

CONTRIBUTED PAPER

Restoring habitat quality for Skylarks in winter cereal fields by manipulating the crop architecture

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Abstract

Losses of suitable foraging and nesting habitats are key drivers for ongoing declines of farmland birds. For Eurasian Skylarks (*Alauda arvensis*), this is reflected by the lack of sparse and short vegetation structure (i.e., crop architecture). Existing countermeasures outside cultivated areas seem unable to offset declines, indicating the need for in-field measures, ideally in cereal fields which cover large shares of agricultural land and ideally without compromising yields.

We experimentally tested whether unsown Skylark strips in intensive winter cereal fields (treatment) provided sparse and short crop architecture throughout the breeding season and whether this improved habitat quality by comparing key parameters of Skylark populations on treatment fields and fields without Skylark strips (control). Further, we tested whether the size and direction of effects of the measure depended on surrounding landscape features and seasonality.

Breeding performance was improved in treatment fields: the odds for nests being successful were 12.5 times that of control fields. During important phases of the breeding season, prey density and parental foraging were increased in treatment fields. Territorial behavior was higher in treatment fields throughout the breeding season, which was also less dependent on other attractants (i.e., proximity to ecotones) compared to control fields. Habitat use was increasingly higher in treatment fields as the breeding season progressed. Further, the availability of small-parceled fields in the surrounding area was related to decreased habitat use in control fields but not in treatment fields. In general, habitat use in cereal fields depended on adjacent habitat types, with the presence of spring sown crops leading to the largest declines.

We conclude that Skylark strips can improve habitat quality for Skylark nesting and foraging in intensive winter cereal fields. Given the previously shown yield stability, this encourages large-scale implementation of this measure for Skylark conservation, which might be most beneficial on large winter cereal fields in landscapes where there are few spring-sown crops.

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KEYWORDS

additional tramlines, agri-environmental scheme, agroecology, conservation, ecological intensification, in-crop, in-field, sward structure, vegetation density

1 | INTRODUCTION

In Europe, large parts of terrestrial biodiversity, such as plants, invertebrates, and birds, have adapted to agricultural conditions and therefore now largely depend on managed habitats (Krebs et al., 1999). Changes in farm management during agricultural intensification, however, reduced the carrying capacity of modern high-yielding farmland to support wildlife (Donald et al., 2001; Krebs et al., 1999; Robinson & Sutherland, 2002; Stoate et al., 2001). As the demand for agricultural products continues to increase, ongoing intensification might pose the greatest threat to farmland biodiversity (Butler et al., 2010; Jeanneret et al., 2021).

Despite great efforts to counteract negative impacts of agricultural practices (e.g., international agreements (European Commission, 2011), agri-environmental schemes (Kleijn & Sutherland, 2003), and the introduction of set asides (Tscharntke et al., 2011)), biodiversity is still declining (Emmerson et al., 2016; Kleijn et al., 2011; Kleijn & Sutherland, 2003). One group of species that is particularly threatened by intensified agricultural practices is farmland birds, whose abundance has halved on average since the 1980s (PECBMS, 2021a; Voříšek et al., 2010), with crop-breeding farmland birds being disproportionately negatively affected (Blösch, Batáry, et al., 2023; PECBMS, 2021b). Evidence is growing that the success of conservation measures scales with the degree to which they are tailored to the needs of species (Batáry et al., 2015; Peach et al., 2001; Pywell et al., 2012). Thus, in the case of crop-breeding birds, the key drivers of population declines, which are loss of nesting and foraging habitat in cropped areas (Butler et al., 2007, 2010), might not have been sufficiently compensated by existing measures.

An example for this is the Eurasian Skylark (*Alauda arvensis*), which has suffered severe declines in both the short and the long term (PECBMS, 2021c). Research in several European countries has independently demonstrated its requirements for a sparse and short crop architecture for successful breeding and efficient foraging (Donald, 2004; Jenny, 1990a, 1990b; Odderskær et al., 1997; Schläpfer, 1988) and multiple nesting attempts to offset high predation rates in order to maintain population levels (Donald, 2004; Wilson et al., 1997). Crops typically fulfill these vegetation-structural requirements only within a limited time period (Schläpfer, 1988;

Wilson et al., 1997, 2005), which is increasingly curtailed and/or mismatched with the breeding season as a result of agricultural intensification.

In particular, the switch from spring-sown to autumn-sown cereals with the earlier growth of winter varieties (Eggers et al., 2011; Fuller, 2000; Hinzman et al., 1986; Robinson & Sutherland, 2002) has rendered large areas of farmland (Eurostat, 2022) relatively unsuitable for Skylarks during most of the breeding season (Chamberlain et al., 1999; Donald & Vickery, 2000; Jenny, 1990b; Siriwardena et al., 2001). As a result of the altered crop architecture, Skylarks inhabiting winter cereals are forced to cease nesting early on (Daunicht, 1998; Donald, 2004) or to shift to nesting sites with a high risk of nest loss, such as unvegetated tramlines within winter cereal fields (Donald et al., 2002; Fischer et al., 2009; Püttmanns et al., 2021), field boundaries (Morris & Gilroy, 2008; Ottens et al., 2013), maize fields (Praus & Weidinger, 2015), or frequently mown meadows (Kuiper et al., 2015). The same is true for foraging: Skylarks nesting in winter cereals are increasingly forced either to feed solely along the tramlines, where food is scarce, or to fly to other habitats to feed, with the associated costs of energy expenditure and exposure to predation (Donald & Morris, 2005; Odderskær et al., 1997; Püttmanns et al., 2022).

Existing potentially suitable countermeasures such as set-asides or conservation headlands on the one hand probably cover too few an area for sufficient compensation as they are associated with conflicting aims (BLW, 2022; Jenny et al., 2002; Weibel, 1999) and are on the other hand considered high-risk habitats (especially for breeding), as predators are also increasingly attracted to them (Donald et al., 2002; Weibel, 1999). This indicates the need for measures that improve habitat conditions within the (winter) crop fields (Butler et al., 2007), but there are currently few whose effectiveness has been evaluated (Blösch et al., 2023b).

Opening up the crop architecture of winter cereals could be such a measure, providing benefits specifically tailored to this species in a relatively predator-safe environment. Also, it is a measure that seems to be able to maintain high yields (Blösch et al., 2023a). Currently, there are three distinct approaches on how the crop architecture of winter cereals can be manipulated in order to open it up: unsown plots (also referred to as Skylark plots), unsown strips (also referred to as Skylark

strips, additional tramlines), or wide-spaced rows (see Blösch et al., 2023b). Generally, Skylark plots and strips seem to be more successful than wide-spaced rows in keeping the crop canopy open throughout the breeding season (Morris et al., 2004), with promising initial results for effects on Skylarks, as suggested in a recent review (Blösch et al., 2023b).

However, evidence is still limited: only a few studies examined important key parameters of Skylark populations, such as breeding performance or prey availability, the latter of which can be particularly critical in winter cereals (Donald & Morris, 2005; Kuiper et al., 2015; Wilson et al., 1997). And none of the studies quantified the impact of the surrounding landscape on the effectiveness of such crop architecture-related measures, although interactions are standing to reason (Blösch et al., 2023b). For example, edges, such as field margins, are considered beneficial for Skylarks, as they form frequently used and arthropod-rich ecotones (Fischer et al., 2009; Jenny, 1990a; Kuiper et al., 2013). Thus, close or long edges might increase the attractiveness of fields, independently of the crop architecture. On the other hand, a winter cereal field with a manipulated crop architecture might be more attractive and thus better accepted by birds in simplified large-parceled monocultures than in small-parceled heterogeneous landscapes, where other crops offer alternative (potentially suitable) crop architectures and nearby fields have large ecotones (Blösch et al., 2023b; Eraud & Boutin, 2002; Teunissen et al., 2010).

