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ORIGINAL ARTICLE

Effects of breeding habitat and field margins on the reproductive performance of Skylarks (*Alauda arvensis*) on intensive farmland

M. W. Kuiper · H. J. Ottens · J. van Ruijven · B. J. Koks · G. R. de Snoo · F. Berendse

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Abstract Field margin management is a common measure employed in Europe to support farmland bird populations. In this study we found and analysed 237 nests of the Skylark *Alauda arvensis* in the Netherlands over a period of 6 years to determine the effects of arable field margins and breeding crop on nest-level reproductive success. Additionally, the effect of field margins on predation was investigated and food availability in crops and field margins was compared. Neither clutch size, nest survival nor nestling body weight were improved by field margin availability, irrespective of the breeding crop used. However, the choice of breeding crop had important effects. Nestling weight was significantly lower in cereals than in grassland and lucerne, corresponding with the low prey densities present in cereals. Nest survival was lowest in grassland due to frequent silage cutting. Predation rates were highest in cereals but were not affected by field margin proximity. The highest reproductive success was achieved in lucerne, which was mown twice a year and retained a suitable height for breeding throughout the breeding season. We conclude that field margins are not sufficient to maintain a Skylark population in this intensively farmed area. The presumably more subtle effects of increased food availability cannot compensate for the high nest failure rates resulting from agricultural operations and predation. In this and similar areas, the provisioning of safe nesting habitat throughout the breeding season is essential to improve breeding performance. Our research suggests that this can be achieved by reducing the frequency of silage cutting on grassland and by increasing the surface area of lucerne.

Keywords Agri-environment · Conservation · Nestling condition · Passerine · Predation · Reproduction

Zusammenfassung

Der Einfluss von Bruthabitat und Ackerrainen auf den Fortpflanzungserfolg der Feldlerche auf intensiv bewirtschaftetem Ackerland

Ackerrain-Management wird in Europa häufig eingesetzt, um Vogelpopulationen in der Agrarlandschaft zu unterstützen. In dieser Untersuchung analysierten wir in den Niederlanden über sechs Jahre hinweg 237 Nestlinge der Feldlerche (*Alauda arvensis*), um herauszufinden, ob die Randstreifen der Äcker und der Anbau von Feldfrüchten auf Nesthöhe einen Einfluss auf den Fortpflanzungserfolg der Lerchen hätten. Darüber hinaus wurde untersucht, ob die Ackerraine einen Einfluss auf die Räuber-Beute-Beziehung hätten, und die Verfügbarkeit von Nahrung an Acker- und Feldrainen wurde miteinander verglichen. Das Vorhandensein von Ackerrainen hatte keinerlei positiven Einfluss auf die Gelegegröße, die Überlebensrate der

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M. W. Kuiper (✉) · J. van Ruijven · F. Berendse
Nature Conservation and Plant Ecology Group, Wageningen University, PO Box 47, 6700 AA Wageningen, The Netherlands
e-mail: marije.kuiper@wur.nl

H. J. Ottens · B. J. Koks
Dutch Montagu's Harrier Foundation, PO Box 46, 9679 ZG Scheemda, The Netherlands

H. J. Ottens
SOVON Dutch Centre for Field Ornithology, PO Box 6521, 6503 GA Nijmegen, The Netherlands

G. R. de Snoo
Institute of Environmental Sciences, Leiden University, PO Box 9518, 2300 RA Leiden, The Netherlands

Nestlinge oder auf deren Körpergewicht, ganz gleich, ob Feldfrüchte auf den Äckern angebaut wurden. Die Feldfrüchte selbst hatten jedoch einen wichtigen Einfluss. Das Körpergewicht der Nestlinge war bei Getreide-Anbau signifikant niedriger als bei Wiesen oder Luzerne-Anbau, was vermutlich an der niedrigeren Dichte von Beutetieren in den Getreiden lag. Wegen des häufigen Mähens von Futtergras war die Überlebensrate der Nestlinge auf Wiesen am niedrigsten; die Beuterate war in Getreideäckern am höchsten, aber unbeeinflusst davon, wie nahe der Ackerrain war. Den größten Fortpflanzungserfolg gab es in Äckern mit Luzerne, die zweimal im Jahr gemäht wurden und während der gesamten Brutperiode ausreichend hoch stand. Wir schließen aus diesen Ergebnissen, dass das Vorhandensein von Ackerrainen für den Erhalt einer Feldlerchen-Population auf intensiv bewirtschaftetem Ackerland nicht ausschlaggebend ist. Die vermutlich eher subtilen Effekte der höheren Nahrungsverfügbarkeit können nicht die häufigeren Brut-Misserfolge aufgrund der landwirtschaftlichen Bearbeitung sowie der Predation wettmachen. Für eine Verbesserung des Bruterfolgs ist in erster Linie die Verfügbarkeit sicherer Brutplätze über die gesamte Brutzeit hinweg wichtig. Unsere Untersuchungen legen nahe, dass dies erreicht werden kann, indem die Wiesen weniger häufig gemäht und auf mehr Ackerflächen Luzerne angebaut werden.

Introduction

Agricultural intensification has been identified as the major driver behind the decline of farmland bird populations in western Europe (Donald et al. 2001a; Robinson and Sutherland 2002; Stoate et al. 2009). To counteract the negative effects of agricultural intensification on biodiversity and ecosystem services, the European Union introduced the possibility of farmers participating in agri-environment schemes. In arable areas, agri-environment schemes often focus on increasing the area of uncropped land, for example in the form of sown field margins or set-aside (Vickery et al. 2002; Tscharntke et al. 2011). Various species living in agricultural areas depend on the presence of uncropped land, including a range of arthropods (Duelli and Obrist 2003; Tscharntke et al. 2005), plants (Hovd and Skogen 2005; Van Dijk et al. 2013), and birds (Fuller et al. 2004; Henderson et al. 2012).

Evaluating the effectiveness of agri-environment schemes for farmland birds can be difficult. A number of studies have compared bird abundances on different farms or in different regions: so-called space-for-time substitution (Smith et al. 2010). However, a comparison of areas with and without agri-environmental measures can be biased in cases where measures were preferentially established in landscapes or farms that already had higher bird abundances (Kleijn and Sutherland 2003). Another difficulty is that changes in bird abundance do not necessarily correlate with changes in reproductive success or survival. Increased bird abundance in areas with agri-environmental management can, for example, be the result of mere bird relocation rather than increased reproduction, turning the area into a potential sink rather than a source (Geertsma et al. 2000). It is therefore essential to complement studies on bird abundances or changes therein with studies that investigate the direct effects of management on demographic processes (Henderson et al. 2012).

In the work reported in the present paper, we studied the nest-level reproductive performance of a rapidly declining farmland bird, the Eurasian Skylark *Alauda arvensis*. Populations of this species have been declining in most western European countries (EBCC 2013); for instance, there has been a 96 % decrease in the Skylark population in the Netherlands since 1960 (SOVON 2012). The decline of the Skylark has been linked to changes in agricultural land use and decreased habitat diversity at the farm and landscape scales, which have reduced the number of breeding attempts that Skylarks undertake per year (Wilson et al. 1997; Chamberlain et al. 1999; Chamberlain and Vickery 2000; Geiger et al. 2010; Guerrero et al. 2012). Additionally, summer and winter food resources for Skylarks have diminished due to increased agrochemical inputs and the loss of semi-natural habitat elements (Wilson et al. 1999; Chamberlain et al. 2000; Geiger et al. 2014).

