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Habitat use of foraging skylarks (*Alauda arvensis* L.) in an arable landscape with wild flower strips

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Summary

1 Skylark (*Alauda arvensis*) populations have dramatically declined during recent decades in central Europe. The modern intensive land use is responsible for this development. A new Swiss agropolicy aims to sustain biodiversity on farmland by introducing ecological compensation sites, e.g. wild flower strips.

2 This study investigates the hypothesis that wild flower strips are a habitat with high relative use by skylarks for foraging. Additionally, the factors which influence feeding frequency and differences between both sexes were investigated. During the breeding season, the habitat use of foraging skylarks was observed. The relative habitat use was calculated by compositional analysis.

3 Skylark females and males did not differ in their feeding rate. The age of the nestlings and the time of day influenced the feeding rate per hour and nestling, but there was no effect of the number of nestlings.

4 The habitats were ranked by the relative use for foraging: wild flower strips > stubble > tracks > grassland > root vegetables > maize > oil rape > spring cereals > winter cereals. Crop categories with low and sparse vegetation had a high relative use. Wild flower strips had the highest relative use in spite of their high and dense vegetation structure.

5 Wild flower strips are particularly attractive for foraging skylarks due to their heterogeneous vegetation structure and a high abundance of invertebrate food.

Keywords: compositional analysis, ecological compensation sites, habitat selection, invertebrate food, skylark, vegetation structure

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Introduction

A decline in the populations of the skylark (*Alauda arvensis*) has been reported in nearly all European countries during the last three decades, reviewed in Tucker & Heath (1994) and Hagenmeijer & Blair (1997). The modern intensive agricultural land use, characterised by loss of winter stubble, increased use of pesticides, reduction in crop rotation and expansion of field size, among others, are the main reasons for these declines (e.g. Schläpfer 1988; Busche 1989). In particular, the reduction in abundance of invertebrate food, due to increased use of insecticides, and food availability, due to denser sown and faster growing crops, are supposed to be responsible for the decreasing size of skylark populations (Schläpfer 1988; Jenny 1990; Evans *et al.* 1995); the situation for the grey partridge (*Perdix perdix*) seems to be similar (Potts 1986).

Height and density of crops affect foraging behaviour and territory distribution of skylarks (Jenny 1990; Wilson *et al.* 1997; Daunicht 1998). The skylark needs sparse vegetation, as the most frequent foraging technique is walking and taking food items from the soil surface or gleaning at plant leaves (Jenny 1990; Tryjanowski 1995). The lack of open ground or sparse vegetation is a severe factor influencing breeding success for many other bird species, e.g. woodlark (*Lullula arborea*; Bowden 1990), and yellow wagtail (*Motacilla flava*; Stiebel 1995).

Skylarks feed their chicks mainly with invertebrates: In a landscape in the Swiss lowlands dominated by grassland the diet was composed of dipterans (adults and larvae), orthopterans and lepidopterans (Jenny 1990), and in arable farmland in southern England of dipterans (adults and larvae), araneae and coleopterans (Poulsen 1993). A preliminary study with the ligature method of nestling diet collected in the intensively used arable Klettgau in 1995, revealed a similar food spectrum to that in the above cited authors (Weibel 1995).

The present agro-economic situation with its implications for the decline of numerous farmland species has led to a new agropolicy in Switzerland, which aims to sustain biodiversity besides the production of food as the main objective of agriculture. The farmers have to make at least 5% (since 1998 7%) of their farmland available for ecological compensation sites, for instance as extensively used meadows, hedgerows and wild flower strips ("Buntbrachen"). Wild flower strips are 3–10 m wide and sown with a seed mixture of annual segetals, biennual ruderals and grassland perennials.

Associated projects on ecological compensation sites assess the beneficial effects of the wild flower strips which were established by the Swiss Ornithological Institute (Sempach) in a 10-year project founded by the Federal Office of Environment, Forest and Landscape (BUWAL). The projects improve practical knowledge about the establishment of ecological compensation sites in arable landscapes, and they promote farmland species, especially grey partridge and brown hare (*Lepus europaeus*; Jenny *et al.* 1997; Pfister 1997).

Wild flower strips are supposed to be beneficial for many species, e.g. endangered segetals, invertebrates, and nesting or foraging farmland birds. The present study investigates the habitat use of foraging skylarks in an intensively used arable landscape, where wild flower strips were established some years ago. The main hypothesis is that wild flower strips sustain a high relative use of foraging skylarks. Besides that, foraging behaviour and feeding of skylark males and females are compared.

