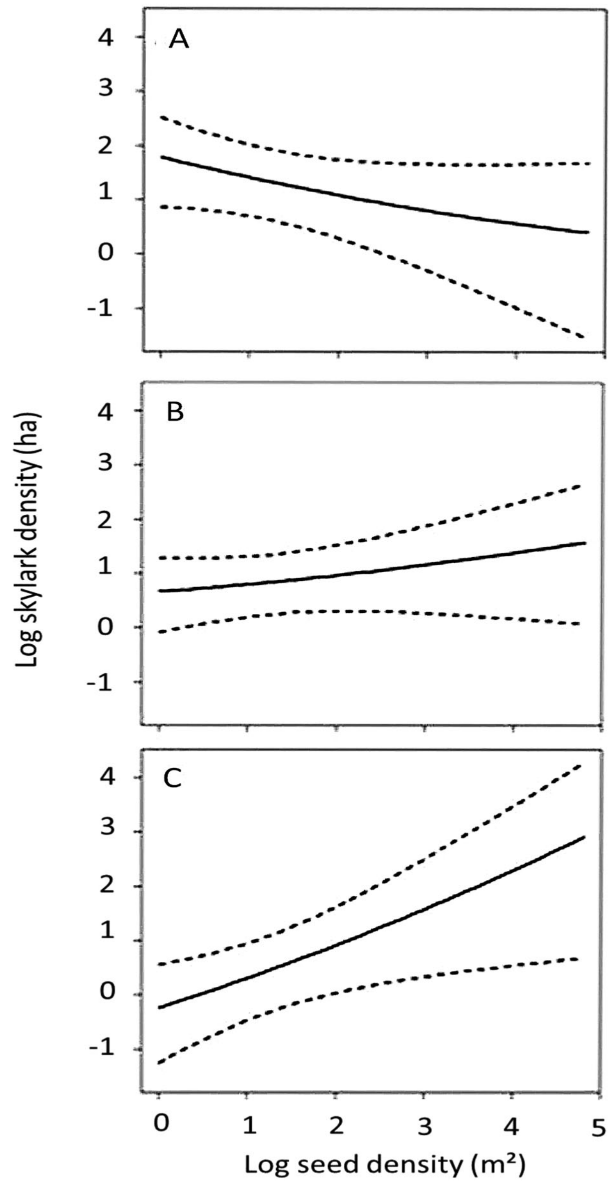

Figure 5. Aggregative responses for Sky Lark *A. arvensis* during the winter 2009–10: (A) January; (B) February; (C) March. These data represent modelled responses from statistical models. Bird and seed densities were log transformed.

compared to winter cereals. In December, grassland, wheat stubble and alfalfa contained the highest densities of seeds, while this difference tended to vanish in late winter. Seed depletion was also greatest on grasslands compared to other habitat types, possibly as a result of greater predation by other granivorous guilds such as rodents and/or carabids (considering no difference in the process of seed natural movements into the deeper soil layers between crop or soil types, Bekker *et al.* 1998).

The seasonal variation in wild seed abundance affected the aggregative response of Sky Larks. During the first weeks of winter, Sky Larks did not