The problem of insufficient food availability during the breeding season can potentially be solved by establishing field margins (Vickery et al. 2002, 2009). Field margins are extensively managed strips of land, often sown with forbs and grasses, that have been established in a range of countries, including the United Kingdom (Vickery et al. 2009), Switzerland (Zollinger et al. 2013), Germany (Denys and Tscharntke 2002), France (Cordeau et al. 2012) and the Netherlands (Noordijk et al. 2010). Field margins generally contain higher densities of arthropods than agricultural land, and they are a highly preferred foraging habitat for Skylarks and other farmland passerines (Perkins et al. 2002; Kuiper et al. 2013). In the United Kingdom, the abundance of Skylarks was positively correlated with the area of uncropped land on a farm, especially with uncropped patches with large perimeter-to-area ratios (Henderson et al. 2012). In both the UK and Switzerland, however, Skylark abundance and population growth rates did not positively correlate with the surface area of field margins (Baker et al. 2012; Meichtry-Stier et al. 2014).

The aim of the present study was to examine the effect of field margin presence and surface area on Skylark reproduction. The effect of field margins was determined at the level of individual nests. We studied three important aspects of reproduction that are known to be linked to population dynamics: clutch size, nestling body weight and nest survival. Birds can adjust their clutch size in response to food availability (Martin 1987; Poulsen et al. 1998), which in turn can affect the productivity of a population (Chamberlain and Crick 1999). The body weight of young birds is an important reproductive parameter because it correlates positively with future survival and reproductive success (Magrath 1991; Lindström 1999).

It is known that the breeding performance of Skylarks differs between crops due to differences in food availability and agricultural management (Jenny 1990; Poulsen et al. 1998; Donald et al. 2002). To increase the effectiveness of field margins, it is therefore important that they are placed alongside crops in which Skylarks have good breeding prospects. In order to assess how various crops can hamper or enhance the potential effects of field margins on reproduction, the effects of field margins were tested in three breeding crops: cereals, grassland and lucerne. Additionally, we compared these breeding crops in terms of food availability, nestling weight, nest survival and predation risk. Finally, the effect of field margins on predation risk was assessed, since earlier work suggests that field margins can attract predators or improve their access to agricultural fields (Morris and Gilroy 2008), which would hamper the use of field margins as a conservation measure.

Methods

The research was carried out from April through July 2007–2012 in the province of Groningen in the northeast of the Netherlands. This province declared the stabilisation of the Skylark population one of the targets of local agri-environmental management, and field margins are the main management instrument used to achieve this target (Provincie Groningen 2008). The research area of ca. 980 ha (N53°11.813, E007°7.787) is situated on marine clay, and agriculture is the main land use. The main crops are winter wheat (~50 %), permanent grassland (~25 %), maize (~8 %), lucerne (~5 %), sugar beet (~5 %) and rape seed (~3 %). Grasslands were exclusively used for silage cutting, with cuttings taking place 4–5 times per year, with a mean time interval of 33 days (SD 5.3, based on 53 cutting intervals on 30 grasslands). Lucerne was also used for silage cutting, which was performed on average twice per year, with a mean cutting interval of 57 days (SD 4.4, based on 18 cutting intervals on nine lucerne fields).

Field margins have been present in the area since 1997. They generally are 12 m wide and 500–1000 m long and remain in place for at least 6 years. They are sown with a mixture of grasses (e.g. *Festuca rubra*, *Phleum pratensei*), forbs (e.g. *Fagopyrum esculentum*, *Glebionis segetum*, *Lupinus* sp., *Carum carvi*) and spring wheat. Each year, 20–70 % of the field margin is cut twice to keep the vegetation open: once between March 1 and April 15 and once between July 15 and September 15. The surface area of field margins in the region varied over the years between 3 and 5 % of the agricultural land. The research area included parts with high field margin densities as well as parts where they were absent. Within Skylark territories, the relative surface area of field margins ranged between 0 and 24.3 %. Among all of the territories containing field margins, the average relative surface area of field margins was 6.3 % (SD 0.048). In these territories, 52 % contained >5 % field margins and 20 % contained >10 % field margins. Other agri-environment schemes included a few patches of bird winter seed, which were grouped with field margins in the analyses because of their small surface areas (<0.5 % of the cropped area). In 2012, two set-aside fields were established in the area, which were sown with a field margin seed mixture and strips of lucerne.

In one part of the research area (680 ha), the number of Skylark breeding pairs was monitored annually as part of a breeding bird monitoring programme. In this area, the proportion of field margins averaged 4.6 % (±0.96) over the six study years (range 3.3–5.5 %). Four times per year, between early April and the end of July, the area was crossed by foot around the time of sunrise, and all territorial and nesting birds were mapped. After the visits, the total number of Skylark breeding pairs was estimated based on standardised methods (Hustings et al. 1989; Van Dijk and Boele 2011).

Survival and productivity

Skylark nests were located by searching for birds that showed signs of breeding behaviour or performed provisioning flights. The fate of nests was verified every 1–4 days either by revisiting the nest or by observing provisioning flights from a distance in order to minimise disturbance. A nest was considered successful when at least one nestling left the nest at the age of 8 days. The number of fledglings was assumed to be equal to the number of alive nestlings that was seen during the last visit before fledging. Causes of nest failure were determined by inspecting the nest site. Nests were regarded as predated when they were found to be empty during incubation or early nestling stages or when egg shells or scattered feathers were found in the vicinity. When the feathers were found intact, the predator was assumed to be a bird; when the feathers were missing their bases, it was assumed that they had been bitten off by a mammal. Nests with dead, underweight nestlings were considered to have failed due to starvation. When the exact failure date was unknown, it was assumed to have occurred halfway between the last two visits.

Hatching success, nest survival and nestling survival were calculated according to the methods described by Mayfield (1961, 1975) and statistically tested using a generalised linear model with binomial error distribution and logit link function (see "Data analyses"). Egg survival was not included in the analyses because partial clutch loss was observed only once. The overall survival S (the chance that an egg survived through fledging) was estimated as $S = H(L^8)(F^{22})$, where H is the proportion of the eggs that hatch, L is the daily nestling survival rate, F is the daily nest survival rate, 8 is the duration of the nestling phase in days, and 22 is the duration of the nesting period in days (Mayfield 1975). The productivity P (the mean number of fledglings per nesting attempt) was estimated as $P = \mathrm{CH}(L^8)(F^{22})$, where C is the mean clutch size and the other variables are as described above (adapted from Donald et al. 2002). Standard errors for survival and productivity were obtained by bootstrapping, resampling 10,000 times from the probability distributions for hatching success (beta distribution), nest survival (beta distribution), nestling survival (beta distribution) and clutch size (normal distribution). Johnson's estimator for the variance in daily survival rate was used to calculate standard errors for daily survival rates of nests and nestlings (Johnson 1979).

Estimates of hatching success were based either on the difference between clutch and brood sizes or, as most nests were found after hatching, on the presence of unhatched eggs in the nest. Since unhatched eggs were found in nests with young of all ages, this method was assumed to give a reliable estimate of true hatching success. To confirm the correctness of this assumption, a generalised linear model was run with a binomial error distribution and a logit link function, with the number of eggs hatched relative to the number of eggs laid employed as the dependent factor, and year and nest found before or after hatching as explanatory factors. There were no differences in the apparent hatching successes of nests found before and after hatching (year: Wald $\chi^2 = 5.327$, df 5, $P = 0.34$; nest found before/after hatching: Wald $\chi^2 = 0.02$, df 1, $P = 0.88$), so all nests were included in the calculations of hatching success. Nest survival rates during the incubation and nestling phases were combined into one estimate of daily nest survival (Mayfield 1975), because nest survival rates did not differ between the incubation and the nestling phases (nest days without/with losses: 290/19 during the incubation phase and 631/62 during the nestling phase, $\chi^2 = 0.08$, df 1, $P = 0.77$).