Here, we therefore analyzed the effect of Skylark strips on breeding and foraging parameters, and how effects might change depending on the surrounding landscape and as the breeding season progresses. More specifically, we first asked whether the crop architecture in Skylark strips was sparser and shorter compared to areas in conventionally sown fields throughout the breeding season (a). Then we asked whether this resulted in enhanced Skylark territorial behavior (b) and habitat use (c), respectively. In this regard, we also addressed whether the effect of the Skylark strips on the territorial behavior and habitat use was dependent on the time in the breeding season (b(i), c(i)), surrounding landscape features (proximity to edge, edge length, size of adjacent parcels, and adjacent habitat types; b(ii), c(ii)), respectively. Further, we asked whether Skylark strips improved breeding performance of Skylarks in terms of more nesting attempts during the whole breeding season (d), and/or higher nest success (e). Finally, we asked whether prey density was increased in winter cereal fields with Skylark strips, and if so when and which arthropod groups (f), and whether this was reflected in parental foraging patterns indicating improved provisioning during the breeding season (g).

2 | METHODS

2.1 | Study sites and treatment (Skylark strips)

To examine the effects of Skylark strips on territorial behavior, habitat use, breeding performance, and parental foraging of Skylarks, we experimentally manipulated the crop architecture on a total of 12 different sites (four in 2019, five in 2020, and three in 2021) in the Swiss lowlands (see Supporting Information for further information on the study area). Each site was split into two fields in a paired approach: on one of the paired fields, the crop architecture was manipulated with Skylark strips (treatment field) and on the other the crop was sown in a conventional way (control field), with control and treatment being randomly assigned within one field pair (Figure 1). Control fields were conventionally sown with row spaces between 12.5 and 16.6 cm and tramlines every 28–36 m, depending on seed drills. Skylark strips in treatment fields were modeled after “improved tramlines”: Skylark strips consisted of an unsown broad strip of 45–50 cm adjacent to one or two unsown narrower strips of 30–37.5 cm, separated by one sown winter cereal row (Figure 1, Figure S1). The distance between two unsown Skylark strips was 3–4 m; their length was 260–730 m, depending on the field length (mean $\pm$ SE: 466 ± 180 m). To reduce the probability of predation, the Skylark strips ended around 20 m away from the field margin and were, therefore, not connected to the field-encircling tramlines on the headlands. Each treatment or control field was a minimum of 4.5 ha (8.1 ± 2.5 ha) in size and could be either a whole parcel or a subdivided parcel. Whole parcels of one field pair were located directly next to each other or at a maximum distance of 30 m from each other and only separated by linear structures of low interference, such as unpaved paths. Areas of fields, which were unsuitable for Skylarks were excluded from the study fields, for example, we established 50 m buffer zones to large trees, hedgerows, or buildings. We focused on winter wheat (*Triticum aestivum*), except for one winter spelt (*Triticum aestivum* subsp. *spelta*) treatment field.

Studies on Skylarks, that is, territorial behavior, habitat use, breeding performance and foraging patterns, were restricted to areas where Skylarks were present. However, to obtain general information on the crop architecture (i.e., vegetation height and density) and prey availability in fields with and without manipulated crop architecture, the 12 sites used for Skylark studies were complemented by field pairs in a surrounding of 26.2 ± 10.8 km. These differed from the “Skylark-study sites” by being smaller (2.1 ± 1.3 ha), having larger distances between treatment and control fields within a pair (at least 300 m), and having

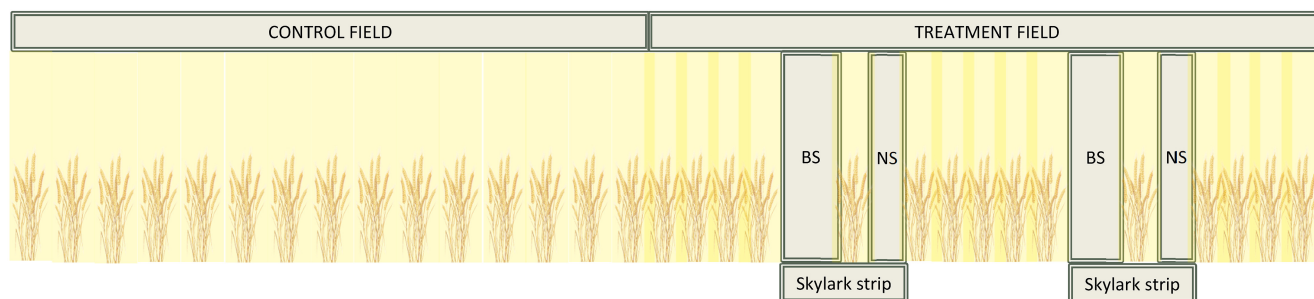


FIGURE 1 Schematic illustration of the study design of one experimental site, which was split into a control field and a treatment field. Control fields were conventionally sown. In treatment fields, Skylark strips were applied, consisting of an unsown broad strip (BS; at least 45 cm wide) and one or two unsown narrower strips (NS; at least 30 cm wide; either on one side of the broad strip or on both sides), repeated all 3–4 m. As seed rate (400 seeds m^{-2}) was not reduced in treatment fields, the areas between the Skylark strips were slightly denser than in control fields.

only the broad strip of the Skylark strips (i.e., no narrower strips). A total of 21 sites were used to collect data on crop architecture and 19 sites on prey availability.

The “Skylark-study area” was characterized by heterogeneous field sizes and crop rotations, which allowed to disentangle interactions between landscape variables and the preference and use of the measure, that is, the manipulated crop architecture, by Skylarks (question b(ii), c(ii)). Agricultural intensity was consistently high on winter cereal fields (two herbicide and fungicide applications, one growth regulator application, fertilization with $143 \pm 40 \text{ kg N ha}^{-1}$) with both treatment and control fields being managed conventionally apart from the sowing pattern. Further, there was no reduction of seed rate (400 seeds m^{-2}) on fields with Skylark strips, with the idea to improve habitat quality for Skylarks while ensuring high and equivalent yields on both treatment and control fields (Blösch et al., 2023a).

2.2 | Crop architecture

To provide data on nesting and foraging habitat within the crop (question a), vegetation height and density as characteristics for the crop architecture were measured once a month between April and July in 2019 and 2020. We took four measurements per field and sampling time, each in $0.2 \times 2.5 \text{ m}$ vegetation-observation plots. In control fields, conventionally sown areas were measured; in treatment fields, broad (unsown) strips were measured. We assessed vegetation density visually by estimating the percentage of vegetation cover. Vegetation height was determined by placing a cardboard of $0.2 \times 1 \text{ m}$ in the middle of the vegetation-observation plots and measuring the height at all four corners.

Vegetation data of conventionally sown winter cereals also provided the basis for categorizing the breeding

season into an early (April and May) and late (June and July) breeding period. Between the measurements in May and June, the average vegetation height reached 60 cm, which is considered the upper limit of the typical range of Skylark nest vegetation in winter cereals (Donald et al., 2002) and average vegetation density exceeded 50%, which is considered the upper limit of optimal cover at nest sites (Jenny, 1990b).

2.3 | Skylark territorial behavior, habitat use, and landscape variables

Measuring scale: To collect systematic, precise, and small-scale data on territorial behavior and habitat use, study plots of 1 ha were established on control and treatment fields with large flexible rods (Figure S2). Accordingly, each study plot was either a control or treatment plot and was observed independently in terms of territorial behavior and habitat use. Treatment and control fields within a field pair were always observed together, whereby the order was randomized. To evaluate how landscape features interact with control or treatment fields, respectively, and how this influences territorial behavior and habitat use patterns of Skylarks, important landscape variables were identified for each study plot (Figure S2).

Territorial behavior (question b): Between April and mid-July, every study plot was visually observed for 10 min (± 1) with minimum intervals of 7 and maximum intervals of 14 days (resulting in 7–15 observations for each plot). During these observations, singing males on territory flights were mapped, and the number of singing males per 10 min in each study plot of control or treatment fields was recorded. Observations were restricted to periods of high Skylark activity from sunrise up to 11.30 am. Frequency of territorial song flights in a plot provides information on occupancy and competition (Pätzold, 1983).

