

Weed seeds, not grain, contribute to the diet of wintering skylarks in arable farmlands of Western France

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Abstract Assessing the diet of farmland birds during the wintering period has important implications for conservation. However, for some species such as the skylark, the diet composition remains poorly known across its wintering range. On the basis of gizzards collected in mid-winter over a 10-year interval and in two regions of Western France, we quantified the contribution of seeds and investigated whether the diet differed between sexes, regions and period and whether seeds entered the diet with respect to their size, nutritive value or their spring occurrence within the farmland landscape. Also, the amount of seeds that birds need to consume for meeting their daily energy requirements was assessed by simulation and compared with estimates measured in captive individuals. Thirty-eight seed species belonging to 16 families were

identified in gizzards. All species but one were weeds, and cereal grains were absent from all gizzards. The diet differed slightly between sexes but contrasted between regions and periods. We found no clear evidence for a selective intake based on seed traits. Conversely, our results suggest that weed seeds would enter the diet with respect to their relative occurrence. Our simulation indicated that birds should ingest about 8 g (4200–5600 seeds) to meet their daily requirements. A mean value of 6.7 g per day was measured in captive skylarks. These results suggest that the maintenance of rich weed habitats is a crucial issue for populations of skylarks that overwinter in agricultural landscapes of Western France.

Keywords Skylark · *Alauda arvensis* · Winter ecology · Diet · Weed seeds · Agroecology

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Introduction

Given their energy content, cereal grains and weed seeds form the bulk of the diet of numerous farmland passerines during the critical wintering period (Wilson et al. 1999). Agricultural intensification over the last decades has, however, reduced the availability of these food resources in arable landscapes, and there is now ample evidence that this process has contributed to the population decline of several farmland specialists (Peach et al. 1999; Siriwardena et al. 2000, 2007). In particular, seed-rich habitats such as overwinter stubbles and fodder crops have become scarce in modern farming landscapes, being replaced by winter-sown cereals, silage or maize (Fuller 2000). Efficient harvesting regimes have also substantially reduced the abundance of split grains on remaining stubble fields (Fuller 2000; Robinson and Sutherland 2002). Concomitantly, changes in the timing of herbicide spray and the introduction of broader-spectrum molecules have modified weed diversity and abundance in arable farmlands (Wilson et al. 1999; Sotherton and

Self 2000; Marshall et al. 2001) and the seed bank (Robinson and Sutherland 2002). In this context, quantifying the importance of particular weed seeds in the diet of farmland birds is a fundamental step to address management and conservation issues. An appraisal of the full range of weed seeds consumed by birds in various farming landscapes is also important for predictive purposes. For instance, it may prove helpful for modelling the impact of new cropping practices (e.g. GMH crops, Watkinson et al. 2000), assessing the effects of the use of new herbicides on key weed seeds for birds or evaluating health risks associated with the exposure to pesticides (Crocker et al. 2002).

The Eurasian skylark *Alauda arvensis* is a common farmland specialist that has shown a steep decline in Europe over the last 30 years (PECBMS 2012). While many studies highlighted how agricultural intensification has caused an overall reduction in the breeding productivity of skylarks' populations (Wilson et al. 1997; Chamberlain and Crick 1999; Chamberlain et al. 2000), other studies suggested that food scarcity during the wintering period may have significantly contributed to the decline (Donald et al. 2001; Gillings et al. 2005). Green (1978, 1980) provided the first detailed account of skylark diet composition. On the basis of faecal analyses, his results showed that cereal grains were the most energetically profitable food and formed the bulk of the diet of skylarks in autumn-winter in the UK. Most subsequent studies on skylark diet almost exclusively come from the UK farmlands (e.g. Donald et al. 2001; Clarke et al. 2003; Robinson 2004), with only few anecdotal studies from elsewhere (Schröpfer 1985; Vignes 1996) or out of the native range of the species (e.g. Garrick 1981). To the best of our knowledge, only one study has investigated the diet of wintering skylarks in modern farmlands elsewhere than in UK (Geiger et al. 2014). Although these studies provide a wealth of knowledge, the generalisation of conclusions for migrating skylarks that congregate by millions in South-western Europe in autumn-winter (Hémery et al. 1992; Spaepen 1995) remains to be addressed for developing effective conservation measures.

France is one of the key wintering grounds for migrating skylarks originating from many parts of Europe (Hémery et al. 1992; Spaepen 1995; Henry et al. 2014). Here, we studied the seed fraction of the diet of Eurasian skylarks wintering in Western France. On the basis of gizzard samples, we quantified the contribution of the weeds and grains and analysed whether the seeds in diet contrasted between sexes, geographical regions and over a 10-year interval period. We further compiled seed traits and used data from botanical surveys carried out in one of the study sites to investigate whether seeds entered the diet with respect to their size, their nutritive value or their occurrence within the farmland landscape. Finally, we simulated the amount of seeds that birds need to consume for meeting their daily energy requirements and compared estimates with those measured on captive individuals.