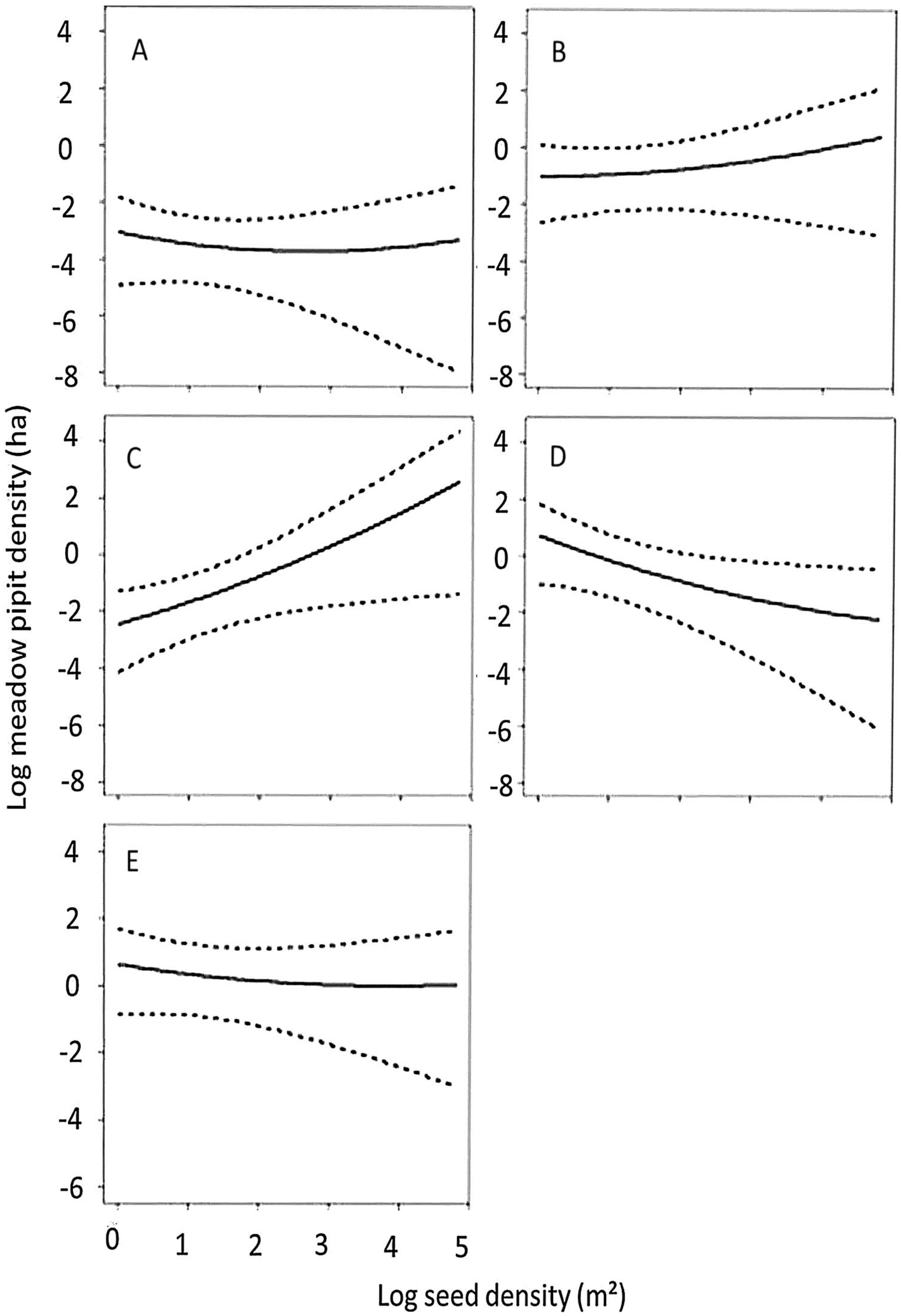

Figure 6. Aggregative responses for Meadow Pipit *A. pratensis* during the winter 2009–10 foraging on (A) winter cereal; (B) wheat stubble; (C) oilseed rape; (D) alfalfa; (E) grassland. These data represent modelled responses from statistical models. Bird and seed densities were log transformed.

show a significant aggregative response with field seed density. However, this relationship became positive and significant as the winter progressed, suggesting that the aggregative response of Sky Lark is not acute when resource is plentiful, but becomes strong once seed densities decline. The absence of an aggregative response in the beginning of winter could be explained by several phenomena. First, and comparative to other farmland landscapes in UK in particular (Robinson & Sutherland 1999, Moorcroft *et al.* 2002), the high quantities of seeds on our study site would allow the birds to find their food independently of seed density, with no advantage in selecting high seed density areas. It is also possible that during these periods of relative abundance, birds select more the quality of seeds than their quantities.

In that case, the fields containing key important species and not a higher quantity would be selected. Alternatively, inter-specific competition between other bird species could involve an absence or even a negative relationship between seed and bird density. Indeed, decreasing the number of individuals in a high seed density area would decrease the inter-specific competition and predation risk (Sutherland 1983).

While Sky Larks were was significantly associated more frequently with alfalfa and oilseed rape, Meadow Pipits showed significant preference for alfalfa and grassland. Winter cereal fields were significantly avoided by both species. Overall the preponderance of positive effects of alfalfa and grassland may indicate a preference for habitats that were less intensively managed. Thus, alfalfa may provide key winter foraging resources in mixed crop areas. However, although grassland seed holds less energy per unit weight than cereal grain (Perkins *et al.* 2007), birds selected permanent habitat types, likely to increase encounter rates with seeds or reduce the seed handling time (Buckingham *et al.* 2011). In contrast to Meadow Pipit, Sky Lark showed a slight avoidance for grassland, as already found in the UK for this species (Donald *et al.* 2001, Gillings & Fuller 2001) suggesting that in addition to seed abundance, vegetation structure may be a significant factor influencing field selection. Following this idea, vegetation height received considerable attention and may be an important determinant of bird distribution for many reasons (Wilson *et al.* 2005, Powolny *et al.* 2015). First, vegetation height affects perceived predation risk (Lima & Dill 1990). For example, European Starlings *Sturnus vulgaris* took longer to respond to an avian predator when foraging within 13 cm long swards than in 3 cm swards (Devereux *et al.* 2006). Chaffinches *Fringilla coelebs* (Butler *et al.* 2005) and Sky Lark (Powolny *et al.* 2014) forage more in short stubble and show shorter vigilance periods than individuals foraging in long stubble when initial seed densities in the patches were equal. Secondly, vegetation height or density may influence seed diversity, abundance and accessibility. It is considerably easier for birds to locate seeds on bare earth than on short grass substrates (Whittingham & Markland 2002). Finally, the thermo-energetic and mobility costs of foraging may be less in short and uniform patches than in dense and heterogeneous vegetation (Butler *et al.* 2005, Wilson *et al.* 2005).