Habitat use (question c): Between mid-April and mid-July, the control and treatment fields were searched for breeding or foraging Skylarks. Therefore, a rope was carried by two observers walking in the tramlines and pulling the rope over the crops to disturb birds on the ground. Locations where Skylarks were flushed were assigned to the respective plot in the data set in terms of habitat use (at ground-level). Maximum intervals between two surveys were 11 days (resulting in at least eight surveys for each plot) and surveys were only conducted in the very early morning (starting with civil twilight, ending at 8.00 am), when Skylarks forage and incubate (Pätzold, 1983).

Surrounding landscape features (questions b(ii) and c(ii)): The following landscape variables were identified for each study plot: “Edge length” and “distance to the nearest edge” were measured to the nearest meter. The “habitat type of the nearest adjacent crop” was classified regarding the crop architecture each habitat type provided, resulting in five categories: winter cereal (except for barley); spring-sown crops; grassland; barley and rape; vegetables (see Table S1 for details). “Parcellation” of adjacent fields was categorized according to whether predominantly large (>2 ha) or small (<2 ha) fields were adjacent to the study plot. See Figure S2 for an exemplary depiction and Table 2 for more details on definition, categories, and range of each variable.

2.4 | Skylark breeding performance and provisioning

Measuring scale: Breeding performance (nesting attempts and nest success) and provisioning (parental foraging patterns and arthropod availability) were observed at field level.

Number of nesting attempts (question d): The same method was used to find nests as for the documentation of habitat use. A systematic search for nests was carried out at locations where Skylarks were flushed. Due to the incubation period of 11 to 14 days (Pätzold, 1983), every nest should have been found in the egg stage in our 11-day interval surveys.

Nest success (question e): Nests were visited every 2–3 days to monitor success. A nest was considered successful when it was found empty at least 8 days after hatching with a well-flattened and undisturbed nest lining and when food-carrying adults were seen or when they were heard giving alarm calls nearby. Co-variables for visibility (and thus conversely concealment) were recorded for each nest to examine their impact on nest success with respect to predator–prey interactions. Visibility of each nest was assessed in an early (after

hatching) and late (after leaving the nest; ca. 8–10 days after hatching) nest stadium. Dates were predicted in case of predation. Visibility was estimated from 20 to 30 cm above the ground (i.e., the approximate height of a medium-sized mammal predator), standing 50 cm from the nest from four angles: entrance, right and left sides, back, to gain the horizontal visibility. Similarly, visibility was estimated from 50 cm above the nest vegetation to gain the vertical visibility representing visibility by avian predators. Single values were averaged, resulting in one value for horizontal visibility and one for vertical visibility per nest.

Parental foraging patterns (question g): As a common method for analyzing the foraging habitats of chick-rearing Skylarks (e.g., Fischer et al., 2009; Kuiper et al., 2013; Morris et al., 2004; Püttmanns et al., 2022), we observed the foraging flights of feeding adults. Foraging locations were mapped one to three times per nest (until at least 10 foraging flights per nest were recorded) as soon as the nestlings were older than 2 days. To do so, we used a hide, such as a camouflaged tent or car (approximately 150 m from the nest) with a clear view of the nest area and all potential foraging habitats and recorded with the help of binoculars whether the foraging location was inside or outside the nest field, that is, the field in which the nest was located.

Arthropod data (question f): To gain information on the prey availability in treatment and control fields, arthropod groups present in Skylark nestlings' diet (Poulsen & Aebischer, 1995; Poulsen et al., 1998; Weibel, 1999) were sampled with pitfall traps and sweep netting during the rearing phases of 2019 and 2020. Sampling locations were approximately in the middle of the fields, in a broad strip in Skylark strips in treatment fields and in a conventionally sown location in control fields, keeping a minimum distance of 10 m to the field edges. Sampling times were once each month in May, June, and July. Pitfall traps (10 cm funnel diameter; 70% ethanol) were opened for 7 days to collect activity density data on ground-dwelling carabids and spiders. Standardized sweep netting (40 sweeps, 40 cm net diameter) was used to collect abundance data of canopy-dwelling Coleoptera (other than carabids), Diptera, Hemiptera, Hymenoptera, and larvae. Overall, we analyzed one sample per sampling method (pitfall trap, sweep net), field (38 fields) and sampling time (May, June, July), summing up to 228 samples.

2.5 | Statistical analyses

Generalized linear mixed models or linear mixed models (depending on the error distribution of the response

TABLE 1 List of response variables. For each variable, it is defined what has been measured, what type of data it was, which categories were available for categorical variables, how model were specified (error distribution and link function), and which research question was addressed.

Response variables	Measurement	Data type	Categories	Error distribution in models (family)	Model link function	Research question
Vegetation density	Vegetation cover (%)	Numeric (continuous); without negative values		Gaussian	Identity	a
Vegetation height	Vegetation height (cm)	Numeric (continuous); without negative values		Gaussian	Identity	a
Territorial behavior	Number of songflights; per observation in a study plot within 10 min	Numeric (discrete); non-negative integer		Poisson	Log	b, b(i), b(ii)
Habitat use (at ground-level)	Number of habitat uses; per survey in a study plot	Numeric (discrete); non-negative integer		Poisson	Log	c, c(i), c(ii)
Nesting attempts	Number of nesting attempts; per period in each field	Numeric (discrete); non-negative integer		Gaussian	Identity	d
Nest success	Observation of the nests; determination of whether a nest was successful or not	Categorical; binary	Successful/not successful	Binomial	Logit	e
Parental foraging patterns	Mapping foraging flights; determination of whether a foraging flight took place in the same field in which the nest was located or not	Categorical; binary	Inside the nest field/outside the nest field	Binomial	Logit	g
Abundance of canopy-dwelling arthropods	Number of canopy-dwelling Coleoptera (other than carabids), Diptera, Hemiptera, Hymenoptera, and larvae, respectively; per month in each sweep net sample	Numeric (discrete); non-negative integer		Poisson	Log	f
Activity density of ground-dwelling arthropods	Number of ground-dwelling carabids or spiders, respectively; per month in each pitfall trap sample	Numeric (discrete); non-negative integer		Poisson	Log	f

variables) were fitted to identify those predictors explaining significant variations in the response variables (*lme4* package, Bates, 2015). Marginal effects were computed to better understand the relationship between predictors and outcome (*emmeans* package, Lenth, 2025). An observation level random factor was added to correct for overdispersion in generalized linear mixed models when necessary (Bolker et al., 2009). Model assumptions were checked according to graphical validation procedures recommended by Zuur et al. (2009). All numerical explanatory variables were standardized prior to the analyses.

Unique field IDs nested within unique site IDs formed the basic random factor-structure, which was included in all models, with additions (nest ID, study plot ID) where necessary. Crop architecture was entered into each model as a fixed factor with two levels (Skylark strip [=treatment], conventionally sown [=control]), representing the experimental design, with treatment effects being of main interest in all research questions. Also, a time variable was added to all models, as changes over the course of the breeding season were another central question. This could have been a factorial period in the case of vegetation structure of crop architecture (four

TABLE 2 List of explanatory variables. Each variable is defined, and its data type is specified. For categorical variables, levels and categories are given, for numeric variables, their range is given. It is defined how variables were prepared for analysis, in which model each explanatory variable was included [models: vegetation density (1); vegetation height (2); territorial behavior, global model (3); territorial behavior, minimum adequate model (3.1); habitat use (at ground-level), global model (4); habitat use (at ground-level), minimum adequate model (4.1), nesting attempts (5), nest success (6), parental foraging patterns (7), abundance of canopy-dwelling arthropods (8), activity density of ground-dwelling arthropods (9)] and whether the explanatory model was part of the “basic model structure,” that is, variables that were part of all analyses.