Nestling body mass

Body mass was measured to the nearest 0.1 g using a spring balance when nestlings were 5–9 days old (average 7.0 ± 1.1 SD days). A condition-independent indicator of growth (tarsus length) was measured to the nearest 0.1 mm using a pair of callipers. Rainfall and temperature may affect nestling body weight and survival (Donald et al. 2001b; Bradbury et al. 2003) and were therefore included in the analyses. Meteorological data were obtained from a weather station in the research area (Nieuw Beerta, N53°11.662, E007°8.966), owned by the Dutch Meteorological Institute (KNMI). For analyses of the effects of temperature and rainfall on nestling weight, the mean temperature and the total duration of rainfall in hours were calculated over the day on which weighing was performed, as well as the preceding 3 days. For analyses of the effects of temperature and rainfall on nest survival, the mean temperature and the total duration of rainfall in hours were calculated over the day of fledging or nest loss and the preceding 3 days.

Effect of field margins

In order to establish whether the presence of a field margin is sufficient to enhance reproduction or whether a minimum surface area of field margins is required, two field margin measures were tested for their effects on breeding success: (1) the presence of at least one field margin within flight distance, and (2) the surface area of field margins within flight distance. Based on foraging distances of Skylarks in the study area, two flight distances were used: 100 and 272 m. The largest effect was expected from margins within 100 m of the nest, because the chance that a field margin was visited by Skylarks during a 1-h or 2-h observation period was 76 % for margins within 100 m of the nest and only 12 % for margins further away (Kuiper et al. 2013). A radius of 272 m was used because this was the 95th percentile of all foraging flight distances recorded in the research area in 2007, 2008, and 2011 (Kuiper et al. 2013).

Field margin availability was used as the explanatory variable, rather than field margin use based on foraging observations. Foraging observations conducted in the study area around the same time showed that the use of field margins by Skylarks was so high and consistent (Kuiper et al. 2013) that we assumed field margin availability could be used reliably as a proxy for field margin use in order to enlarge the sample size. The presence and surface area of field margins were calculated in ArcGIS 10.1 (ESRI, Redlands, CA, USA), using agricultural maps from the Ministry of Economic Affairs (Dienst Regelingen).

Invertebrate sampling

Invertebrates were sampled in 2011 and 2012 to compare food abundance between field margins, grassland, lucerne and winter wheat. Five catch rounds per year took place between the middle of May and the middle of July at fixed time intervals, irrespective of the cutting cycles of lucerne and grassland. Five field margins were sampled in both years. For each crop, two fields were sampled in 2011 and five in 2012. The results of the 2011 sampling effort are published in Kuiper et al. (2013).

Invertebrates were collected by vacuum sampling using a modified leaf vacuum (McCulloch MAC GBV 345) with a 12-cm-diameter suction tube. Sampling was conducted in sunny and dry weather conditions only. Each sample consisted of five subsamples of 15-s vacuum sessions performed within a bottomless circular frame (50 cm diameter), thus sampling a total area of 0.982 m^2 per sample. Invertebrates were identified to the order level and allocated to three size classes (3–5, 6–8 and >8 mm). Only those invertebrate groups that were recorded by Holland et al. (2006) and Smith et al. (2009) as being found in the Skylark diet were included in the analysis: individuals larger than 5 mm in the taxa *Arachnida*, *Coleoptera*, *Diptera*, *Lepidoptera*, *Orthoptera*, *Hemiptera* and *Hymenoptera*, including adults and larvae.

Data analyses

All statistical analyses were performed in SPSS 19 (IBM, Armonk, NY, USA). Means are given with standard errors in parentheses, unless indicated otherwise.

Reproduction and nestling weight

Clutch size was analysed using generalised linear models (type III sums of squares) with a Poisson distribution and identity link ($n = 191$). Nestling weight was analysed using generalised linear mixed models (type III sums of squares) with nest ID as a random variable ($n = 357$ nestlings in 111 nests). Body mass was log-transformed to achieve normality of residuals. Nest survival was modelled using generalised linear models with a binomial error distribution and logit link function (i.e. Mayfield logistic regression, Aebischer 1999; Hazler 2004; $n = 169$ nests). For all three analyses, only nests located in the four most commonly used breeding habitats were analysed, which were grassland, lucerne, cereals (mainly winter wheat, but there were also a few nests in spring wheat and barley) and non-crop habitat (including field margins, set-aside, road verges and ditch banks).

The models of all three dependent variables included the factors year and breeding habitat and the covariates temperature, rainfall and laying date (the estimated date that the first egg of a clutch was laid). Brood size was added as a covariate to the models for nest survival and nestling weight. The model for nestling weight also contained the covariate tarsus length to control for differences in nestling age and structural size (Gilroy et al. 2009; Labocha and Hayes 2012) as well as the interaction between tarsus length and year, because we expected that the relation between body weight and tarsus length would differ between years as a result of varying weather conditions and food availability.

Field margin effects

The effects of the four field margin variables (presence and surface area of field margins within 100 and 272 m of the nest) were tested by adding them one by one to the basic model described above. Possible interactions between field margin variables and breeding habitat were also considered, because it was expected that the effect of field margins would be influenced by crop management and food availability. Only nests located in grassland, lucerne and cereals were included in this analysis.

To assess whether nests located closer to field margins experienced increased predation rates, a generalised linear model with a binomial error distribution and logit link function (i.e. Mayfield logistic regression; Aebischer 1999; Hazler 2004) was used to model predation as a binary variable (predated or not predated) relative to the nest exposure time. For nests that failed due to other causes than predation, the last nest exposure day was omitted, and only the days that the nest survived and was not predated were counted. Explanatory variables included breeding habitat (factor), distance to the nearest field margin (covariate) and the interaction between the two. Only nests located in grassland, lucerne and cereals were included in this analysis.

Invertebrate abundance

Differences in invertebrate abundance between habitat types were analysed using a linear mixed model. Habitat type, catch round and year were included as fixed factors. The interaction between habitat type and catch round was included to compare the change in food availability between the habitat types throughout the breeding season. When this interaction appeared significant, post hoc tests were performed to further explore the differences. Sampling site was included as a random factor to account for the repeated measurements performed at the same locations. The number of prey items was square root transformed in order to achieve normality of residuals.

Results

Skylark nests and population trend

Over the six study years, 237 nests were found, 27 % of which were in the incubation stage. Most nests were located in silage grassland (87), lucerne (62) and winter wheat (48). Smaller numbers were found in field margins (10), sugar beet (7), set-aside (6), spring wheat (6), barley (4), rape seed (1) and maize (1). A few nests were located outside agricultural land in road verges (4) and ditch banks (1).

The number of Skylark breeding pairs in the central part of the research area was monitored annually and decreased steadily from 63 pairs (9.3 per 100 ha) in 2007 to 38 pairs (5.6 per 100 ha) in 2012, an overall decrease of 40 %.