Oilseed rape held high Sky Lark densities, despite having high vegetation height (mean ± se = 12.3 ± 3.8 cm, $N = 12$) and comparatively few seeds. We suggest that the attractiveness of rape fields was a result of specific energetic needs (high fat content in rape seed) or green material rather than seed abundance. During winter, periods of snow-cover and prolonged frost limit foraging access to the ground. Therefore, seeds remain unavailable and birds have to adapt their diet and may consume green material (Green 1978). Such observations were described for Woodpigeon *Columba palumbus* feeding on White Clover *Trifolium repens* and more particularly on oilseed rape leaf (Inglis *et al.* 1997). Oilseed rape represents an abundant source of green material, consumed by Sky Lark and Meadow Pipit in winter (Donald *et al.* 2001; pers. obs.). Furthermore, for dicotyledonous species such as oilseed rape, the energy content is higher compared with the leaf of winter cereal (Green 1978).

Conservation implications

Temporal variation across and within fields in Sky Lark densities indicates that localized reduction of seed resources may limit the number of individuals, especially in late winter. Concomitant with agricultural intensification, food abundance has been reduced by improved harvesting techniques that spill less grain (Wilson *et al.* 1999), post-harvest herbicides (Moreby & Southway 1999), tillage and the early ploughing of stubble (Newton 2004). The availability of seed for granivorous birds is greatly reduced after the end of January, when many stubble fields and seed crops are ploughed according to European directives (2000/60/CE), making any remaining seed unavailable to birds. Within our study area, stubbles showed a clear decline in seed availability through the winter and cover crop areas fell dramatically during February. The progressive loss of areas of seed-rich habitat through the winter will add to the limitations on resource availability caused by the ongoing deterioration in quality of these habitats as seed is depleted. As well as consumption by birds of conservation concern, seeds will also be taken by other bird species, mammals and invertebrates and will become unavailable through germination (especially in late winter), decomposition and covering by soil. Our results, therefore, support the hypothesis that ambient food resources for granivorous farmland birds are at their scarcest in late winter (Siriwardena *et al.* 2008). Given the likely dependence of farmland bird population trends on overwinter survival (Siriwardena *et al.* 2000b) and the observation that declines can be halted by effective increases in winter food availability (Siriwardena *et al.* 2007), it is most likely that food supplies in late winter are the most critical and that this ‘hungry gap’ needs to be filled if population declines are to be reversed. Current agri-environment scheme options do attempt to address the shortfall in winter food availability for farmland birds, but it is very possible that they do not provide sufficient resources in late February and March. Revision of existing agri-environment measures is thus urgently needed to fill this gap. Two forms of change are required: extension of the period (into spring) over which seed-rich habitats are allowed to remain, and management to improve seed content in fields (Robinson 2003). Our study reinforces the view that the conservation of wild plants considered to be weeds in arable crops is an important issue for wintering populations of Sky Larks. In this context, maintaining overwinter stubble and minimizing the use of broad-spectrum herbicides on these fields in autumn are likely to benefit several granivorous bird species (Eraud *et al.* 2015). Hence, the consequences of nitrate-fixing intermediate crops used in France (implementation of the European nitrates directive in France; Arrêté du 23/10/2013. NOR: DEVL1326188A) may have important consequences for wintering populations of passerine birds.

Acknowledgements

We thank Steve Augiron, Willy Gerbault, Rémi Huot, Jean-François Blanc (CEBC-CNRS) and Hervé Bidault (ONCFS) for assistance during fieldwork and reviewers for comments. We are very grateful to the late L. Bruneteau from INRA Lusignan for help during seed germination work. This work is also part of ANR AGROBIOSE.

Funding

This work was supported by the Office National de la Chasse et de la Faune Sauvage (ONCFS) and by the Agence National de la Recherche [ANR ADVHERB].

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