Explanatory variables	Definition	Data type	Categories/range	Preparation	Included in model	Basic model structure
Crop architecture	Whether fields were manipulated (with Skylark strips = treatment) or not (= control)	Categorical, two levels	Control/treatment		1, 2, 3, 3.1, 4, 4.1, 5, 6, 7, 8, 9	Yes
Time variable: day of the year	Ordinal day number, i.e., sequential day numbers starting with day 1 on January 1st	Numeric (discrete); non-negative integer	92–205	Scaled	1, 2, 3, 3.1, 4, 4.1, 7	Yes
Time variable: breeding period	The early breeding period was in April and May, the late period in June and July; defined by using vegetation data	Categorical, two levels	Early breeding season/late breeding season		5	Yes
Time variable: monthly period	Calendar month	Categorical, three levels	May/June/July		8, 9	Yes
Year	Calendar year	Categorical, three levels	2019/2020/2021		1, 2, 3, 4, 5, 7, 8, 9	Yes
Landscape feature: habitat type of the nearest adjacent crop	For each study plot, the nearest field was defined and characterized into habitat types depending on the vegetation structure (see Table S1)	Categorical, five levels	Winter cereal (except for barley)/spring-sown crops/grassland/barley and rape/vegetables		3, 4, 4.1	No
Landscape feature: edge length	For each study plot, the length of the edge structure, that is, the transitional zone where two different cover types meet, was measured (m)	Numeric (continuous); without negative values	0–140	Scaled	3, 3.1, 4, 4.1	No
Landscape feature: distance to the nearest edge	For each study plot, the distance to the next edge, that is, a transitional zone where two different cover types meet, was measured (m)	Numeric (continuous); without negative values	20–285	Scaled	3, 3.1, 4, 4.1	No
Landscape feature: parcellation of adjacent fields	For each study plot, the adjacent parcels were identified and characterized according to whether they were predominantly small (<2 ha) or large (>2 ha)	Categorical, two levels	Small/large		3, 4, 4.1	No
Visibility: vertical	For each nest, the visibility of the nest from above was estimated, with “0” meaning that 0% of the nest was visible and “1” meaning that 100% of the nest area was visible	Numeric (continuous); without negative values	0–0.9	Scaled	6	No

(Continues)

TABLE 2 (Continued)

Explanatory variables	Definition	Data type	Categories/range	Preparation	Included in model	Basic model structure
Visibility: horizontal	For each nest, the visibility of the nest from the side was estimated, with “0” meaning that 0% of the nest was visible and “1” meaning that 100% of the nest area was visible	Numeric (continuous); without negative values	0.02–0.5	scaled	6	No
Crop architecture of nest location	Whether the nest was located in a treatment or control field	Categorical, two levels	Control/treatment		7	No
Arthropod group (canopy-dwelling)	Groups of canopy-dwelling arthropods that are part of the diet of Skylark nestlings	Categorical, five levels	Coleoptera (other than carabids)/Diptera/Hemiptera/Hymenoptera/larvae		8	No
Arthropod group (ground-dwelling)	Groups of ground-dwelling arthropods that are part of the diet of Skylark nestlings	Categorical, two levels	Spiders/carabids		9	No

levels: April, May, June, and July), arthropod data (three levels: May, June, and July), number of nests (two levels: early and late breeding period) or a numeric single time point of observation (day of the year, in case of territorial behavior, habitat use, and parental foraging patterns), depending on the research question and temporal resolution of the response variable. Only in the case of nest success did the data situation not allow the implementation of a time variable. Interactions between crop architecture and the time variable were fitted in all models, which contained these basic variables. Furthermore, the year from which the respective data originated was implemented as a fixed factor in all models to address annual fluctuations, again with the exception of the nest success model. These variables (crop architecture, time variable, crop architecture: time variable, year) formed the basic structure of our models, which was supplemented with further explanatory variables for individual response variables with specific research questions.

For the models including the potential influence of (various) landscape variables, model selection (*MuMIn* package, function *dredge*, Barton & Barton, 2015) was used to reduce the global model to the minimum adequate model (MAM), from which statistical inferences were drawn (Zuur et al., 2009). For the prey availability-analysis, we show inferential interpretation of the confidence intervals (CIs) of the plotted model predictions, which convey an overall pattern of results at a quick glance (Cumming & Finch, 2005). However, these results were double-checked

by deriving post hoc contrasts from the average marginal effects from the models (Lenth, 2025). Analyses were performed using R ver. 4.0.3 (R Core Team, 2020). Effects were defined as significant when $p < .05$ or marginally significant when $.05 \leq p < .10$.

In the following subsections, each analysis is described in detail. In addition, Table 1 provides an overview and model details of the response variables, and Table 2 of the explanatory variables, including data structure, preparation, and inclusion in models.

2.5.1 | Crop architecture

First, crop architecture was analyzed for its vegetation structure-related differences during each month of the breeding period, with vegetation density and height as separate response variables to assess whether Skylark strips in treatment fields provided a more sparse and short vegetation during the whole breeding season (question a). Vegetation height was log-transformed to achieve normally distributed residuals and avoid heteroscedasticity.

2.5.2 | Skylark territorial behavior, habitat use, and landscape variables

Territorial behavior and habitat use were analyzed for their improvement by Skylark strips (questions b and c)

during the breeding season (b(i) and c(i)), including how landscape features influenced such potential effects (b(ii) and c(ii)). Thus, we fitted global models for both response variables (frequency of territorial behavior or habitat use, respectively) with the basic model structure, all landscape variables, and their interactions with the crop architecture. The random structure was supplemented by nesting the plot ID (of the study plots) in the basic random factor structure. To determine relevant predictors out of the global models, we used model selection based on small-sample corrected Akaike Information Criterion (AICc) (Johnson & Omland, 2004). The MAM with the smallest AICc was used for statistical inference (Zuur et al., 2009). Model-averaged coefficients from model averaging (*MuMIn* package, function *model.avg*, Barton & Barton, 2015) of all candidate models with $\Delta \text{AICc} \leq 7$ (Burnham et al., 2011) are shown in Tables S2 and S3.

2.5.3 | Skylark breeding performance and provisioning

Whether breeding performance of Skylarks was increased in fields with Skylark strips was analyzed via the number of nesting attempts and nest success rate in treatment and control fields (questions d and e). The numeric response variable “number of nests” was log-transformed to achieve normally distributed residuals and avoid heteroscedasticity. The interaction between the breeding period (early, late) and crop architecture (treatment field, control field) was to be used to identify a potential dependence of the effect of the measure from the breeding period. Nest success was analyzed in a binomial model. Due to the strong negative correlation between successfulness and predation of nests (correlation coefficient: -0.91), we refrained from a separate analysis of the predation rate. Instead, concealment variables (vertical visibility [from above], horizontal visibility [mean from four sides]) were entered as additional explanatory variables into the nest success model to gain information on predator–prey interactions. Due to the small amount of nest data, the time variable and the year were excluded from the analysis. Estimated nest success rates were derived by back-transforming the coefficients from the model using the inverse logit function. From this, the odds ratio for nests being successful in treatment or control fields were calculated.

Whether provisioning was improved in fields with Skylark strips was analyzed based on prey availability and parental foraging patterns (questions f and g). Parental foraging was tested via the ratio of foraging within or outside the nest field as the response variable

in a binomial model. Random structure was supplemented by the nest ID. For the arthropod data, two models were fitted to test whether the abundance of canopy-dwelling arthropods (from sweep net samples) or the activity density of ground-dwelling arthropods (from pitfall samples), respectively, were higher in areas with Skylark strips than in the control areas. To differentiate effects for the individual arthropod groups and months, a fixed factor for the arthropod groups was entered, and interactions with crop architecture and period were fitted. Model predictions were plotted and analyzed using graphical interpretation of the 95% CIs, using plots with a linear y-axis. According to Cumming and Finch (2005), *p*-values were defined as less than or equal to .05 when the overlap of the 95% CIs is no more than about half the average margin of error; that is, when proportion overlap is about .5 or less. In addition, *p*-values were defined as less than or equal to 0.01 when the CIs do not overlap; that is, when proportion overlap is about 0 or there is a positive gap.

3 | RESULTS

3.1 | Crop architecture

Vegetation density and height were significantly lower in vegetation-observation plots in Skylark strips than in those in control fields throughout the breeding season (Table S4, Figure 2). Both parameters increased during the growing season for both treatment and control vegetation-observation plots, with vegetation height significantly more strongly increasing in those in control fields (Table S4, Figure 2). Vegetation-observation plots in treatment fields did not exceed average values for density and height typically classified as suitable for breeding (Jenny, 1990b) throughout the breeding season, while those in control plots did from May onward (Figure 2).