Study area and methods

STUDY AREA

The study took place in the Klettgau (Canton Schaffhausen, Switzerland) in 1995. The study area (5.3 km^2; 450 m a.s.l.) is an intensively used arable landscape with calcareous soil of low fertility. The climate is relatively warm and dry (8.5 °C annual average; 915 mm annual average precipitation; 1931–1990); the meteorological data are from the climate station Hallau 3 km west of the study area. Agriculturally used land within the study area covers 483.2 ha, and settlements 46.3 ha. Agricultural land use is dominated by winter cereal farming (wheat and barley 30%, resp. 9%), and other important crops are maize (13%), sugar beet (8%) and oil rape (7%); the area of intensively used grassland is 38 ha (8%): besides that 12 other crop types, including vineyards, set-asides and ecological compensation sites, were cultivated (25%). The average field size is 0.81 ha (range 0.1–5.5 ha). The biologically enhancing of the arable landscape is mainly realised with wild flower strips (5.4 ha) and extensively used grassland (7.2 ha). The total length of grassy tracks is 36 km (16.2 ha).

Observations of skylarks

In total, foraging skylarks were observed for 47 h on 38 days in 24 territories (27 nests) between 5.30 a.m. and 9.00 p.m. Observation hours were unequally distributed within the breeding season (April: 1 h, May: 4 h, June: 15 h, July: 27 h) and the time of day (morning 5.30 to 10.30 a.m.: 34 h; midday 10.31 a.m. to 3.30 p.m.: 8 h; afternoon/evening 3.31 to 9.00 p.m.: 5 h). For all observations a tent was used as a hide at a suitable distance from the nest and they were started 15 min after setting up the tent.

During the observation hour all activities of the females and the males, e.g. foraging, feeding, songflight and antagonistic behaviour, were recorded; also the time spent foraging in a particular crop type. The nests were visited after the observation to obtain information on the age of the nestlings (mean 7.3 days, range 3–11 days) and the number of nestlings (mean 3.5, range 2–5).

Besides a small size difference, the sexes of the skylarks are distinguishable not by field characteristics but by their behaviour. Males show a more conspicuous behaviour than females, as sitting on perches, songflights and antagonistic behaviour (Delius 1963). During the observations the sexes of the birds could be easily determined.

Vegetation types

The vegetation height for each crop type in the observed home range was measured to the nearest 5 cm with three replicates per field. The vegetation cover was estimated to the nearest 5% in one 1 m^2 plot per crop type.

The size of all home ranges was mapped during the entire breeding season and analysed in a geographical information system (GIS, ARC/INFO®) to get the areas of the different crop types per home range and the total size.

Statistical analyses

Feeding frequencies of females and males were compared by a paired *t*-test. Multiple regressions were calculated with several explanatory variables for feeding rate per hour and per nestling of the female, male, and pair. The feeding frequencies were square-root-transformed to obtain normal distributions of the residuals.

The calculation of the relative use of the different crops, based on the number of foraging flights or time spent for foraging, was done with the compositional analysis (Aitchison 1986; Aebischer *et al.* 1993). The calculation of preference indices (e.g. Jenny 1990; Griesser 1996) is statistically not correct because of the non-independence of the proportion of habitat composition. In a territory with D crop types the individual proportional habitat use is described by $x_1, x_2, ..., x_D$, where x_i is the proportion of the individual's foraging flight per hour in crop type i. These proportions summing to 1, called a composition, are not independent. To render linear independence the log-ratio transformation $y_i = ln(x_i/x_j)$

*Table 1. Factors affecting feeding frequencies of skyarks females, males, and pairs. For the multiple regression feeding rate per hour and nestling was square-root-transformed. The feeding rates were independent of the number of nestlings, the month of observation, and the constant was not significant (significance levels: *, P < 0.05; **, P < 0.01; ***, P < 0.001)*

	Estimate	df	Sum of squares	*F*
Female				
Age	0.04	1	0.32	4.7*
Weather+	–0.10	1	0.39	5.7*
Residual		44	3.01	
Model $r^2 = 0.20$				
Male				
Age	0.05	1	0.60	15.0***
Time of day#	–0.09	1	0.20	5.0*
Residual		44	1.77	
Model $r^2 = 0.27$				
Pair				
Age	0.06	1	0.79	11.4**
Weather+	–0.08	1	0.27	5.0*
Residual		44	3.06	
Model $r^2 = 0.26$				

+ Sunny or slightly cloudy *vs.* overcast or rainy
# 10.31 a.m. to 3.30 p.m. *vs.* 5.31 to 10.30 a.m., resp. 3.31 to 8.30 p.m.