Methods

Data collection

The determination of skylark diet was based on the analysis of 123 gizzards obtained from birds collected by hunting bags (Table 1). Collections were made across two broad geographical regions: Central-western France (departments 17, 79; approximate coordinates 46.2° N, 0.4° W) and South-western France (department 82; approximate coordinates 43.8° N, 1.2° E) where skylarks are known to congregate during the winter (Eraud and Boutin 2008). Both study areas are dedicated to arable farming but slightly contrast in their agricultural regimes: in Central-western France, the primary crops were winter wheat, rape, sunflower, maize and artificial and temporary grasslands, while in South-western France, the primary crops were similar but with more maize and non-rotational set-aside fields. Birds were collected from early December to late January during three winters in Central-western France (1999–2000, 2000–2001 and 2010–2011) and during the winter 2010–2011 in the South (Table 1). The sex of each bird was determined either by molecular analyses performed on tissue samples or by inspection of gonads during post-mortem dissection. Gizzards were stored in 90° alcohol or frozen until examination.

Dietary analysis and seed characteristics

The seed fraction of each gizzard was inspected using a binocular microscope (M125, Leica Microsystems), and seeds were counted and identified on the basis of their size, shape, colour and a reference collection held at the French National Institute for Agricultural Research (INRA, Dijon). A total of 3626 seeds were counted (see Online Resource 1). For 88.9 % of them, the identification was achieved at the species level and for 10.9 % at the genus level. In this later case, plausible species were provided for 79 % of seeds. We failed to identify 0.1 % of all seeds. The taxonomic nomenclature followed the

Table 1 Details on skylark gizzards collected in France

	Past winter 1999–2000	Recent winter 2000–2001	Total	2010–2011
Central-western				
Males	20	23	43	24
Females	7	8	15	9
Total	27	31	58	33
South-western				
Males	–	–	–	18
Females	–	–	–	14
Total				32

Sample sizes are given by region, wintering periods and sex

classification of Kerguelen and Bock (2011). Food items other than seeds (e.g. leaves, invertebrates, grit) were ignored.

The richness and diversity (Shannon index) of the seed fraction were calculated for each gizzard on the basis of seed number. Diet composition was expressed as the frequency of occurrence (i.e. proportion of gizzards in which a particular weed species was detected) and as the percentage of the dry biomass assessed as the product of the number of seeds and their specific dry weights obtained from various sources (see Online Resource 2). For species identified at the genus level, we used the mean dry mass calculated from the most plausible species. When plausible species were undefined, means were based on data from a sample of species of the same genus (see Online Resource 2). To assess the dry mass of unidentified seeds, we used fitted values from the linear relationship between seed specific mass and volume. Assuming that seeds were ellipsoids, the specific volume (expressed in mm^3) was calculated following the formula: $\pi/6 \times \text{length} \times \text{height} \times \text{width}$ (Wright et al. 2000). Using morphological data collated for weed seeds identified at the species/genus level in skylark gizzards ($n=31$, Online Resource 2), we assessed the relationship between specific dry mass and volume as follows: $\log_{10}\text{Mass (mg)} = -0.026 + 0.805(\log_{10}\text{Volume in mm}^3)$; $R^2 = 0.852$. For *Ranunculus parviflorus* (L.) and *Sorghum halepense* (L.) Pers., size measurements were lacking, and the reverse relationship ($\log_{10}\text{Volume (mm}^3) = 0.054 + 1.058(\log_{10}\text{Mass (mg)})$) was used to estimate their dry mass after they were measured using a digital colour camera (DFC295, Leica Microsystems) and an imaging software (LAS V3.7).

We also compiled data on major seed constituents, including the fraction (in percent of dry mass) of lipids and proteins. The data were obtained from the Seed Information Database

(Royal Botanic Gardens Kew, 2008), Azimova and Glushenkova (2012), Ucciani et al. (1996) and Gardarin et al. (2011) and from Bretagnolle et al. (in revision). These data were used to assess the amount of each constituent (as fraction in % of dry mass \times seed dry mass) and derive a crude estimate of the gross energy provided by one seed (or per g^{-1} dry mass). The mineral content was missing for most seed species. Hence, it was omitted in our calculations by considering that the sum of the three major constituents equalled the seed dry mass. Following Gibbons et al. (2006), the seed energy content (kJ seed^{-1} or kJ g^{-1}) was therefore calculated as the sum of the energy provided by seed lipids, proteins and carbohydrates. A conversion factor of 38.94 kJ g^{-1} was used for lipids, and a value of 17.17 kJ g^{-1} was used for both proteins and carbohydrates (Glück 1985 in Diaz 1990; Gibbons et al. 2006). For species identified at the genus level, the fraction of each constituent was assumed as the mean calculated from the most plausible species. When plausible species were undefined, means were based on data from a sample of species of the same genus. Because data (in percent of dry mass) for carbohydrates were lacking, values were calculated as 100 minus the sum of the lipid and protein fractions. When only the lipid fraction was known and assuming a similar energetic equivalence of proteins and carbohydrates, the seed energy content was assessed as follows: $(\text{lipid amount} \times 38.94 \text{ kJ g}^{-1}) + ((\text{seed dry mass} - \text{lipid amount}) \times 17.17 \text{ kJ g}^{-1})$. All data are compiled in Online Resource 3.

Assessment of daily requirements based on gizzard content

The daily food intake (in wet weight, g) was estimated following Crocker et al. (2002) as follows:

$$\frac{\text{Energy Expenditure (kJ day}^{-1}\text{)}}{\text{Energy provided by food (kJ g}^{-1}\text{ dry mass)} \times (1 - \text{Moisture}) \times \text{Assimilation efficiency}}$$

where both moisture and assimilation efficiency are proportions ranging from 0 to 1.