3.2 | Skylark territorial behavior and habitat use

Model selection resulted in the following explanatory variables for territorial behavior: crop architecture, observation date, distance to the nearest edge, edge length, and interaction between crop architecture and distance to the nearest edge. The model for habitat use included the same variables plus habitat type of the nearest adjacent crop, parcellation of adjacent parcels, interaction between crop architecture and observation date, and interaction between crop architecture and parcellation of adjacent parcels (compare Table 2).

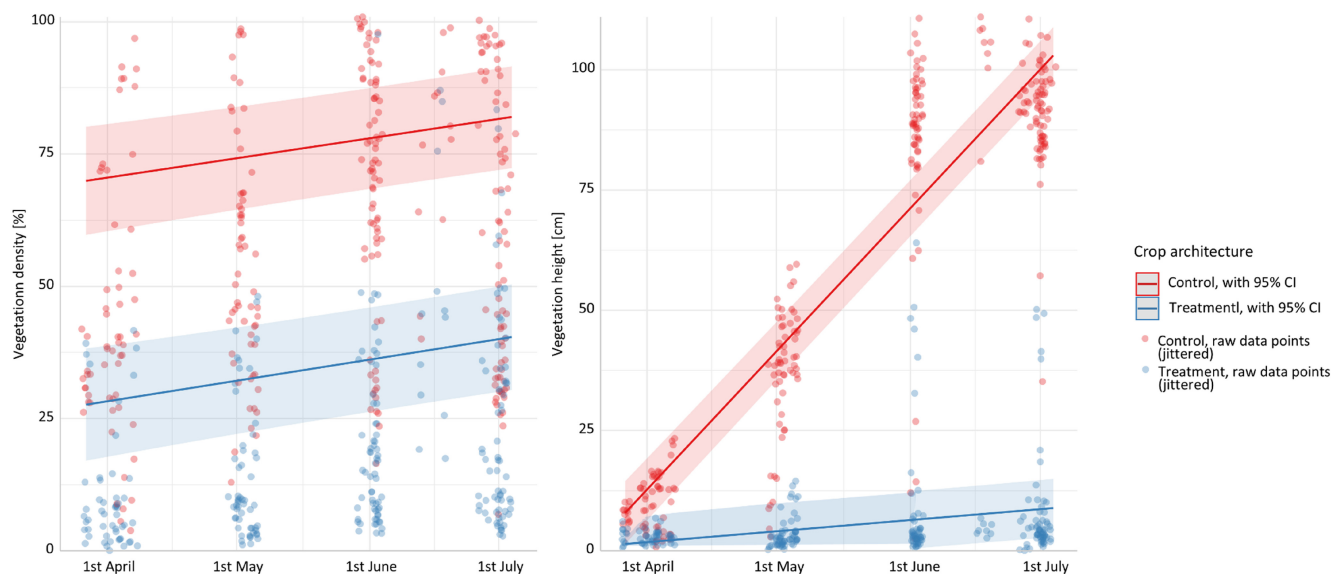


FIGURE 2 Vegetation density (on the left, measured as vegetation cover in percent) and vegetation height (on the right, measured in cm height) in Skylark strips (treatment) or conventionally sown winter cereal fields (control) during the breeding period of Skylarks. Mean predicted values from linear mixed models, jittered raw data from response by predictor on the x-axis, and 95% CI-bands are depicted.

TABLE 3 Model summaries for the minimum adequate generalized linear mixed models (MAGLMM) explaining differences in the territorial behavior or habitat use (at ground-level), respectively, in dependence on the crop architecture (treatment = plot with Skylark strips, control = conventionally sown plot) and landscape variables during the breeding season. SE = standard error, LV = landscape variable. $p \leq .05$ are presented in bold.

Model	Terms	Fixed effects	Estimate	SE	Z value	p value
Territorial behavior	Intercept (crop architecture)	Control	−0.99	0.19	−5.33	<.001
	Crop architecture	Treatment	0.29	0.11	2.60	.009
	Time variable	Day of the year	−0.37	0.04	−10.01	<.001
	LV (edge)	Distance to nearest edge	−0.68	0.13	−5.16	<.001
	LV (edge)	Edge length	−0.22	0.07	−3.16	.002
	LV (edge): crop architecture	Distance to nearest edge: treatment	0.52	0.15	3.57	<.001
Habitat use (at ground-level)	Intercept (crop architecture, habitat type, parcellation)	Control and cereals and large	−1.12	0.18	−6.32	<.001
	Crop architecture	Treatment	0.27	0.19	1.39	.164
	Time variable	Day of the year	−0.29	0.08	−3.72	<.001
	LV (habitat type)	Spring-sown	−0.93	0.32	−2.97	.003
	LV (habitat type)	Grassland	−0.20	0.27	−0.74	.460
	LV (habitat type)	Vegetable	0.06	0.28	0.20	.844
	LV (habitat type)	Barley and rape	0.02	0.21	0.12	.906
	LV (parcellation)	Small	−1.11	0.47	−2.33	.020
	LV (edge)	Distance to nearest edge	−0.36	0.12	−3.08	.002
	LV (edge)	Edge length	−0.26	0.09	−2.80	.005
	LV (parcellation): crop architecture	Small: treatment	1.39	0.52	2.66	.008
	Time variable: crop architecture	Day of the year: treatment	0.22	0.10	2.09	.037

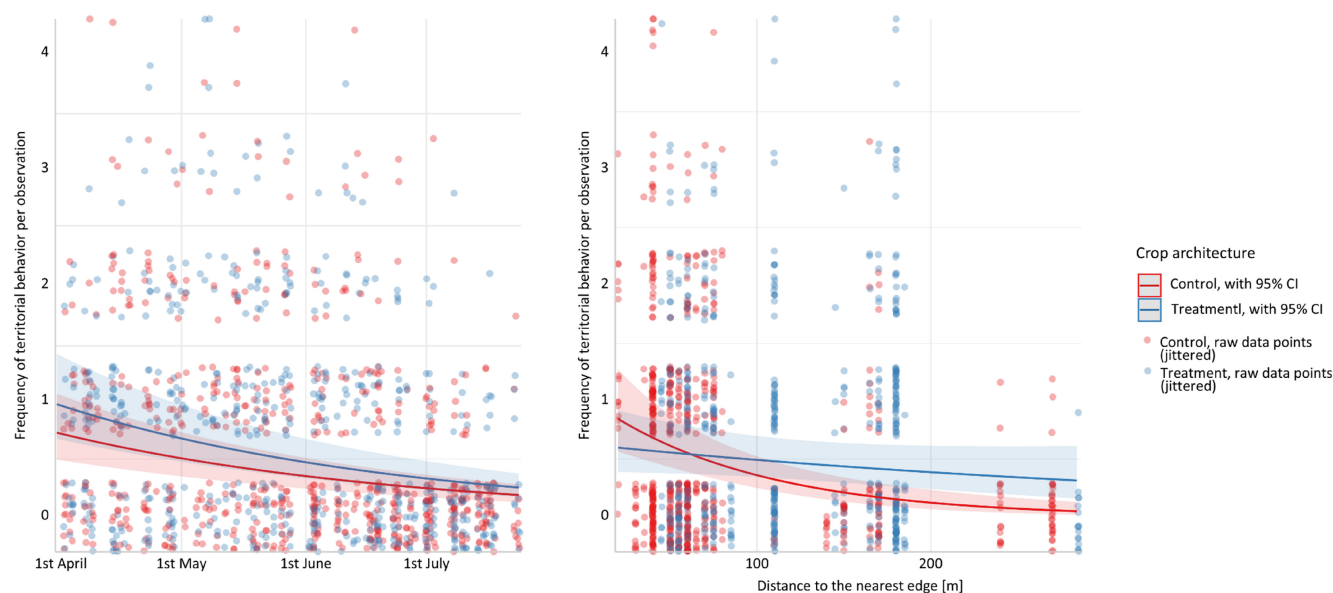


FIGURE 3 Territorial behavior, measured as frequency of territorial behavior per observation and plot, in dependence on crop architecture and observation date (on the left) or crop architecture and distance to the nearest edge (on the right), respectively. Mean predicted values from generalized linear mixed models (back-transformed to the response scale), jittered raw data from response by predictor on the x-axis, and 95% CI-bands are depicted.