(i = 1, ..., D; $i \neq j$) for any component x_i has to be calculated (Aitchison 1986; Aebischer *et al.* 1993). The crop types were stratified in nine categories to reduce the number of non-used habitats; available but non-used habitats were set as 0.01. For each observation the log-ratios were calculated and then pooled to determine the matrix of standardised log-ratio differences. A separate compositional analysis for females and males could not be calculated as too many habitat types were unused because of low feeding rates. The comparison between ranking according to compositional analysis by number of flights and time spend was done with a Spearman rank correlation.

To explain the log-ratios by vegetation structure (height and cover), a multiple linear regression was calculated in which the collinearity of the explanatory variables was corrected with a path analysis (Sokal & Rohlf 1995). The relations between time and log-ratios, vegetation cover and height per crop category were analysed with regression models. The statistical analysis are done with the JMP 3.2.1 software package (SAS institute).

Results

Feeding frequencies

Females and males showed no differences in feeding frequencies per hour and nestling (paired t-test; $t = 1.60$, df = 46, $P > 0.05$). The feeding frequencies per hour and nestling had a range from 1.7 to 6.0, and depended for females and pairs on the age of the nestlings and the weather conditions, and for males on the age of the nestlings and the time of day (Table 1). Feeding frequencies of females and pairs increased with the age of the nestlings and were higher on sunny or slightly cloudy days than for rainy and overcast weather. The feeding frequency of the males also increased with

Table 2. Habitat use of foraging skylarks in arable farmland. Matrix of standardised log-ratio differences of numbers of foraging flights per crop category of the compositional analysis, and the resulting ranking of the relative habitat use

	Stubble	Tracks	Grassland	Root vegetables	Maize	Oil rape	Winter cereals	Spring cereals	Rank
Wild flower strip	1.33	2.08	2.29	2.63	4.39	6.31	6.38	7.50	1
Stubble		0.74	0.96	1.30	3.06	4.98	5.05	6.17	2
Tracks			0.21	0.55	2.32	4.24	4.30	5.43	3
Grassland				0.34	2.10	4.02	4.09	5.21	4
Root vegetables					1.76	3.68	3.75	4.87	5
Maize						1.92	1.99	3.11	6
Oil rape							0.07	1.19	7
Winter cereals								1.12	8
Spring cereals									9

Table 3. Habitat use of foraging skylarks in arable farmland. Matrix of standardised log-ratio differences of time spent per crop category of the compositional analysis, and the resulting ranking of the relative habitat use

	Stubble	Grassland	Root vegetables	Tracks	Maize	Oil rape	Spring cereals	Winter cereals	Rank
Wild flower strip	2.08	2.85	3.22	3.49	5.52	8.45	8.62	9.96	1
Stubble		0.76	1.14	1.41	3.43	6.37	6.54	7.87	2
Grassland			0.37	0.64	2.67	5.60	5.77	7.11	3
Root vegetables				0.27	2.30	5.23	5.40	6.74	4
Tracks					2.03	4.96	5.13	6.47	5
Maize						2.93	3.10	4.44	6
Oil rape							0.17	1.51	7
Spring cereals								1.34	8
Winter cereals									9

the age of the nestlings and was lower during midday. The feeding rates were independent of the number of nestlings, the months of observations, and the constant is not significant.

RELATIVE USE OF DIFFERENT HABITAT TYPES

The compositional analysis of the number of foraging flights and of time spent in a certain habitat within the home range both indicated a significant non-random utilisation of the total available habitats (Wilk's r = 0.25, $P <$ 0.001; r = 0.31, $P <$ 0.001, resp.). The habitat ranking according to the log-ratio matrix is shown in Tables 2 and 3 (from "1" for high use to "9" for low use). The Spearman rank correlation indicated a highly significant correlation between the habitat ranking of the number of foraging flights and of the time spent in a certain habitat ($r_s = 0.95$, $P < 0.001$, $n = 9$).