The daily energy expenditure (DEE) was assumed to be $101.4 \text{ kJ day}^{-1}$, following Tieleman et al. (2004). Energy in food was estimated by the amount of energy (kJ g^{-1} dry mass) provided by a typical diet encompassing all species consumed by skylarks. Each seed was assumed to contribute to the diet according to its relative frequency calculated on dry biomass. For our analyses, one gizzard containing a cultivated seed was excluded (see “Results” section). Accordingly, the typical diet was defined on the basis of data from 122 birds (body mass

$40.53 \pm 0.37 \text{ g (SE)}$). Moisture content of weed seeds was set to 11.9 % (Crocker et al. 2002), and assimilation efficiency (i.e. the absorbed fraction of food) was set to 78 % (Christensen et al. 1996; see also Green 1978 for a value of 77.3 %). The daily food intake was separately estimated by region and period because consumed weeds differed.

Weed abundance survey

During the springs 2006–2011, 2030 fields distributed over a 450-km^2 study area were surveyed for weed diversity. This

study area was located in Central-western France (LTER “Zone Atelier Plaine et Val de Sèvre” (ZA-PVS) south of the Département des Deux Sèvres, 46° 11' N, 0° 28' W) and was representative of the arable farming systems of the sites where skylarks were collected in this region. Practically, the occurrence of weed species was recorded at the centre of each sampled field, in 32 plots of 2 m×2 m positioned along the eight arms of a star-shaped array (see Gaba et al. 2010 for more details). Observations were made from March to June. Overall, 135 weed species belonging to 93 genera were identified in winter wheat, while a total of nearly 400 different weed species were counted (all crop types, including grasslands). Plants were identified and named according to Hanf (1982), Jauzein (1995) and Marmarot et al. (1997), except for a few taxa for which small seedling size and the absence of reproductive parts constrained the identification to the genus level. Weed abundance in spring was assessed using frequency of occurrence (i.e. proportion of fields in which a particular weed species was detected; Online Resource 2), and this value was used as a proxy of the presumed seed abundance during the wintering period.

Daily food intake in captive birds

The daily amount of seed intake by skylarks was measured on 17 individuals (10 males and 7 females) temporarily held in captivity. All the birds were wild skylarks trapped by mist netting along the French Atlantic coast during the fall migration (October and November 2009). Individuals were sexed by molecular analysis. Before experiments, birds were housed in outdoor aviaries and fed ad libitum with a commercial seed mix, grit, oilseed rape and tap water (see Powolny et al. 2012 for further details). For experiments, birds were individually housed in cages ($L \times l \times W$, 30×30×30 cm) in late afternoon (mean 16:42 pm) and provided with 10 g (wet) of millet seeds. Mean body mass (\pm SE) prior to the trial was 39.8 (\pm 0.72 g) for males and 33.4 (\pm 0.54 g) for females. Twenty-four hours after the start of the trial, birds were removed and all the remaining seeds were carefully collected from each cage and feeder and then weighed. Experiments were conducted under both natural ambient temperature (mean 7.6 °C \pm 1.8 °C) and light regime, from 28 November to 13 December 2009 at the *Centre d'Etudes Biologiques de Chizé*.

Statistical analyses

The number of seeds, richness and diversity of the diet per gizzard was compared between sexes, regions and periods (1999/2000 and 2000/2001 vs. 2010/2011) using generalised linear models (GLM) fitted with either gaussian (diversity), poisson (richness) or quasipoisson (number of seeds) error distributions and two-way interactions (either region \times sex or period \times sex, see below). Non-significant terms were

sequentially removed by comparing nested models that expressed competing hypotheses. Model selection followed a backward procedure starting by first removing the non-significant interaction, then the least significant main effect. The significance of the last main effect remaining in the model structure was assessed by comparison with the null model. Depending on the error distribution, comparisons were based on either F (for gaussian and quasipoisson errors) or chi-square (poisson error) statistics.

In order to compare seed composition between periods, sex and regions, we used an analysis of similarity (ANOSIM, Clarke 1993) based on Bray-Curtis distance matrices derived from presence/absence data, number of seeds and estimated dry biomass. This analysis uses gizzards and their weed species composition and tests (by permutation, $n=999$) the degree of separation between a priori groups (i.e. sex, region or period). Since our design was imbalanced (e.g. no samples were available for South-western France during the first period), analyses were carried separately on subsets of data : comparisons between regions only included gizzards collected during the winter 2010–2011 whereas the difference between periods was investigated using only gizzards collected in the Central-western France. Because we found some evidence that diet characteristics varied somewhat according to periods and geographical regions (see “Results” below), the relationships between seed traits and the diet composition were explored in separate analyses using Pearson’s correlation coefficients. Similarly, we used Pearson’s correlation coefficient to assess whether the diet composition of skylarks wintering in Central-western France during the winter 2010–2011 reflected the abundance of weed species in this region. We considered for analyses only 33 weed species that were consumed by skylarks (all periods and regions pooled), and for which, field occurrence was assessed. ANOSIM, richness and diversity indices were calculated using the library “vegan” (version 2.0–10, Oksanen et al. 2013) *R* package (R Development Core Team 2008). All other statistical analyses were performed using Statistica 7.1. Unless otherwise specified, means are given \pm 1SD.