Clutch size

The average clutch size was 3.85 eggs and did not differ between breeding habitats (Tables 1, 2). Clutch size tended to be higher in cereals than in grassland, but this trend was not significant. The presence or surface area of field margins around the nest did not affect clutch size (Table 2).

Nestling body weight

Nestling body weight differed significantly between breeding habitats (Table 2), being lower in cereals than in grassland ($P < 0.001$), lucerne ($P < 0.01$) and extensive habitat ($P < 0.05$) (Table 1). Nestling body weight was significantly affected by the interaction between breeding habitat and the presence of a field margin within 100 m of the nest (Table 2). This interaction was caused by field margin presence affecting nestling body weight in lucerne ($P < 0.05$) but not in grassland ($P = 0.43$) or cereals ($P = 0.44$). In lucerne, mean body weight was lower when a field margin was present within 100 m of the nest ($n = 56$; model-estimated mean weight 28.1 ± 1.0 g) than when no field margin was present ($n = 57$; model-estimated mean weight 29.4 ± 1.0 g). Mean body weight varied significantly between years, which also significantly affected the relationship between tarsus growth and weight gain (tarsus × year, Table 2). Brood size, temperature and rainfall did not affect nestling body weight.

Survival and productivity

Forty-seven unhatched eggs were found among 747 eggs and nestlings in 202 nests, giving a mean hatching success of 0.936 (Table 1). Partial brood loss was observed for 21 nests, with 29 nestlings lost during 2,401 nestling exposure days. The loss of nine nestlings could be attributed to starvation; the cause of the partial brood loss could not be established in the other cases. The daily nestling survival rate was 0.988 (Table 1), resulting in a nestling survival probability of 90.7 % (±1.6) for the entire nestling phase of 8 days. The daily nest survival rate was 0.919 (Table 1), equalling a nest survival probability of 15.7 % (±3.2) over

Table 1 Skylark nestling body weight and nest survival in the four most commonly used breeding habitats and in total, averaged over the years 2007 through 2012

	Nests	Nestling weight (g)	Nest days	Nests lost	Nestling days	Nestlings lost	Clutch size[b]	Hatching success[c]	Daily nest survival	Daily nestling survival[d]	Overall survival[e]
Cereals	48	25.3 (0.73)	231	15	633	2	4.10 (0.23)	0.933 (0.018)	0.935 (0.016)	0.997 (0.002)	20.8 % (7.9)
Grassland	73	27.3 (0.89)	314	41	725	10	3.65 (0.18)	0.921 (0.017)	0.869 (0.019)	0.986 (0.004)	3.8 % (2.0)
Lucerne	48	29.5 (1.01)	301	14	672	13	3.95 (0.14)	0.960 (0.014)	0.953 (0.012)	0.981 (0.005)	28.8 % (8.1)
Non-crop[a]	18	30.5 (1.59)	77	8	257	4	3.63 (0.26)	0.933 (0.028)	0.909 (0.032)	0.984 (0.008)	10.1 % (9.0)
All habitats	195	29.1 (0.49)	1002	81	2401	29	3.85 (0.09)	0.936 (0.009)	0.919 (0.009)	0.988 (0.002)	13.3 % (2.7)

Data show mean ± SE

[a] Set-aside, field margins, road verges and ditch banks

[b] Clutch size of nests found in the incubation phase

[c] Hatching success of eggs present at hatching time

[d] Daily survival of individual nestlings in surviving nests

[e] Product of hatching success, nest survival over 22 days and nestling survival over 8 days

Table 2 Factors influencing Skylark clutch size (GLM, $n = 191$), nestling body weight (GLMM, $n = 111$ nests) and nest survival (Mayfield logistic regression, $n = 169$)

	Clutch size Wald $\chi^2_{(df)}$	Nestling weight $F_{(df)}$	Nest survival Wald $\chi^2_{(df)}$
Intercept	$28.3_{(1)}$***	$203_{(1,339)}$***	$38.4_{(1)}$***
Year	$0.77_{(5)}$	$12.2_{(5,339)}$***	$2.76_{(5)}$
Breeding habitat	$0.66_{(2)}$	$7.79_{(2,339)}$***	$9.81_{(2)}$**
Lay date	$0.30_{(1)}$	$5.04_{(1,339)}$*	$0.03_{(1)}$
Temperature	$0.02_{(1)}$	$0.56_{(1,339)}$	$0.17_{(1)}$
Rainfall	$0.02_{(1)}$	$1.68_{(1,339)}$	$0.12_{(1)}$
Brood size	–	$0.53_{(1,339)}$	$2.08_{(1)}$
Tarsus length	–	$616_{(1,339)}$***	–
Tarsus × year	–	$27.6_{(5,339)}$***	–
FM presence within 100 m	$0.31_{(1)}$	$0.17_{(1,336)}$	$0.47_{(1)}$
FM presence within 272 m	$0.02_{(1)}$	$1.91_{(1,336)}$	$0.08_{(1)}$
FM surface area within 100 m	$0.23_{(1)}$	$3.53_{(1,336)}$	$0.80_{(1)}$
FM surface area within 272 m	$0.28_{(1)}$	$3.05_{(1,336)}$	$0.41_{(1)}$
FM presence within 100 m × breeding habitat	$0.48_{(2)}$	$3.42_{(2,336)}$*	$0.67_{(2)}$
FM presence within 272 m × breeding habitat	$0.58_{(2)}$	$0.77_{(2,336)}$	$2.03_{(2)}$
FM surface area within 100 m × breeding habitat	$0.87_{(2)}$	$1.25_{(2,336)}$	$0.28_{(2)}$
FM surface area within 272 m × breeding habitat	$0.39_{(2)}$	$0.92_{(2,336)}$	$0.85_{(2)}$

Only nests located in cereals, grassland and lucerne were included (data collected between 2007 and 2012)

Significant variables are shown in bold

FM field margin

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

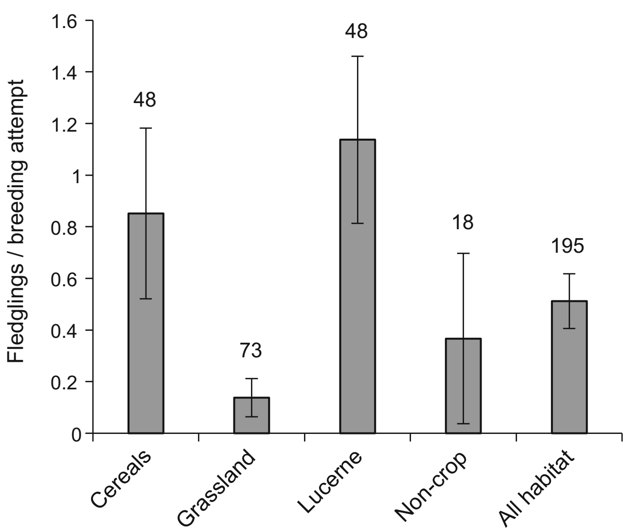

Fig. 1 Mean number of Skylark fledglings produced per breeding attempt (±SE) in the four most commonly used breeding habitats and in total, averaged over the years 2007 through 2012. *Numbers above bars* indicate sample sizes (number of nests)

the whole nesting period. The average productivity (the number of fledglings produced per nesting attempt) over all years was 0.51 (±0.11).