TABLE 3.1 Marginal effects within the MAGLMM on territorial behavior. Estimated marginal means are shown for different distances to the nearest edge, contrasting effects on territorial behavior in plots with different crop architectures (i.e., control or treatment). Upper triangle = Tukey-adjusted p -values with $p \leq .05$ presented in bold. Diagonal = Estimated marginal means (in brackets). Lower triangle = Estimates between contrast levels (i.e., control and treatment). Results are given on the log (not the response) scale.

Model: territorial behavior	Crop architecture	Control	Treatment
Distance to the nearest edge = 0 m	Control	[0.05]	0.020
	Treatment	0.51	[−0.46]
Distance to the nearest edge = 50 m	Control	[−0.5]	0.439
	Treatment	0.10	[−0.58]
Distance to the nearest edge = 100 m	Control	[−1.01]	0.007
	Treatment	−0.31	[−0.71]
Distance to the nearest edge = 150 m	Control	[−1.55]	<0.001
	Treatment	−0.72	[−0.83]
Distance to the nearest edge = 200 m	Control	[−2.08]	<0.001
	Treatment	−1.13	[−0.95]
Distance to the nearest edge = 250 m	Control	[−2.61]	<0.001
	Treatment	−1.54	[−1.07]
Distance to the nearest edge = 300 m	Control	[−3.14]	<0.001
	Treatment	−1.95	[−1.19]

The MAM on territorial behavior revealed that plots with Skylark strips were significantly more frequently occupied and contested by territorial individuals than plots in control fields throughout the whole breeding season (Table 3, Figure 3). Overall, however, the frequency of territorial behavior decreased over time (Table 3, Figure 3). Proximity to edges had a strong positive effect on territorial behavior for plots in control fields, but not for plots with Skylark strips

(Tables 3, 3.1, Figure 3, Figure S3). Large edge lengths reduced the frequency of territorial behavior within the study plots (Table 3).

Habitat use (at ground-level) was significantly characterized by interactions between the crop architecture and date: while there was no significant difference in the frequency of utilizations at the beginning of the breeding season between treatment and control plots, these became increasingly less

TABLE 3.2 Marginal effects within the MAGLMM on habitat use (at ground-level). Estimated marginal means are shown for different days of the year, contrasting effects on habitat use (at ground-level) in plots with different crop architectures (i.e., control or treatment). Upper triangle = Tukey-adjusted p-values with $p \leq .05$ presented in bold. Diagonal = Estimated marginal means (in brackets). Lower triangle = Estimates between contrast levels (i.e., control and treatment). Results are averaged over the levels of the nearest adjacent habitat type and parcellation and are given on the log (not the response) scale.

Model: habitat use (at ground-level)	Crop architecture	Control	Treatment
1st April	Control	[−1.19]	0.175
	Treatment	−0.45	[−0.74]
1st May	Control	[−1.53]	0.010
	Treatment	−0.70	[−0.83]
1st June	Control	[−1.88]	<0.001
	Treatment	−0.96	[−0.92]
1st July	Control	[−2.21]	<0.001
	Treatment	−1.20	[−1.01]

frequent in control plots from May onwards (Tables 3, 3.2, Figure 4, Figure S4). Furthermore, small-parcelled adjacent fields (i.e., small parcellation compared to large fields, i.e., large parcellation) led to significant reductions in habitat use in control plots but not in treatment plots (Tables 3, 3.3, Figure S5). The frequency of use of the study plots varied depending on the nearest adjacent habitat type, with the presence of spring-sown crops leading to the greatest declines (Tables 3, 3.4, Figure S6). Proximity to field edges boosted utilizations (Table 3).

3.3 | Skylark breeding performance and provisioning

While there was no effect of crop architecture on the number of nesting attempts in the early or late breeding period, nest success in fields with Skylark strips (estimated nest success rate: 67%; raw data: 7 from 12 nests were successful) tended to be higher than in control fields

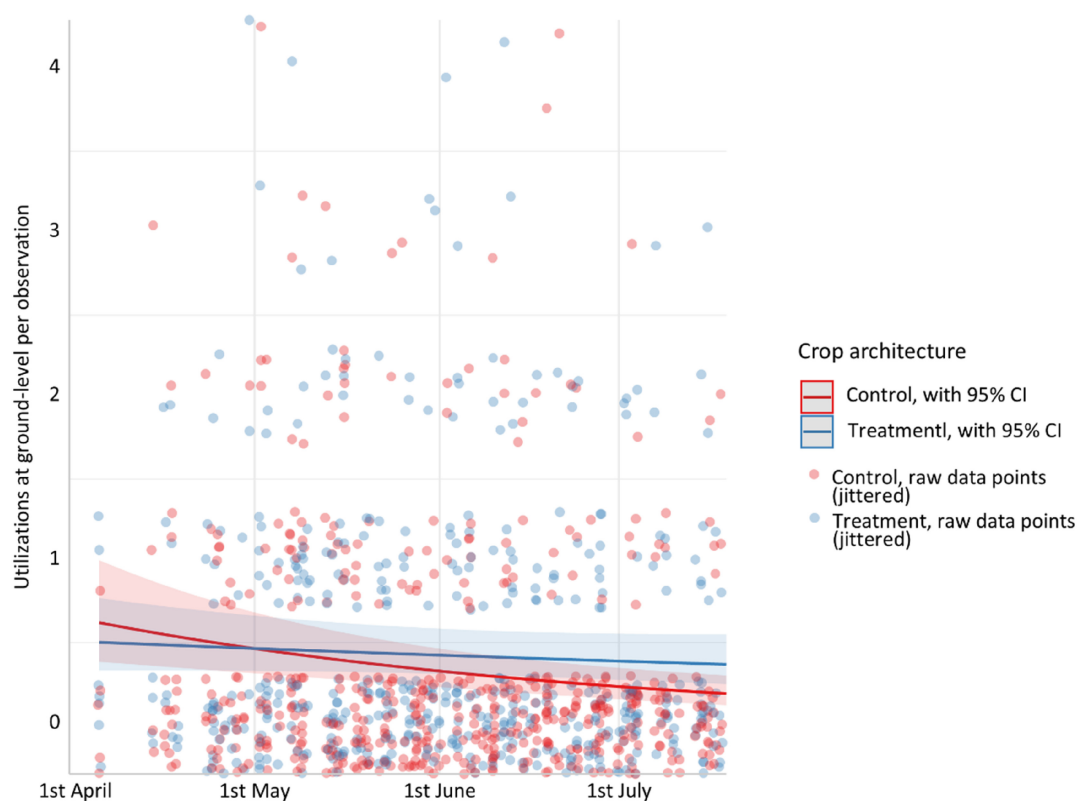


FIGURE 4 Habitat use, measured as frequency of habitat utilizations (at ground-level) per survey, in dependence on crop architecture and observation date. Mean predicted values from generalized linear mixed models (back-transformed to the response scale), jittered raw data from response by predictor on the x-axis, and 95% CI bands are depicted.

TABLE 3.3 Marginal effects within the MAGLMM on habitat use (at ground-level). Estimated marginal means are shown for different adjacent parcellation or crop architecture categories, respectively, contrasting effects on habitat use (at ground-level) in plots with different crop architectures (i.e., control or treatment) or different adjacent parcellation category (i.e., large or small). Upper triangle = Tukey-adjusted p -values with $p \leq .05$ presented in bold. Diagonal = Estimated marginal means (in brackets). Lower triangle = Estimates between contrast levels (i.e., control and treatment or large and small parcellation, respectively). Results are averaged over the levels of the nearest adjacent habitat type and are given on the log (not the response) scale.