Results

Seed abundance, richness and diversity

The mean number of seeds per gizzard was 29.5 (\pm 33.5, range 1–223, $n=123$). Seed abundance per gizzard did not differ between sexes, periods or regions (Table 2). The analysis of gizzards revealed the presence of 38 species, belonging to 16 identified families (Table 4). All species but one (sunflower, *Helianthus annuus*) were weeds. Most of them were dicots with the exception of *Setaria viridis*, *Setaria pumila* and

Table 2 Models explaining variation in abundance, richness and diversity of seeds in the skylark gizzards

Variables	Recent winter ($n=65$)			Central-western France ($n=91$)		
	Effect	Test	<i>P</i> value	Effect	Test	<i>P</i> value
Number of seeds	Region	$F_{1,63}=0.090$	<i>0.765</i>	Period	$F_{1,89}=1.559$	<i>0.215</i>
	Sex	$F_{1,62}=0.225$	<i>0.637</i>	Sex	$F_{1,88}=0.032$	<i>0.859</i>
	Sex \times region	$F_{1,61}=0.808$	<i>0.372</i>	Sex \times period	$F_{1,87}=1.248$	<i>0.267</i>
Richness	Region	$\chi^2_1=2.741$	<i>0.098</i>	Period	$\chi^2_1=4.226$	0.040
	Sex	$\chi^2_1=0.179$	<i>0.672</i>	Sex	$\chi^2_1=1.488$	<i>0.223</i>
	Sex \times region	$\chi^2_1=0.034$	<i>0.853</i>	Sex \times Period	$\chi^2_1=0.255$	<i>0.614</i>
Diversity	Region	$F_{1,63}=3.589$	<i>0.063</i>	Period	$F_{1,89}=7.169$	0.009
	Sex	$F_{1,62}=0.034$	<i>0.855</i>	Sex	$F_{1,88}=1.827$	<i>0.179</i>
	Sex \times region	$F_{1,61}=0.404$	<i>0.527</i>	Sex \times period	$F_{1,87}=0.114$	<i>0.736</i>

Analyses were separately carried out on subsets of data to conform to our imbalanced design. *P* values in italic refer to values when non-significant terms were dropped from the model following a backward elimination. Significant *P* values are in bold

Echinochloa crus-galli. On average, gizzards contained 2.8 (± 1.7 , range 1–10) seed species. Seed richness and diversity differed neither between sexes nor between regions but contrasted between periods in Central-western France (Table 2). Gizzard contents were less rich and less diverse during the past (i.e. 1999–2001) than during the more recent period (respectively, means \pm SE; richness 2.57 ± 0.23 vs. 3.33 ± 0.27 ; Shannon index 0.50 ± 0.06 vs. 0.75 ± 0.08).

Diet composition

Prior to performing analyses on the dry biomass, the single gizzard containing the seed of *Helianthus annuus* was excluded to focus on weed seeds only. Analyses showed that the most frequent seeds were also those that contributed the most to the ingested biomass (overall diet; Pearson's correlation test between occurrence and proportion of the dry biomass, $r=0.856$, $P<0.001$, $n=37$ species and 122 individuals).

Across study periods and regions, three weed species were particularly common: *Chenopodium album*, *Fallopia convolvulus* and *Polygonum aviculare* (Table 4) and 27 species were rare (i.e. $<5\%$ in frequency of occurrence). Similarly to seed richness and diversity, the weed species composition in skylarks' gizzards differed significantly between periods, but the difference was slight (ANOSIM, all $R \leq 0.07$; Table 3). *Lysimachia arvensis*, *Setaria viridis* and *Solanum nigrum* tended to be more frequent in gizzards collected in the past, whereas the inverse was observed during the winter 2010–2011 for *Heliotropium europaeum*, *Polygonum aviculare*, *Geranium* spp. and *Mercurialis annua* (Table 4). When considering the gizzards collected in Central-western France, ANOSIM analyses indicated a significant difference between sexes (ANOSIM, all $R \leq 0.11$; Tables 3 and 4), which was no longer apparent on the basis of the gizzards collected in the South-western region (Table 3). More significantly, our

results showed a clear contrast between regions (ANOSIM, all $R \geq 0.39$, Table 3). Four weed species commonly consumed in Central-western France (*F. convolvulus*, *Polygonum aviculare*, *Geranium* spp. and *Heliotropium europaeum*) were uncommon or absent in gizzards from the South-western region. Inversely, *Persicaria* spp., *E. crus-galli*, *Sorghum halepense* and *Datura stramonium* were more frequently consumed in the South-western region (Table 4).

Appraisal of seed selection

All seeds consumed by skylarks measured at least 1 mm long, most of them (i.e. 93.4 %) being comprised between 1 and 3 mm. In terms of mass and volume, 84.4 and 86.7 % of seeds were lighter than 2 mg and smaller than 3 mm³, respectively. On the basis of weed species found in skylark gizzards, we found no significant correlations between their contribution in the diet (either frequency of occurrence or proportion of dry biomass) and their mass, volume, major constituents or energy content (see Online Resources 2–4).

Conversely, the availability of weed seeds measured in spring within the farmland landscape was correlated with their contribution to the diet, both in terms of frequency of occurrence or proportion in biomass (Pearson's correlation test, $n=33$, $r=0.54$, $P=0.001$ and $r=0.63$, $P<0.001$, respectively; Fig. 1). Some striking exceptions were, however, found. For instance, *Convolvulus arvensis* was found in nearly 60 % of field surveys but did not occur in the gizzards. Another example includes *M. annua* which was found in about 56 % of field surveys but accounted for a mere 2 % of the ingested seed biomass. Conversely, one species frequently consumed by skylarks (i.e. *Heliotropium europaeum*) was detected as a rare weed species during spring botanical surveys (Fig. 1).