The vegetation height and cover of the crop categories ranked by the log-ratio differences of the number of foraging flights are shown in Fig. 1 and 2. The collinearity between vegetation height and the arcsin transformed cover values was $r = 0.75$. The multiple regression between the log-ratios and the vegetation cover and height, corrected by a path analysis, has a total determination of $r^2 = 0.80$. The

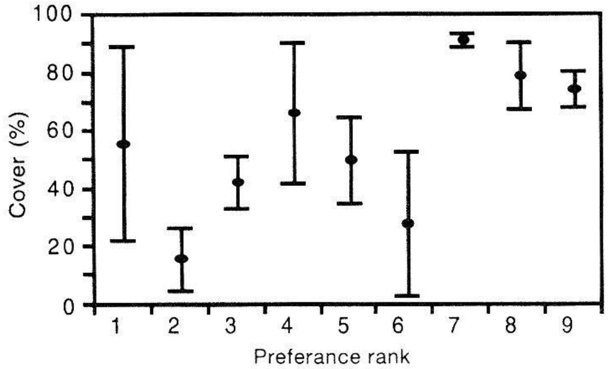

Fig. 1. Vegetation cover of the crop categories arranged according to the ranking of relative habitat use; (from "1" for high use to "9" for low use)(mean ± 1SD) (1, wild flower strips; 2, stubble; 3, tracks; 4, grassland; 5, root vegetables; 6, maize; 7, oil rape; 8, spring cereals; 9, winter cereals).

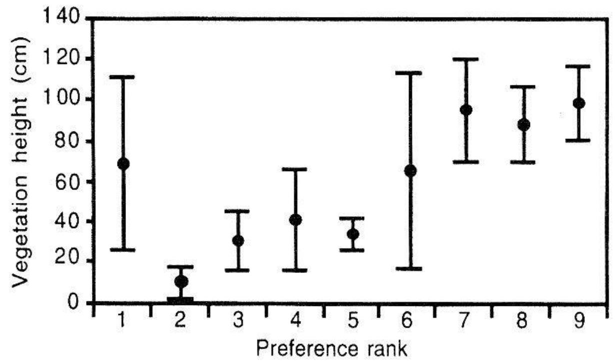

Fig. 2. Vegetation height of the crop categories arranged according to the ranking of relative habitat use (mean ± 1 SD) (1, wild flower strips; 2, stubble; 3, tracks; 4, grassland; 5, root vegetables; 6, maize; 7, oil rape; 8, spring cereals; 9, winter cereals).

slope parameters were $b = -0.41$ for vegetation height and $b = -0.13$ for cover.

The relation between log-ratios of the number of flights per crop category and time, expressed as weeks of a year, was for no crop category statistically significant (simple regressions; $P > 0.05$). Vegetation cover and height increased during the time of observation in all crop categories, except in the grassland (simple regressions; $P < 0.05$ for cover of stubble, root vegetables, maize, and winter cereal; for height of wild flower strips, maize, and winter cereal).

Discussion

FEEDING FREQUENCIES

The feeding frequencies of the skylarks were nearly fourfold lower than those reported by Delius (1963), and threefold lower than by Poulsen (1993), but slightly higher than by Jenny (1990), when compared for feeding rate per nestling and per hour at the sixth day after hatching. The great difference between Poulsen (1993) and this study is quite surprising, since both studies were carried out in an arable landscape. The similarities among the two English studies (Delius 1963; Poulsen 1993), and among the Swiss studies (Jenny 1990; this study) are remarkable. Poulsen (1993, 1996) has observed an inverse correlation between feeding rate and feeding distance, and he reported that the birds with a longer feeding distance bring more food items per nest visit, which is consistent with the "central place foraging theory" (Charnov 1976; Orians & Pearson 1979). However, decisive is not the number of nest visits per time unit and nestling, but the metabolizable energy per time and it might be that the skylarks in this study bring more food items per nest visit than in the British investigations (Delius 1963; Poulsen 1993). The design of this study did not allow these findings to be tested, but it was remarkable that the skylarks nearly always foraged at the same place in subsequent flights and rarely changed the crop types without feeding the nestlings.