Model: habitat use (at ground-level)	Crop architecture	Control	Treatment
Parcellation = large	Control	[−1.33]	0.164
	Treatment	−0.27	[−1.07]
Parcellation = small	Control	[−2.44]	0.001
	Treatment	−1.65	[−0.79]
Model: habitat use (at ground-level)	Parcellation	Large	Small
Crop architecture = control	Large	[−1.33]	0.020
	Small	1.11	[−2.44]
Crop architecture = treatment	Large	[−1.07]	0.474
	Small	−0.28	[−0.79]

TABLE 3.4 Marginal effects within the MAGLMM on habitat use (at ground-level). Estimated marginal means are shown for the different categories from the nearest adjacent habitat type, contrasting effects on habitat use (at ground-level). Upper triangle = Tukey-adjusted p -values with $p \leq .05$ presented in bold. Diagonal = Estimated marginal means (in brackets). Lower triangle = Estimate between contrast levels (i.e., the different habitat types). Results are averaged over the levels of the crop architecture and parcellation and are given on the log (not the response) scale.

Model: habitat use (at ground-level)	Habitat type	Cereal	Spring-sown	Grassland	Vegetables	Barley and rape
	Cereal	[−1.20]	0.025	0.947	1.000	1.000
	Spring-sown	0.93	[−2.13]	0.245	0.062	0.018
	Grassland	0.20	−0.74	[−1.39]	0.944	0.926
	Vegetables	−0.06	−0.99	−0.25	[−1.14]	1.000
	Barley and rape	−0.02	−0.96	−0.22	0.03	[−1.17]

(estimated nest success rate: 14%; raw data: two from nine nests were successful) (Table 4). The estimated odds for nests being successful in treatment fields were 12.5 times the odds for nests being successful in control fields. Furthermore, nests tended to be rather successful when the vertical visibility was low; that is, when the nests were more concealed from above (Table 4).

The number of foraging flights within the nest field varied significantly with both crop architecture and date: there were more within-field foraging flights for nests that were located in fields with Skylark strips than for those that were located in control fields from June onwards (Tables 4, 4.1, Figure S7). This corresponded to the majority of the period in which nests were active (early May to mid-July).

There were monthly fluctuations for nearly all arthropod groups, partly depending on the crop architecture (Figure 5). For sweep-net samples that collected canopy-active arthropods, the abundance of Coleoptera (other than carabids), Diptera, Hemiptera, and Hymenoptera

was not influenced by crop architecture (Figure 5). In contrast, comparing Skylark strips to control plots, there were more larvae in May ($p \leq .01$, Figure 5). For ground-dwelling arthropods caught by pitfall traps, there were no differences in the activity density of carabids between control fields and Skylark strips, but there were significantly more spiders in June in Skylark strips ($p \leq .01$), expressed by a large increase in the catch numbers, which more than doubled from an average of 32 (± 25) to 75 (± 48) per trap (calculated from raw data, sampling duration = 7 days). Detailed model statistics and results from double-checking via post hoc contrasts are shown in Tables S5, S5.1, S6, and S6.1, Figures S8 and S9.

4 | DISCUSSION

Our results suggest that the implementation of Skylark strips in winter cereal fields has the potential to restore habitat quality for Skylarks in high-yielding winter cereal

TABLE 4 Model summaries for (generalized) linear mixed models ((G)LMM) explaining differences in breeding parameters (number of nesting attempts, success rate of nests and parental foraging locations), in dependence of the crop architecture (treatment = fields with Skylark strips, control = conventionally sown fields) during the breeding season; except for the nest success-model, where data did not allow the implementation of a time variable and the nest visibility was additionally entered into the model. SE = standard error, df = degrees of freedom. $p \leq .05$ are presented in bold.

Model	Terms	Fixed effects	Estimate	SE	df	T value	Z value	p value
Nesting attempts	Intercept (crop architecture and time variable and year)	Control and early and 2019	0.60	0.17	23.54	3.58		.002
	Crop architecture	Treatment	0.03	0.20	24.00	0.16		.875
	Time variable	Late	−0.12	0.20	24.00	−0.61		.548
	Year	2020	−0.36	0.15	7.00	−2.36		.051
	Crop architecture: time variable	Treatment: late	0.00	0.28	24.00	0.00		1.000
Nest success	Intercept (crop architecture)	Control	−1.84	0.97			−1.90	.058
	Crop architecture	Treatment	2.53	1.31			1.93	.054
	Visibility	Vertical	−1.35	0.76			−1.78	.074
	Visibility	Horizontal	−0.75	0.70			−1.07	.286
Parental foraging patterns	Intercept (crop architecture of nest location and year)	Control and 2019	0.45	0.56			0.79	.429
	Crop architecture of nest location	Treatment	2.32	0.88			2.63	.008
	Time variable	Day of the year	1.51	1.40			1.08	.280
	Year	2020	2.90	2.12			1.37	.172
	Crop architecture of nest location: time variable	Treatment: day of the year	2.22	0.83			2.69	.007

TABLE 4.1 Marginal effects within the GLMM on parental foraging patterns. Estimated marginal means are shown for different days of the year (during which foraging flights were observed), contrasting effects on foraging flight ratio in fields with different crop architectures (i.e., control or treatment). Upper triangle = Tukey-adjusted p -values with $p \leq .05$ presented in bold. Diagonal = Estimated marginal means (in brackets). Lower triangle = Estimates between contrast levels (i.e., control and treatment). Results are averaged over the levels of year and are given on the log (not the response) scale.

Model: parental foraging patterns	Crop architecture	Control	Treatment
1st May	Control	[−1.28]	0.064
	Treatment	2.35	[−3.63]
15th May	Control	[−0.12]	0.406
	Treatment	0.65	[−0.77]
1st June	Control	[1.28]	0.039
	Treatment	−1.42	[2.70]
15th June	Control	[2.44]	0.005
	Treatment	−3.12	[5.56]
1st July	Control	[3.76]	0.004
	Treatment	−5.06	[8.82]

fields. The key resources “foraging habitat” and “nesting habitat” were improved in the existing cropped area, both important factors in driving Skylark populations (Butler et al., 2007, 2010). Thus, it seems that this measure has the potential to allow Skylarks to return to our fields as “agricultural by-products.” However, our results also suggest that the effectiveness of Skylark strips can depend on surrounding landscape features. Thus, when implementing this measure, the landscape context should be taken into account.

Changes in nest survival rates have been shown to drive population trends in ground-breeding farmland birds (Tapper et al., 1996). This is encouraging for our finding that the estimated nest success rate increased strongly in fields with Skylark strips (67%) compared to fields without Skylark strips (14%). Such a success rate exceeds previously found values for set-asides, which fluctuate between 18% and 45% (Donald et al., 2002; Weibel, 1999; Wilson et al., 1997), with low levels probably being due to increased attraction of predators to rather isolated and longitudinal set-asides and concentrated prey (Donald et al., 2002; Weibel, 1999). Indeed, the commonest cause of nest failure is considered predation across a wide diversity of species and habitats