Table 4 The seed contribution in the diet of wintering skylarks according to periods, regions and sexes

	Overall		Periods				Regions				Sexes			
	Occurrence	Biomass	Occurrence		Biomass		Occurrence		Biomass		Occurrence		Biomass	
	(123)	(122)	Past (58)	Recent (33)	Past (58)	Recent (33)	West (33)	South (32)	West (33)	South (31)	F (24)	M (67)	F (24)	M (67)
<i>Chenopodium album</i> L.	43.9	16.4	44.8	45.5	15.7	15.8	45.5	40.6	15.8	19.1	41.7	46.3	20.6	14.4
<i>Fallopia convolvulus</i> (L.) Á. Löve	32.5	28.9	34.5	54.5	33.8	34.1	54.5	6.3	34.1	7.4	16.7	50.7	18.7	38.2
<i>Polygonum aviculare</i> L.	32.5	15.8	29.3	66.7	16.1	24.7	66.7	3.1	24.7	1.4	37.5	44.8	27.3	16.8
<i>Persicaria</i> spp. (1)	23.6	7.8	19	12.1	3.3	2.2	12.1	43.8	2.2	29.1	12.5	17.9	4.1	2.6
<i>Lysimachia arvensis</i> (L.) U. Manns & Anderb.	17.9	2.7	25.9	6.1	4.4	0.2	6.1	15.6	0.2	1.6	16.7	19.4	7.9	1.5
<i>Setaria viridis</i> (L.) P. Beauv.	17.9	5.8	34.5	6.1	10.8	0.2	6.1	–	0.2	–	16.7	26.9	3.9	8.0
<i>Echinochloa crus-galli</i> (L.) P. Beauv.	17.1	1.9	1.7	6.1	0.1	0.7	6.1	56.3	0.7	8.5	4.2	3.0	1.1	0.1
<i>Solanum nigrum</i> L.	16.3	3.0	19	9.1	4.3	0.7	9.1	18.8	0.7	2.9	8.3	17.9	1.7	3.4
<i>Geranium</i> spp. (2)	13.8	5.8	12.1	30.3	7.1	7.1	30.3	–	7.1	–	12.5	20.9	7.2	7.1
<i>Amaranthus</i> spp.	11.4	0.6	13.8	12.1	0.9	0.1	12.1	6.3	0.1	0.3	12.5	13.4	0.1	0.8
<i>Heliotropium europaeum</i> L.	11.4	1.2	1.7	39.4	0.5	3.4	39.4	–	3.4	–	25.0	11.9	2.4	1.2
<i>Sorghum halepense</i> (L.) Pers.	4.9	3.1	–	–	–	–	–	18.8	–	16.7	–	–	–	–
<i>Datura stramonium</i> L.	4.1	1.6	–	–	–	–	–	15.6	–	8.7	–	–	–	–
<i>Mercurialis annua</i> L.	3.2	0.6	1.7	9.1	0.1	2.0	9.1	–	2.0	–	8.3	3.0	1.2	0.6
<i>Erodium cicutarium</i> (L.) L'Hér.	2.4	0.5	–	9.1	–	1.7	9.1	–	1.7	–	4.2	3.0	0.2	0.7
<i>Euphorbia helioscopia</i> L.	2.4	0.3	1.7	6.1	0.4	0.3	6.1	–	0.3	–	4.2	3.0	1.3	0.1
<i>Setaria pumila</i> (Poir.) Roem. & Schult.	2.4	0.1	–	–	–	–	–	9.4	–	0.6	–	–	–	–
<i>Stellaria media</i> (L.) Vill.	2.4	0.2	3.4	–	0.4	–	–	3.1	–	0.1	–	3.0	–	0.3
<i>Digitaria sanguinalis</i> (L.) Scop.	1.6	0.3	–	–	–	–	–	6.3	–	1.4	–	–	–	–
<i>Poa annua</i> L.	1.6	<0.1	–	–	–	–	–	6.3	–	0.1	–	–	–	–
<i>Ranunculus</i> spp. (3)	1.6	0.1	–	–	–	–	–	6.3	–	0.5	–	–	–	–
<i>Vicia sativa</i> L.	1.6	1.2	–	3.0	–	3.5	3.0	3.1	3.5	1.3	–	1.5	–	1.6
<i>Alopecurus myosuroides</i> Huds.	0.8	0.1	–	3.0	–	0.3	3.0	–	0.3	–	4.2	–	0.5	–
<i>Chenopodium hybridum</i> L.	0.8	<0.1	1.7	–	0.1	–	–	–	–	–	4.2	–	0.2	–
<i>Convolvulus arvensis</i> L.	0.8	0.6	1.7	–	1.1	–	–	–	–	–	–	1.5	–	0.9
<i>Helianthus annuus</i> L.	0.8	–	–	–	–	–	–	3.1	–	–	–	–	–	–
<i>Kickxia</i> spp. (4)	0.8	0.2	1.7	–	0.3	–	–	–	–	–	–	1.5	–	0.3
<i>Lolium</i> spp.	0.8	0.1	–	3.0	–	0.3	3.0	–	0.3	–	4.2	–	0.5	–
<i>Ranunculus parviflorus</i> L.	0.8	<0.1	1.7	–	0.1	–	–	–	–	–	–	1.5	–	0.1
<i>Ranunculus sardous</i> Crantz	0.8	0.1	1.7	–	0.3	–	–	–	–	–	4.2	–	0.7	–
<i>Rumex</i> spp.	0.8	0.1	1.7	–	0.1	–	–	–	–	–	–	1.5	–	0.1
<i>Sherardia arvensis</i> L.	0.8	0.6	–	3.0	–	2.3	3.0	–	2.3	–	–	1.5	–	1.0
<i>Silene</i> spp.	0.8	0.1	–	3.0	–	0.4	3.0	–	0.4	–	–	1.5	–	0.2
<i>Verbena officinalis</i> L.	0.8	<0.1	1.7	–	<0.1	–	–	–	–	–	–	1.5	–	<0.1
Unidentified (four species)	3.2	0.2	1.7	6.0	0.1	0.1	6.0	3.1	0.1	0.3	12.5	–	0.5	<0.1