Breeding crop was the only variable affecting nest survival (Table 2). Survival in grassland was lower than in lucerne ($P < 0.001$) and in cereals ($P < 0.01$; Table 1). Nest survival in non-crop habitat was slightly higher than in grassland but the difference was statistically non-significant ($P = 0.060$). Fledgling productivity was 0.14 (±0.07) in grassland, 0.37 (±0.33) in non-crop habitat, 0.85 (±0.33) in cereals and 1.14 (±0.32) in lucerne (Fig. 1). Nest survival was unaffected by the presence or surface area of field margins.

Mowing and predation were the most important causes of nest loss (Table 3). Of the 34 nests that were lost to mowing, 30 were located in grassland and 4 in lucerne. Nest proximity to field margins did not affect predation rate (Wald $\chi^2 = 1.5$, *df* 1, $P = 0.23$). This effect was independent of breeding crop (breeding habitat × field margin proximity interaction, Wald $\chi^2 = 3.9$, *df* 2, $P = 0.14$). However, predation rates differed significantly between breeding crops (Wald $\chi^2 = 9.4$, *df* 2, $P < 0.01$). Predation was significantly higher in winter cereals than in grassland (Wald $\chi^2 = 9.1$, *df* 1, $P < 0.01$) and lucerne (Wald $\chi^2 = 4.6$, *df* 1, $P < 0.05$). For ten nests (29 % of all predated nests), the predator type could be identified based on the feather remains. The predator was a bird in seven cases and a mammal in three cases. Ten broods were lost due to starvation or abandonment and three to unknown or other causes, including a nest located in a road verge that failed after one of the adult birds was killed by traffic.

Food abundance

Invertebrate prey abundance differed significantly between the four habitat types that were sampled (field margins, grassland, lucerne and winter wheat; $F_{3,23} = 10.0$, $P < 0.001$) but not between the five catch rounds ($F_{4,27} = 2.5$, $P = 0.070$) or study years ($F_{1,27} = 0.0$, $P = 0.99$). The interaction between habitat type and catch round was significant ($F_{12,27} = 4.5$, $P < 0.001$), indicating

Table 3 Causes of Skylark nest failure in the four most commonly used breeding habitats and in total, summed over the years 2007 through 2012

	Cereals	Grassland	Lucerne	Non-crop[a]	All
Mowing	0 (0 %)	30 (41 %)	4 (8 %)	0 (0 %)	34 (17 %)
Predation	12 (25 %)	7 (10 %)	9 (19 %)	4 (22 %)	34 (17 %)
Starvation/abandonment	3 (6 %)	3 (4 %)	0 (0 %)	3 (17 %)	10 (5 %)
Other/unknown	0 (0 %)	1 (1 %)	1 (2 %)	1 (6 %)	3 (2 %)
Total	15 (31 %)	41 (56 %)	14 (29 %)	8 (44 %)	81 (42 %)

The percentage of nests lost relative to the total number of nests found within the breeding habitat is shown in parentheses

[a] Set-aside, field margins, road verges and ditch banks

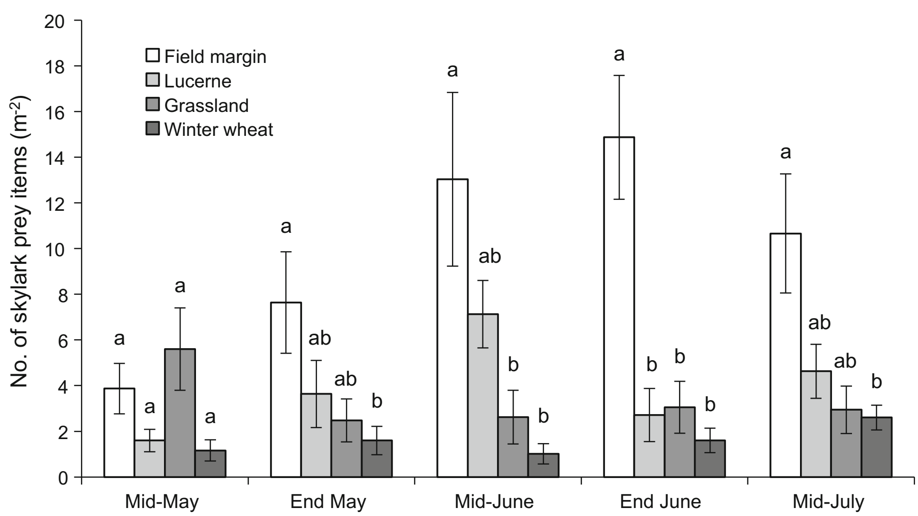

Fig. 2 Invertebrate prey availability in field margins and crops throughout the breeding season, averaged over 2011 and 2012. *Different letters* indicate significant differences between habitat types within catch rounds ($P < 0.05$)

that the differences in prey abundance between habitat types changed over time. There were no differences in prey abundance between habitat types during the first catch round in the middle of May. Throughout the rest of the sampling period (from the end of May until the middle of July), prey abundance was significantly higher in field margins than in winter wheat (Fig. 2). Field margins contained more prey than grassland in the middle and at the end of June, and more prey than lucerne at the end of June. Prey densities in the three crops did not differ from each other at any point in time, although densities were generally lower in winter wheat than in grassland and lucerne.

Discussion

Skylark reproduction

Low food availability in agricultural landscapes has been identified as one of the causes of the declines in farmland bird populations in Western Europe (Newton 2004; Butler et al. 2007). The establishment of agri-environment schemes that increase food availability, such as field margins, was expected to improve bird reproductive performance. Yet, the relationship between food availability and nestling condition or survival is not consistently positive, perhaps because factors like accessibility, prey profitability and nutrient composition are not always accounted for. Although some studies found improved nestling weight and survival when food availability around the nest was higher, for example for Yellowhammer *Emberiza citrinella* (Hart et al. 2006), Linnet *Carduelis cannabina* (Bradbury et al. 2003) and Corn Bunting *Miliaria calandra* (Brickle et al. 2000; Boatman et al. 2004), other studies could not detect such correlations for Chaffinch *Fringilla coelebs* (Bradbury et al. 2003), Yellowhammer (Bradbury et al. 2003) and Yellow Wagtail *Motacilla flava* (Gilroy et al. 2009).

For Skylarks, there are indications that nestling condition is significantly affected by the abundance of chick food within 100 m of the nest (Boatman et al. 2004). Our results point in the same direction, with broods located in winter wheat—the crop with the lowest food abundance—being in poorer condition than broods in grassland and lucerne. This suggests that the establishment of invertebrate-rich elements such as field margins would be most effective in wheat fields. Surprisingly, however, we did not find a positive effect of field margins on nestling weight in any of the breeding crops, even when taking into account field margin surface area. This result is similar to findings from Switzerland, where the area of field margins (wildflower strips) did not affect Skylark nestling weight, although a significant effect was found on feather growth (Weibel 1999). It is difficult to understand why field margins did not have a positive effect on weight, because food abundance was on average 4.4 times higher in field margins than in the sampled crops. Field margins are widely and frequently used by the Skylarks in this area, so the vegetation composition and management of the margins do not seem to hamper their use (Kuiper et al. 2013). The lack of effect cannot be explained by an increase in clutch size near field margins (as was found previously) either (Weibel 1999; Donald et al. 2001b), since clutch size was not affected by the availability of field margins nor by breeding habitat.