The results indicate no differences in feeding frequencies between the sexes, contradicting the statement of Delius (1963). However, the age of the nestling is an important factor affecting feeding rate. The remaining variation in feeding rate could only partly be explained by the data available, especially for the females (Table 1). The rather small sample size and the unequal distribution during breeding season and time of day, and the lack of meteorological data on a local scale might be responsible. A similar relation between feeding frequency and age of the nestlings was also described by Delius (1963) and Poulsen (1993). The diurnal variation is similar to other species (O'Conner 1984), but contrasts with the results of Poulsen (1993) who reports the most frequent nest visits in late afternoon and evening. Most observations in this study were carried out during the second half of the breeding period, where during the rather hot midday period the activity of the skylarks was generally low, while Poulsen's study (1993) comprised observations of the entire breeding season. Weather is known to affect feeding frequencies (O'Conner 1984), but might also affect the diurnal variation in feeding rate.

RELATIVE HABITAT USE

This study revealed a high relative use of crop categories with low and sparse vegetation, with the exception of wild flower strips, which have the highest relative use but high and dense vegetation. Skylarks need, because of their foraging technique, sparse vegetation below 50% cover (Jenny 1990). In crop categories with high and dense vegetation (oil rape, winter and spring cereal) skylarks forage at unsown plots, tramlines and field edges (pers. observ.), which was also shown in spring barley fields by Odderskær *et al.* (1997). A dense vegetation strucure hinders the movement, and the high relative use of tramlines and unsown plots is not due to a higher food abundance, but a consequence of the lower and sparser vegetation in these microhabitats (Odderskær *et al.* 1997).

Maize fields had an average cover of 28% which should allow foraging. The attractivity of maize as foraging habitat depends on the management of the site during the previous winter, i.e. grassland or bare ground (Jenny 1990). The cultivation of maize in the study area is very intensive with frequent application of pesticides and rarely a preceding grassland cultivation. Thus, the availability of invertebrates seems to be too low for efficient foraging despite the sparse vegetation. The high relative use of stubble, tracks and root vegetables can be explained by the low vegetation cover and height (<50%, <50 cm, resp.). Grassland had a quite high relative use in spite of an average cover of 66% and height of 41 cm. An explanation for this is the evidence that meadows and set-aside grassland support a much higher availability of invertebrate foods for skylarks than winter cereals (Jenny 1990; Poulsen 1993).

Wild flower strips had the highest relative use despite their dense and tall vegetation. The vegetation structure of the wild flower strips was very heterogeneous with a small scaled mosaic of dense and sparse vegetation, and they have a greater density of invertebrates than adjacent fields (Lys 1994; Frank & Nentwig 1995).

The influence of weather (in particular dew) affected the spatial and temporal foraging pattern in this study as reported by Jenny (1990). Tracks, for example, receive a high relative use especially during wet weather (pers. observ.).

The relations between log-ratios, vegetation cover and height, and time for the crop categories were weak because of unequal observation distribution during the breeding season with the greater part between end of June and mid of July. The lack of some observations in the first half of the breeding period prevents an extrapolation to the entire breeding period. A decreasing utilization of dense and tall growing crop types for foraging and nesting are described by several authors (e.g. Schläpfer 1988; Jenny 1990; Poulsen 1993). In the modern arable landscape with large field sizes, a short crop rotation and a high use of pesticides and fertilisers skylark experience a food shortage during the breeding period, due to reduced invertebrate food abundance and the lack of sparse vegetation.

PRACTICAL IMPLICATIONS

Foraging skylarks benefit from the wild flower strips due to their heterogeneous vegetation structure and a greater invertebrate abundance, that means overall a greater invertebrate food availability. It is very important to sow the wild flower strips at a low density, i.e. <5000 g ha^{-1} with a standard seed mixture (Jenny *et al.* 1997), and in a heterogeneous pattern, which benefits foraging skylarks. Besides the attractivity of wild flower strips as foraging place they have also a high relative use as nesting habitat (Weibel *et al.*, in prep. a) and the nestlings in home ranges which contain wild flower strips have a greater growth rate (Weibel *et al.*, in prep. b). Other bird species, e.g. corn bunting (*Miliaria calandra*), stonechat (*Saxicola torquata*) and quail (*Coturnix coturnix*), also benefit from wild flower strips (Jenny *et al.* 1997). To maintain the value as foraging habitat for skylarks during the following years the wild flower strips have to be partly harrowed and ploughed every 2–3 years depending on the vegetation structure.

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