Data are expressed in percentages and refer to either the proportion of gizzards in which a particular seed species was detected (Occurrence) or the proportion of the dry biomass summed by periods, regions or sexes (Biomass). Periods refer to past (1999–2001) and recent winters (2010–2011) and concern only individuals collected in Central-western France (West). The comparison between regions is based only on gizzards collected during the winter 2010–2011. Sex-specific diets are shown and include only gizzards collected in the Central-western region over all periods. Sample sizes are given in brackets. Plausible species are either (1) *P. lapathifolia* (L.) Delabre or *P. maculosa* Gray, (2) *G. columbinum* L. or *G. dissectum* L., (3) *R. bulbosus* L. or *R. repens* L. or (4) *K. elatine* (L.) Dumort or *K. spuria* (L.) Dumort

Table 3 Results of analyses of similarity (ANOSIM) based on similarity matrices derived from occurrence data, number of seeds and dry biomass

Grouping factor	Similarity matrix	ANOSIM statistics		Dataset
Period	Occurrence ($n=91$)	$R=0.066$	$P=0.016$	Region: Central-western France Period: past and recent winters
	No. of seeds ($n=91$)	$R=0.052$	$P=0.042$	
	Biomass ($n=91$)	$R=0.030$	$P=0.175$	
Sex	Occurrence ($n=91$)	$R=0.097$	$P=0.018$	Region: Central-western France Period: past and recent winters
	No. of seeds ($n=91$)	$R=0.080$	$P=0.036$	
	Biomass ($n=91$)	$R=0.107$	$P=0.018$	
Sex	Occurrence ($n=32$)	$R=0.035$	$P=0.208$	Region: South-western France Period: recent winter
	No. of seeds ($n=32$)	$R=0.022$	$P=0.291$	
	Biomass ($n=31$)	$R=0.031$	$P=0.238$	
Region	Occurrence ($n=65$)	$R=0.430$	$P=0.001$	Region: all Period: recent winter
	No. of seeds ($n=65$)	$R=0.394$	$P=0.001$	
	Biomass ($n=64$)	$R=0.400$	$P=0.001$	

The subsets of data from which analyses were performed are indicated. Sample sizes are given in brackets. Significant P values are in bold and denote dissimilarities between groups

Daily food intake

On the basis of our estimates of what could be a typical diet in free-ranging skylarks, 1 g (dry mass) would provide about 19 kJ, depending of the region and period (Online Resource 5). Assuming a DEE of $101.4 \text{ kJ day}^{-1}$ and a diet exclusively based on seeds, we thus estimated that birds should ingest about 7.9 g (wet) of seeds to meet their daily requirements. Taking into account the seed-specific energetic content, this would represent from 4200 to 5600 seeds per day (Online Resource 5). On average, captive skylarks ingested 6.7 (± 0.3 g) of millet seeds during a day. Males consumed a larger amount than females (7.0 ± 0.4 vs. 6.1 ± 0.6 g, respectively).

Discussion

The absence of wheat grain in skylark diet

In his seminal study, Green (1978) reported that *cereal grain was the main food in autumn*, and this actually held true also later in winter (Green 1978). This result was further supported in the late 1990s by Donald and Vickery (2000) and Donald et al. (2001), showing that cereal grains contributed significantly to the seed fraction ingested by wintering skylarks in various crop types. In contrast, our study did not find a single wheat seed in any regions nor periods of study. Actually, whatever the region or period, our results clearly indicated that weeds, not grain, were the predominant seeds. Similar findings were reported by Clarke et al. (2003) and Robinson (2004) in UK and more recently by Geiger et al. (2014) in Netherlands, though in these studies, at least some cereal grains were found. Here, only one crop seed species was detected in only one gizzard. As skylarks do not remove husk

(Cramp 1988), it is unlikely that the absence of cereal grains in gizzards was due to a pre-digestion process, but rather reflected the actual level of consumption (see also Robinson 2004). Two issues are thus raised by our results in comparison to Green's study: why cereal grains are absent from French skylark diet, and could this absence result from a recent decline of grain contribution to skylark diet, as it seems to be observed in the UK and the Netherlands?