A possible explanation is that Skylark parents were able to compensate for a poorer environment by increasing their foraging efforts (Bradbury et al. 2003; Gilroy et al. 2009). When parents make longer or more frequent foraging flights, this can ultimately lead to reduced condition, elevated mortality rates or a reduced number of breeding attempts per year (Martin 1995; Siriwardena et al. 2000). An alternative possibility is that Skylark nestlings were able to maintain a normal growth rate under poor conditions at the cost of lowered immune functioning. In this case, the body weight indicates good health while the deprived immune system reduces long-term survival (Chin et al. 2005; Hegemann et al. 2013).

Nest survival rates were not improved by field margin availability. Most likely, food abundance was not the limiting factor for nest survival. Only a few nests were lost due to starvation; the majority of the nest failures was caused by agricultural practices and predation. In contrast to earlier findings, nest predation rates did not increase in the proximity of field margins (Morris and Gilroy 2008). Rather, our field observations led to the idea that predation risk was enhanced by food shortage. Nests with underweight nestlings or deserted broods were often found to be predated at a later visit (not further quantified). It is known that hungry nestlings increase the frequency and volume of their begging calls, which attracts the attention of predators and increases predation rates (Redondo and Castro 1992; Evans et al. 1997). Although predators were not identified, birds of prey seemed to be the most frequent predators based on feather remains, similar to the results of Praus and Weidinger (2010).

Grassland was one of the most commonly used breeding habitats, but, in line with earlier work, nest survival rates in grassland were very low (Jenny 1990; Wilson et al. 1997; Donald et al. 2002). The studied fields were cut in their entirety to collect silage every 33 days on average, a time interval that is generally too short for Skylarks to complete their nesting cycle. It is therefore not surprising that the mean number of chicks produced per nest in grassland was only 0.14. The number of nestlings that survive until independence will probably be even lower, considering that nests that were destroyed at the incubation stage may have been missed and that productivity was calculated up to the moment that the chicks left the nest, while they can only fly short distances and escape from cutting machinery after several more days. The high cutting frequency of grasslands, enhanced by the use of fertilizer, improved drainage and fast-growing grass species, is a strong limitation on successful breeding in grassland (Chamberlain and Vickery 2000). In non-grassland habitats, there were little or no agricultural practices that directly affected nest survival. In lucerne, a legume which is cut twice per year for silage, nest survival and productivity were the highest among the four considered breeding habitats. We suspect that few nests were lost to mowing in lucerne because this crop grows tall and dense quite rapidly, while Skylarks prefer to nest in low and sparse vegetation (Wilson et al. 1997; Toepfer and Stubbe 2001), so the majority of nests were initiated shortly after mowing.

Data on adult and juvenile survival rates are not available for the study population, but we can estimate the minimum reproductive rate necessary for a stable population based on a different Skylark population in the Netherlands, which showed average annual return rates of 0.7 for adults and 0.2 for juveniles (Hegemann 2012). Assuming that the same return rates apply to our study population, it would require on average three fledglings per pair per year in order to maintain the population size. With 2.5–3 breeding attempts per year (Delius 1965), the minimum number of fledglings required per breeding attempt is 1.0–1.2. In our study area, the mean number of fledglings produced per breeding attempt—averaged over all study years and all breeding habitats—was only 0.5, and this is probably an underestimate because nests that fail during the early nesting stages are often missed (Jenny 1990). The annual monitoring of Skylark breeding pairs confirmed that this reproduction rate was insufficient, leading to a gradual decline of 9.5 % per year between 2006 and 2012. Lucerne was the only crop in which the reproductive output exceeded the minimum, with 1.14 nestlings produced per breeding attempt. There is not sufficient data on emigration, immigration and juvenile and adult survival rates to draw final conclusions, but the low productivity rates in cereals and particularly grassland seem to be at least partly responsible for the population decline.

Implications for agri-environmental management

Sufficient food availability on farmland is important for Skylark populations, not only during the breeding season but also in winter (Donald et al. 2001c; Geiger et al. 2014). Yet, for effective conservation of the Skylark, it is essential to implement measures that not only improve food availability but also provide a safe nesting habitat. Although field margins can be used as a nesting habitat by Skylarks (Weibel 1999), only a few birds nested in the field margins in our study area. Survival rates in field margins are low and perhaps Skylarks avoided this breeding habitat to reduce predation risk. Based on our findings, we see two main possibilities for increasing the availability of safe nesting habitat for Skylarks in the study area and in similar agricultural landscapes. First, the safety of grassland as a breeding habitat could be improved by reducing the number of silage cuts, preferentially in combination with lowered inputs of fertilizer to reduce grass growth, thereby lengthening the cutting interval and allowing the birds more time to raise their brood (Wilson et al. 1997; Vickery et al. 2001; Donald et al. 2002; Stein-Bachinger and Fuchs 2012). This is particularly important because Skylarks greatly prefer grassland as a breeding habitat, especially in June and July when winter wheat becomes too tall and other suitable crops are only scarcely available.

Late-season availability of suitable breeding crops can also be improved by increasing the use of spring-sown cereals (Chamberlain et al. 1999; Kragten et al. 2008; Eggers et al. 2011) or lucerne that is mown with low frequency (Eraud and Boutin 2002; Stein-Bachinger and Fuchs 2004). In the present study, the highest nestling productivity was reached in lucerne. The low-frequency mowing of lucerne allows sufficient time for Skylarks to raise their young but also repeatedly returns the vegetation to a height and coverage that is suitable for nesting, explaining the high use of this crop as a breeding habitat throughout the entire breeding season. Another advantage of lucerne is the relatively high availability of invertebrates compared to other crops, probably because lucerne is a perennial crop and requires no pesticide (Bretagnolle et al. 2011). Previous work suggests that increasing the surface area of lucerne may also benefit other passerines, such as Corn Bunting (*Emberiza calandra*), Yellow Wagtail (*Motacilla flava*) and Whinchat (*Saxicola rubreta*) (Stein-Bachinger and Fuchs 2012). For Montagu's Harrier (*Circus pygargus*), lucerne is one of the most preferred hunting habitats, especially shortly after mowing, when voles and mice become more easily visible (Trierweiler et al. 2010). In France, an increase in the surface area of extensively managed lucerne helped to locally reverse the decline of the endangered Little Bustard *Tetrax tetrax* (Bretagnolle et al. 2011) while simultaneously slowing down the decline of the untargeted Skylark (Brodier et al. 2013).

An important advantage of promoting certain production crops for agri-environmental purposes is that such measures are more cost-effective than nonproductive agri-environment schemes. In the study area, farmers received a payment of approximately €2150 for each hectare of field margin to fully compensate for the income loss associated with not using the land to grow winter wheat, the most profitable crop in the region. In comparison, the sum required to compensate for the income difference between lucerne and winter wheat would be approximately €1200 per ha, or €1000 when the positive effects of lucerne on soil quality and future pest pressure are incorporated (personal communication from local farmers). Thus, by promoting crops such as lucerne as agri-environmental measures, farmers can provide safe breeding habitat for birds at relatively low costs, even when additional measures are taken that reduce farming intensity in order to increase the ecological value of the crop (e.g. limiting the number of silage cuts per year).

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References

Aebischer NJ (1999) Multi-way comparisons and generalized linear models of nest success: extensions of the Mayfield method. Bird Study 46:22–31

Baker DJ, Freeman SN, Grice PV, Siriwardena GM (2012) Landscape-scale responses of birds to agri-environment management: a test of the English Environmental Stewardship Scheme. J Appl Ecol 49:871–882

Boatman ND, Brickle NW, Hart JD, Milsom TP, Morris AJ, Murray AWA, Murray KA, Robertson PA (2004) Evidence for the indirect effects of pesticides on farmland birds. Ibis 146:131–143

Bradbury RB, Wilson JD, Moorcroft D, Morris AJ, Perkins AJ (2003) Habitat and weather are weak correlates of nestling condition and growth rates of four UK farmland passerines. Ibis 145:295–306

Bretagnolle V, Villers A, Denonfoux L, Cornulier T, Inchausti P, Badenhausser I (2011) Rapid recovery of a depleted population of little bustards *Tetrax tetrax* following provision of alfalfa through an agri-environment scheme. Ibis 153:4–13

Brickle NW, Harper DGC, Aebischer NJ, Cockayne SH (2000) Effects of agricultural intensification on the breeding success of corn buntings *Miliaria calandra*. J Appl Ecol 37:742–755
Brodier S, Augiron S, Cornulier T, Bretagnolle V (2013) Local improvement of skylark and corn bunting population trends on intensive arable landscape: a case study of the conservation tool Natura 2000. Anim Conserv 17:204–216
Butler SJ, Vickery JA, Norris K (2007) Farmland biodiversity and the footprint of agriculture. Science 315:381–384
Chamberlain DE, Crick HQP (1999) Population declines and reproductive performance of Skylarks *Alauda arvensis* in different regions and habitats of the United Kingdom. Ibis 141:38–51
Chamberlain D, Vickery JA (2000) Spatial and temporal distribution of breeding Skylarks *Alauda arvensis* in relation to crop type in periods of population increase and decrease. Ardea 88:61–73
Chamberlain DE, Wilson AM, Browne SJ, Vickery JA (1999) Effects of habitat type and management on the abundance of skylarks in the breeding season. J Appl Ecol 36:856–870
Chamberlain DE, Fuller RJ, Bunce RGH, Duckworth JC, Shrubb M (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. J Appl Ecol 37:771–788
Chin EH, Love OP, Clark AM, Williams TD (2005) Brood size and environmental conditions sex-specifically affect nestling immune response in the European starling *Sturnus vulgaris*. J Avian Biol 36:549–554
Cordeau S, Petit S, Reboud X, Chauvel B (2012) Sown grass strips harbour high weed diversity but decrease weed richness in adjacent crops. Weed Res 52:88–97
Delius JD (1965) A population study of skylarks *Alauda arvensis*. Ibis 107:466–492
Denys C, Tscharntke T (2002) Plant-insect communities and predator–prey ratios in field margin strips, adjacent crop fields, and fallows. Oecologia 130:315–324
Donald PF, Green RE, Heath MF (2001a) Agricultural intensification and the collapse of Europe's farmland bird populations. P R Soc Lond B Bio 268:25–29
Donald PF, Muirhead LB, Buckingham DL, Evans AD, Kirby WB, Gruar DJ (2001b) Body condition, growth rates and diet of Skylark *Alauda arvensis* nestlings on lowland farmland. Ibis 143:658–669
Donald PF, Buckingham DL, Moorcroft D, Muirhead LB, Evans AD, Kirby WB (2001c) Habitat use and diet of skylarks *Alauda arvensis* wintering on lowland farmland in Southern Britain. J Appl Ecol 38:536–547
Donald PF, Evans AD, Muirhead LB, Buckingham DL, Kirby WB, Schmitt SIA (2002) Survival rates, causes of failure and productivity of Skylark *Alauda arvensis* nests on lowland farmland. Ibis 144:652–664
Duelli P, Obrist MK (2003) Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. Basic Appl Ecol 4:129–138
EBCC (2013) Pan-European Common Bird Monitoring Scheme. European Bird Census Council. http://www.ebcc.info/pecbm.html
Eggers S, Unell M, Pärt T (2011) Autumn-sowing of cereals reduces breeding bird numbers in a heterogeneous agricultural landscape. Biol Conserv 144:1137–1144
Eraud C, Boutin J-M (2002) Density and productivity of breeding Skylarks *Alauda arvensis* in relation to crop type on agricultural lands in western France: small field size and the maintenance of set-aside and lucerne are important to ensure high breeding pair densities and productivity. Bird Study 49:287–296
Evans AD, Smith KW, Buckingham DL, Evans J (1997) Seasonal variation in breeding performance and nestling diet of cirl buntings *Emberiza cirlus* in England. Bird Study 44:66–79
Fuller RJ, Hinsley SA, Swetnam RD (2004) The relevance of non-farmland habitats, uncropped areas and habitat diversity to the conservation of farmland birds. Ibis 146:22–31
Geertsma M, van Berkel H, Esselink H (2000) Are high fitness values sufficient to maintain a Dutch population of the red-backed shrike (*Lanius collurio*)? Ring 22:79–88
Geiger F, Bengtsson J, Berendse F, Weisser WW, Emmerson M, Morales MB, Ceryngier P, Liira J, Tscharntke T, Winqvist C, Eggers S, Bommarco R, Pärt T, Bretagnolle V, Plantegenest M, Clement LW, Dennis C, Palmer C, Oñate JJ, Guerrero I, Hawro V, Aavik T, Thies C, Flohre A, Hänke S, Fischer C, Goedhart PW, Inchausti P (2010) Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic Appl Ecol 11:97–105
Geiger F, Hegemann A, Gleichman M, Flinks H, De Snoo GR, Prinz S, Tieleman BI, Berendse F (2014) Habitat use and diet of Skylarks (*Alauda arvensis*) wintering in an intensive agricultural landscape of the Netherlands. J Ornithol 15:507–518
Gilroy JJ, Anderson GQA, Grice PV, Vickery JA, Watts PN, Sutherland WJ (2009) Foraging habitat selection, diet and nestling condition in yellow wagtails *Motacilla flava* breeding on arable farmland. Bird Study 56:221–232
Guerrero I, Morales MB, Oñate JJ, Geiger F, Berendse F, Snoo GD, Eggers S, Pärt T, Bengtsson J, Clement LW, Weisser WW, Olszewski A, Ceryngier P, Hawro V, Liira J, Aavik T, Fischer C, Flohre A, Thies C, Tscharntke T (2012) Response of ground-nesting farmland birds to agricultural intensification across Europe: landscape and field level management factors. Biol Conserv 152:74–80
Hart JD, Milsom TP, Fisher G, Wilkins V, Moreby SJ, Murray AWA, Robertson PA (2006) The relationship between yellowhammer breeding performance, arthropod abundance and insecticide applications on arable farmland. J Appl Ecol 43:81–91
Hazler KR (2004) Mayfield logistic regression: a practical approach for analysis of nest survival. Auk 121:707–716
Hegemann A (2012) Strive to survive: the Skylark's ecology and physiology in an annual-cycle perspective. PhD thesis. Rijksuniversiteit Groningen, Groningen, pp 16
Hegemann A, Matson KD, Flinks H, Tieleman I (2013) Offspring pay sooner, parents pay later: experimental manipulation of body mass reveals trade-offs between immune function, reproduction and survival. Front Zool 10:77
Henderson IG, Holland JM, Storkey J, Lutman P, Orson J, Simper J (2012) Effects of the proportion and spatial arrangement of uncropped land on breeding bird abundance in arable rotations. J Appl Ecol 49:883–891
Holland JM, Hutchison MAS, Smith B, Aebischer NJ (2006) A review of invertebrates and seed-bearing plants as food for farmland birds in Europe. Ann Appl Biol 148:49–71
Hovd H, Skogen A (2005) Plant species in arable field margins and road verges of central Norway. Agri Ecosyst Environ 110:257–265
Hustings MFH, Kwak RGM, Opdam PFM, Reijnen MJSM (1989) Vogelinventarisatie. Achtergronden, richtlijnen en verslaglegging. Pudoc Wageningen, Nederlandse Vereniging tot Bescherming van Vogels, Zeist
Jenny M (1990) Territorialität und Brutbiologie der Feldlerche *Alauda arvensis* in einer intensiv genutzten Agrarlandschaft. J Ornithol 131:241–265
Johnson DH (1979) Estimating nest success: the Mayfield method and an alternative. Auk 96:651–661
Kleijn D, Sutherland WJ (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? J Appl Ecol 40:947–969
Kragten S, Trimbos KB, de Snoo GR (2008) Breeding skylarks (*Alauda arvensis*) on organic and conventional arable farms in the Netherlands. Agr Ecosyst Environ 126:163–167