There is evidence that stubbles are the primarily source for cereal grains in skylark diet (Green 1978; Donald et al. 2001; Robinson 2004; Geiger et al. 2014). However, it is unlikely that the lack of grain consumption in our study reflects the lack of stubble fields because in both regions and periods, at least some stubbles were available. Alternatively, hunters may have searched for skylarks in cover types other than cereal stubbles. Hunters are known for searching skylarks in fields holding high bird densities, and stubbles are usually selected with this respect. A survey conducted among volunteers involved in sample collection during the winter 2010–2011 indicated that several of them had collected skylarks on cereal stubbles in Western France, and this was actually the case for all skylarks collected in South-western France. Hence, a plausible hypothesis is that cereal grains were virtually absent from the soil seed bank in our study sites. Gizzards were collected at mid-winter (mean = 2 Jan ± 17 days), and at that time, cereal grains might have totally disappeared from the soil surface. Causes for this depletion might include consumption by granivorous birds and/or small mammals (Whelan et al. 2008) during previous months, degradation and/or incorporation into the soil matrix (Westerman et al. 2006) as well as the advanced germination of grains at mid-winter. Alternatively, cereal grains may have become scarce due to low loss during harvesting, thanks to better harvesting machines. Whether the first or second hypotheses are correct (and both may be), the result is that cereal grain may have

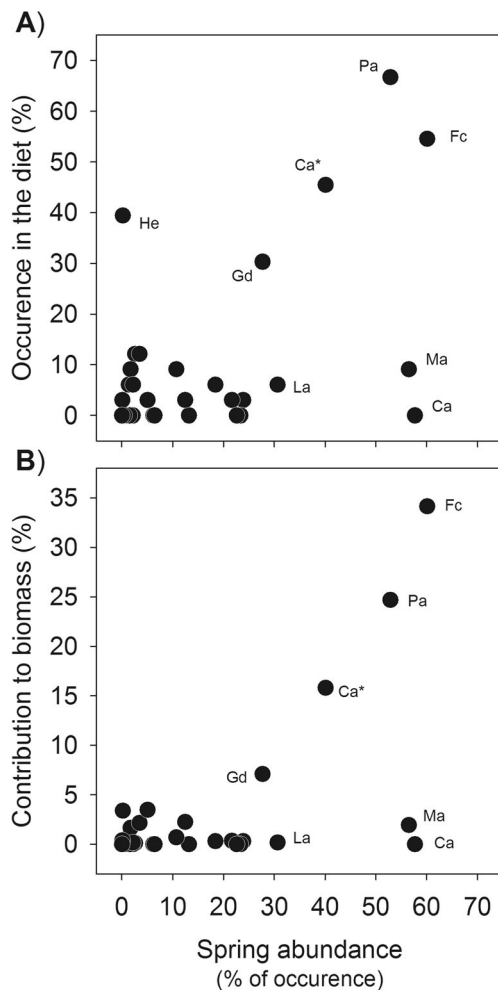


Fig. 1 Relationship between weed abundance ($n=33$) estimated from botanical surveys conducted in spring in Central-western France and their relative contribution to the diet of skylarks wintering in the same geographical region during the 2010–2011 period. Response variables are **a** the frequency of occurrence of seeds in the diet ($r=0.54$, $P=0.001$) and **b** the contribution to the diet in percent of dry biomass ($r=0.63$, $P<0.001$). Main species cited in the text are shown: *Ca* *Convolvulus arvensis*, *Ca** *Chenopodium album*, *Fc* *Fallopia convolvulus*, *Gd* *Geranium dissectum*, *He* *Heliotropium europaeum*, *La* *Lysimachia arvensis*, *Ma* *Mercurialis annua*, *Pa* *Polygonum aviculare*. Note that for our purposes, *Geranium* spp. was assumed as being *Geranium dissectum* (see Online Resource 2)

completely vanished from early December onwards and that this resource does not contribute at all to the diet of wintering skylarks in modern farmlands (and other farmland birds). This conclusion is in agreement with the recent study of Geiger et al. (2014), showing that the proportion of grains in the diet is marginal in the heart of the winter.

The contribution and selection of weed seeds

Given the absence of grain in diet, weeds contributed solely to the seed fraction of the skylark food regime in winter, with at least 37 species recorded. Despite the wide variety of ingested weed seeds, only few species dominated gizzard contents. In

Central-western France, all dominating species were annual weeds such as *Chenopodium album*, *F. convolvulus* and *Polygonum aviculare*, therefore adhering to the pattern of results observed in South-eastern England (Clarke et al. 2003; Robinson 2004) or in Netherlands (Geiger et al. 2014). In South-western France, annual weeds were also dominating but species differed. In this region, gizzards were collected earlier in the season ($24 \text{ Dec} \pm 2 \text{ days}$ vs. $12 \text{ Jan} \pm 10 \text{ days}$); therefore, the difference might reflect a change in the availability of seeds during the season. However, those weed species are generally found in spring crops such as maize which may have been more abundant in the south-west. Hence, the difference of diet between the two regions might also reflect a contrast in local availability of weed seeds. Similarly, the slight difference in the occurrence of some species between periods and sexes in the Central-western region might also result from local differences in weed availability at sites where the birds were retrieved. However, we cannot exclude that this result, as well as the observed differences in both seed richness and diversity between periods, mirrored temporal changes in the weed communities or flora.

In agreement with Green (1978), the vast majority of seeds eaten by skylarks were small (i.e. $<2 \text{ mg}$). Our findings also suggest that weed seeds would enter the diet with respect to their relative occurrence in the farmland landscape, therefore supporting the view that skylark would be a generalist opportunistic forager in such landscapes in winter (Robinson 2004). Weeds in gizzards were mostly therophytes that produce seeds at the end of summer and in autumn, and the most frequent seeds found in gizzards, i.e. *Chenopodium album* and *F. convolvulus*, produce large number of seeds (typically, several tens of thousands per individual; Zimdahl 2007). However, we found discrepancies between the contribution of some weeds to the diet and their frequency of occurrence in the farmland landscape, which may suggest some level of food selectivity by skylarks. In addition to their large size (see “Results” above), some species may be counter selected because of lower seed production per plant (*Convolvulus arvensis* only produces 50 seeds per plant, Zimdahl 2007) or lagged seed production.