Kuiper MW, Ottens HJ, Cenin L, Schaffers AP, van Ruijven J, Koks BJ, Berendse F, de Snoo GR (2013) Field margins as foraging habitat for skylarks (*Alauda arvensis*) in the breeding season. Agr Ecosyst Environ 170:10–15

Lindström J (1999) Early development and fitness in birds and mammals. Trends Ecol Evol 14:343–348

Magrath RD (1991) Nestling weight and juvenile survival in the blackbird, *Turdus merula*. J Anim Ecol 60:335–351

Martin TE (1987) Food as a limit on breeding birds: a life-history perspective. Annu Rev Ecol Syst 18:453–487

Martin TE (1995) Avian life history evolution in relation to nest sites, nest predation, and food. Ecol Monogr 65:101–127

Mayfield H (1961) Nesting success calculated from exposure. Wilson Bull 73:255–261

Mayfield HF (1975) Suggestions for culculating nest success. Wilson Bull 87:456–466

Meichtry-Stier KS, Jenny M, Zellweger-Fischer J, Birrer S (2014) Impact of landscape improvement by agri-environment scheme options on densities of characteristic farmland bird species and brown hare (*Lepus europaeus*). Agr Ecosyst Environ 189:101–109

Morris AJ, Gilroy JJ (2008) Close to the edge: predation risks for two declining farmland passerines. Ibis 150:168–177

Newton I (2004) The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. Ibis 146:579–600

Noordijk J, Musters C, van Dijk J, de Snoo G (2010) Invertebrates in field margins: taxonomic group diversity and functional group abundance in relation to age. Biodivers Conserv 19:3255–3268

Perkins AJ, Whittingham MJ, Morris AJ, Bradbury RB (2002) Use of field margins by foraging yellowhammers *Emberiza citrinella*. Agr Ecosyst Environ 93:413–420

Poulsen JG, Sotherton NW, Aebischer NJ (1998) Comparative nesting and feeding ecology of skylarks *Alauda arvensis* on arable farmland in southern England with special reference to set-aside. J Appl Ecol 35:131–147

Praus L, Weidinger K (2010) Predators and nest success of Sky Larks *Alauda arvensis* in large arable fields in the Czech Republic. Bird Study 57:525–530

Provincie Groningen (2008) Meer doen in minder gebieden. Actieprogramma Weidevogels-Akkervogels. Provincie Groningen, Groningen

Redondo T, Castro F (1992) The increase in risk of predation with begging activity in broods of magpies *Pica pica*. Ibis 134:180–187

Robinson RA, Sutherland WJ (2002) Post-war changes in arable farming and biodiversity in Great Britain. J Appl Ecol 39:157–176

Siriwardena GM, Baillie SR, Crick HQP, Wilson JD (2000) The importance of variation in the breeding performance of seed-eating birds in determining their population trends on farmland. J Appl Ecol 37:128–148

Smith B, Holland J, Jones N, Moreby S, Morris AJ, Southway S (2009) Enhancing invertebrate food resources for skylarks in cereal ecosystems: how useful are in-crop agri-environment scheme management options? J Appl Ecol 46:692–702

Smith HG, Öckinger E, Rundlöf M (2010) Biodiversity and the landscape ecology of agri-environment schemes. Asp Appl Biol 100:225–232

SOVON (2012) Vogelbalans thema boerenland. SOVON, Nijmegen

Stein-Bachinger K, Fuchs S (2004) Wie kann der Lebensraum Acker im großflächigen Okologischen Landbau für Feldvögel und Feldhase optimiert werden? In: Proc "Naturschutz als Aufgabe des Okologischen Landbaus," Witzenhausen, Germany, 16–17 Oct 2003

Stein-Bachinger K, Fuchs S (2012) Protection strategies for farmland birds in legume–grass leys as trade-offs between nature conservation and farmers' needs. Org Agr 2:145–162

Stoate C, Báldi A, Beja P, Boatman ND, Herzon I, van Doorn A, de Snoo GR, Rakosy L, Ramwell C (2009) Ecological impacts of early 21st century agricultural change in Europe—a review. J Environ Manage 91:22–46

Toepfer S, Stubbe M (2001) Territory density of the Skylark (*Alauda arvensis*) in relation to field vegetation in central Germany. J Ornithol 142:184–194

Trierweiler C, Drent RH, Komdeur J, Koks BJ (2010) Travels to feed and food to breed. In: Home range size and habitat selection of the endangered Montagu's harrier *Circus pygargus* in NW Europe: implications for conservation. PhD thesis. Rijksuniversiteit Groningen, Groningen, pp 47–67

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. Ecol Lett 8:857–874

Tscharntke T, Batáry P, Dormann CF (2011) Set-aside management: how do succession, sowing patterns and landscape context affect biodiversity? Agr Ecosyst Environ 143:37–44

Van Dijk AJ, Boele A (2011) Handleiding SOVON Broedvogelonderzoek. SOVON, Nijmegen

Van Dijk WFA, Schaffers AP, Leewis L, Berendse F, De Snoo GR (2013) Temporal effects of agri-environment schemes on ditch bank plant species. Basic Appl Ecol 14:289–297

Vickery JA, Tallowin JR, Feber RE, Asteraki EJ, Atkinson PW, Fuller RJ, Brown VK (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. J Appl Ecol 38:647–664

Vickery J, Carter N, Fuller RJ (2002) The potential value of managed cereal field margins as foraging habitats for farmland birds in the UK. Agr Ecosyst Environ 89:41–52

Vickery JA, Feber RE, Fuller RJ (2009) Arable field margins managed for biodiversity conservation: a review of food resource provision for farmland birds. Agr Ecosyst Environ 133:1–13

Weibel UM (1999) Nest site selection and breeding success of skylarks *Alauda arvensis* in an intensively used arable landscape with special reference to wildflower strips. In: Effects of wildflower strips in an intensively used arable area on skylarks (*Alauda arvensis*). PhD thesis. Swiss Federal Institue of Technology, Zurich, pp 11–37

Wilson JD, Evans J, Browne SJ, Jon RK (1997) Territory distribution and breeding success of skylarks *Alauda arvensis* on organic and intensive farmland in Southern England. J Appl Ecol 34:1462–1478

Wilson JD, Morris AJ, Arroyo BE, Clark SC, Bradbury RB (1999) A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. Agr Ecosyst Environ 75:13–30

Zollinger J-L, Birrer S, Zbinden N, Korner-Nievergelt F (2013) The optimal age of sown field margins for breeding farmland birds. Ibis 155:779–791