It should be stressed that the abundance of weeds was assessed in spring and in a somewhat different area than the collection of birds. Accordingly, we cannot exclude that this discrepancy might have influenced the relationship between the abundance of weeds and their contribution to the diet of birds. For instance, *M. annua*, and *L. arvensis* produce seeds from summer to early autumn; thus, seeds may be unavailable on soil surface in mid-winter for various causes (depletion by other seed predators such as seed-eating carabids and rodents, percolation or germinating of seeds after harvesting). Conversely, some species frequently consumed by skylarks (e.g. *Heliotropium europaeum*) may have been missed during spring botanical surveys because their germination period occurs in summer.

Recently, seed selection by skylarks was experimentally shown by Gaba et al. (2014) who revealed that their foraging decision seems to be mainly based on seed size that is presumably a “proxy” for weed seed energy content. In the current study, we found no evidence that seeds entered the diet with respect to their mass, volume, major constituents or energy content. We acknowledge, however, that in comparison to experiments, the relevance of results from our correlative approaches should be regarded with some caution.

Daily requirements

Guyomarc’h and Guillet (1996) reported that skylarks housed in individual cages and fed with a mix of seeds (e.g. millet, moha or awned canary-grass) and commercial food ingested a daily amount of 6–7 g (wet). We found identical values in our study: skylarks kept in captivity ingested an average of 6.7 g (wet) of millet *Panicum miliaceum* seeds. Assuming an energetic content of about 17.66 kJ g⁻¹ millet (Kelrick and MacMahon 1985) and an assimilation rate of 78 %, this would represent around 81 kJ bird⁻¹ day⁻¹. Our simulations based on the respective contributions of seed species suggested a higher value (about 7.9 g day⁻¹ (wet)). For our calculations, a higher value of DEE has been used, based a priori on the value provided by Tieleman et al. (2004). Given that captive skylarks were deprived from flight, provided with ad libitum food and housed under mild climatic conditions, one may expect a reduced DEE in comparison to free-ranging parents feeding nestlings. We emphasize, however, that during the experiment, the birds have lost -5.6 (SE±0.4 %) of their initial body weight (Wilcoxon signed-rank test, $Z=3.62$, $P<0.001$, $n=17$) which may suggest either a stress or that the food intake was not sufficient to meet their needs. Yet, we acknowledge that the actual DEE for wintering skylarks is a major unknown, as well as its level of variability according to environmental conditions. Nevertheless, the results from our simulations, even based on crude approximations for both seed energy content and DEE, provide some interesting background information with regard to the coverage of daily needs.

Hence, our coarse estimates—based under the assumption that a typical diet included the whole diversity of weed seeds found in gizzards—suggest that skylarks should ingest a huge amount of seeds (4200–5600 seeds) to meet their daily energy needs. Assuming a successful pecking rate of about 0.1 seed per second (Green 1978, on ploughed land) or, alternatively, an estimated time delay of 5.49 s for successfully taking one seed (Green 1980), skylarks should seek their food for a duration that may seem unrealistic given the day length in mid-winter. On average, gizzards contained only a small number of seed species (i.e. mean 3), suggesting that birds might focus on fewer items, which, depending to their profitability, could enable covering the needs in a shorter time. For instance, captive birds fed exclusively with large seeds of

millet covered their daily needs by consuming an estimated mean of 950 seeds (average seed mass 0.007 g (wet); estimated upper value=1 160 seeds day⁻¹). Similarly, a bird feeding on profitable weed seeds like *F. convolvulus* or *D. stramonium* would be expected to need a reduced number of items and, plausibly, to spend less time in foraging. Therefore, our results suggest that wintering skylarks should not feed exclusively on weed seeds but have to complement their diet with green material. Existing recent studies suggest that in some months, weed seeds would not represent the main fraction of the diet of wintering skylarks, the bulk being formed by plant leaves (Donald et al. 2001; Geiger et al. 2014). While this aspect was not addressed in our study, this does not call into question the importance of weed seeds as well as the need to better understand how they contribute to maintain the energy balance of wintering skylarks but also their needs for specific nutrients related to important physiological functions (e.g. Surai 2002).

Conservation implication

Our study reinforces the view that the conservation of arable weeds is an important issue for wintering populations of skylarks (Clarke et al. 2003) and also plausibly for migrants that transit through the Western France (Hémery et al. 1992), especially in a context where cereal grains are not (or less) available anymore. In this context, maintaining overwinter stubbles and minimizing the use of broad-spectrum herbicides on these fields in autumn are likely to benefit several granivorous bird species including the skylark (see also Geiger et al. 2014). However, the present modalities of implementation of the European nitrates directive in France (Arrêté du 23/10/2013. NOR: DEVL1326188A) promote nitrate-fixing intermediate crops at the expense of regenerating cereal stubbles. Furthermore, by providing high and dense vegetation, these crops may not suit the foraging requirements and predator escape strategies (e.g. Butler and Gillings 2004; Butler et al. 2005; Powolny et al. 2014) of skylarks. France is one of the main wintering and stopover areas for a large part of European skylark populations. Hence, the consequences of nitrate-fixing intermediate crops deserve further investigations to assess whether the objective to protect the water quality does not conflict with those of conserving bird populations.

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Conflict of interest The authors declare that they have no conflict of interest

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