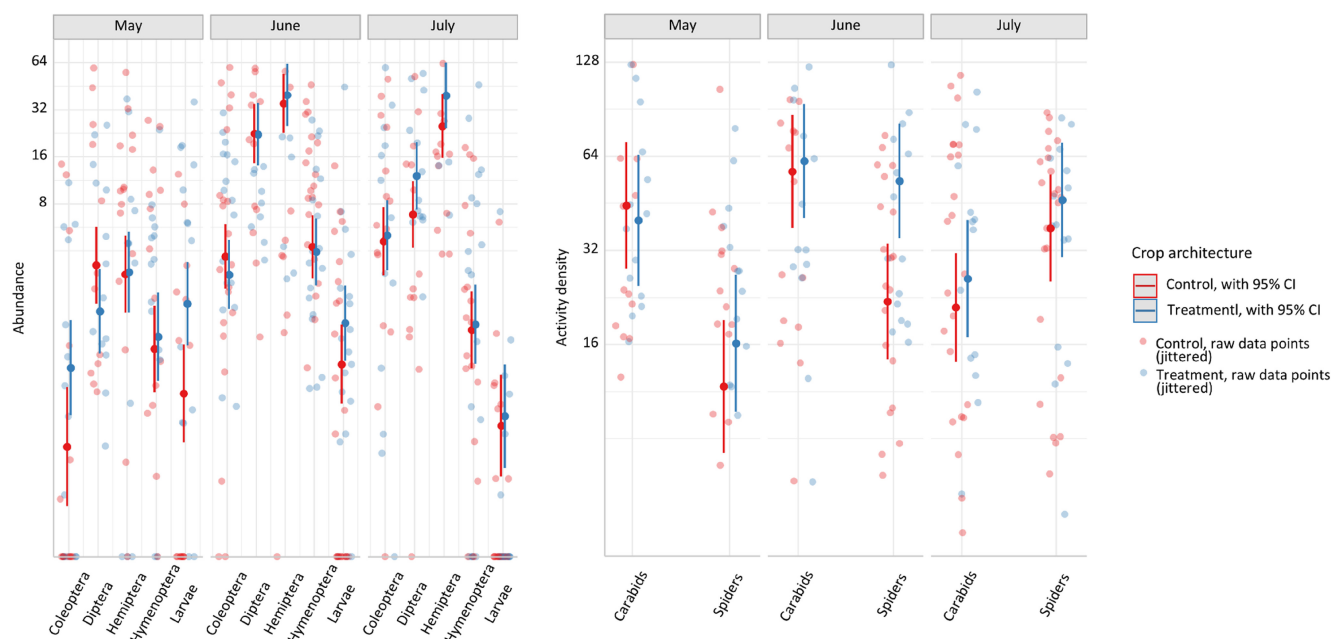


FIGURE 5 Abundance of canopy-dwelling arthropod groups (Coleoptera [other than carabids], Diptera, Hemiptera, Hymenoptera, larvae) from sweep netting (on the left) and activity density of ground-dwelling arthropod groups (carabids, spiders) from pitfall traps (on the right), in dependence of crop architecture and sampling date. Mean predicted values from generalized linear mixed models (back-transformed to the response scale), jittered raw data from response by predictor on the x-axis, and 95% CI-bars are depicted.

(Martin, 1993), which is in line with the high correlation of nest success and predation rate in our study. According to the potential-prey-site hypothesis (Martin, 1993), we suggest that the creation of numerous potential nest sites (i.e., areas with sparse and short crop architecture) in fields with Skylark strips might have reduced predation rates in treatment fields compared to control fields as the probability of the discovery of nests decreases with increasing numbers of unoccupied potential sites (Martin, 1993). Nest success rates were only influenced in terms of vertical but not horizontal visibility, suggesting that avian predators (which seek their prey from the air) could play a major role in nest losses in our study sites. This could indicate that the approach of not connecting the Skylark strips with the field-encircling tramlines on the headlands was effective in providing a physical barrier (by blocking access routes) to predatory mammals. There was no difference in the total number of nesting attempts between fields with and without Skylark strips. This suggests that Skylarks did not cease nesting in conventionally sown winter cereal fields but found poorer conditions (indicated by low nest success). In general, however, sample sizes were low (12 nests in treatment fields, 9 nests in control fields; no breeding activity in 2021 probably due to extremely wet and cold weather), which is most likely the reason why the large increase in the success rate only showed a statistical trend (rather than significance) and which causes the results to be

treated with caution. In sum, we nevertheless conclude that Skylark strips may be an effective tool for Skylark conservation by addressing the lack of suitable nesting sites in intensive arable areas.

Beside the lack of nesting sites, the lack of suitable foraging sites with sufficient prey densities is a further determinant of Skylark population declines (Butler et al., 2007, 2010). In this context, we found the activity density of spiders in Skylark strips to be twice as high as in conventionally sown fields. This is notable in consideration of high absolute numbers and the fact that spiders can contribute more than 20% to Skylark nestlings' diet (Poulsen & Aebischer, 1995; Poulsen et al., 1998; Weibel, 1999). Similarly, increased larvae abundance in Skylark strips in May might be particularly important for early nests when arthropod densities were found to be generally low. To our knowledge, to date no improvement in prey densities has been observed in crop architecture-related measures (Smith et al., 2009; but see Blösch et al., 2023a). As open crop architecture is associated with higher foraging efficiency due to better detectability of prey (prey can be searched for over a greater range, prey items can be more easily seen; Odderskær et al., 1997; Whittingham & Evans, 2004), higher densities of prey in Skylark strips may result in synergistic benefits in the provisioning of nestlings. Even though we were not able to evaluate whether provisioning was sufficient in terms of optimal nestling or parent fitness, we

consider the increase in food supply in winter cereals, which is regarded as critical in this respect (Donald & Morris, 2005; Kuiper et al., 2015; Wilson et al., 1997), to be an important advantage implying the possibility to mitigate the scarcity of suitable foraging habitat of Skylarks (and other farmland birds) in intensive arable areas.

Skylarks seemed to have responded positively to increased prey densities and accessibility in fields with Skylark strips: parental foraging flights were more frequently within the nest field for nests located in treatment than in control plots from June onwards. Consequently, Skylarks had to forage further away from the nest in control fields, with associated costs of energy expenditure and exposure to predation during this important part of the breeding period (Donald & Morris, 2005; Wilson et al., 1997). Although no direct evidence exists from this study, the higher success of nests in treatment fields could also be attributable to food availability, as reduced parental effort in nest-guarding for birds that forage further away from the nest can result in increased predation. In addition, hungry nestlings have been shown to be more vocal and hence more prone to predation (Brickle & Harper, 1999; Evans et al., 1997; Morris et al., 2004).

The fact that Skylark strips in winter cereal fields provide nesting habitat in a relatively predator-safe environment might be the most substantial and unique favor of this measure. Arguably, however, it would be pointless for Skylarks if Skylark strips were implemented in landscapes where they lack effectiveness for them, for example, when landscape features outcompete the attractiveness of winter cereal fields with Skylark strips. In this context, we found that the presence of spring-sown crop fields reduced the habitat use of adjacent cereal fields the most (and more than e.g., vegetable fields [only trend] or barley and rape fields [significant]). Spring-sown crops are known to offer suitable vegetation structure for Skylarks; however, at the cost of low cover and the associated predation risk, for example, in maize (Prau & Weidinger, 2015). In terms of the surrounding landscape parcellation, we found that habitat use of cereal fields was significantly affected by the (manipulated) crop architecture of such fields: while small parcels (with e.g., large proportions of frequently used ecotones [Fischer et al., 2009; Jenny, 1990a; Kuiper et al., 2013]) reduced the habitat use of adjacent control cereal fields, Skylark strips seemed to increase the attractiveness of cereal fields to such an extent that there was no longer a negative effect of small adjacent fields. From this, we conclude that the benefits of Skylark strips come into effect in small- and large-parcelled landscapes but not (to the full extent) in landscapes where spring-sown crops are abundant. In addition, we found that territorial

behavior was less dependent on positive attractants of the surrounding (here proximity to edges, i.e., ecotones) in fields with Skylark strips compared to conventionally sown fields. Thus, we conclude that Skylark strips can especially improve habitat quality in large winter cereal fields. On the other hand, the edges of fields (i.e., field margins) have been associated with a high risk of predation (Morris & Gilroy, 2008), suggesting that a potentially reduced use of these structures along fields (of all sizes) with manipulated crop architecture could have further beneficial effects on Skylark demography. In sum, this shows that the effectiveness of crop architecture-related measures can depend on the landscape context, which is likely to apply equally to production levels (Kirk et al., 2020). These findings not only advise against over-generalization but can also help to ensure optimal allocation of available resources for (Skylark) conservation.

About the temporal development of effectiveness, we found that fields with Skylark strips were utilized increasingly more frequently for ground-level activities from May onwards compared to fields without Skylark strips. This indicates a habitat quality improvement by Skylark strips compared to otherwise dense winter cereal swards in control fields, the quality of which was increasingly deteriorating over the course of the breeding season (see also Eraud & Boutin, 2002). Although this is the basic hypothesis for crop architecture-related measures in winter cereal fields, to our knowledge, this is one of the first times that such a crop architecture $\times$ time variable effect has been demonstrated (Fischer et al., 2009; Morris et al., 2004; Schmidt et al., 2017). This, possibly because studies so far focused only on territorial behavior and habitat use at ground level, has not been examined systematically before.

Congruently, fields with Skylark strips were preferred by territorial individuals over fields without Skylark strips throughout the breeding season in our study. With regard to the finding that there was an overall decrease in territorial activity over the course of the breeding season, seasonal fluctuations in the expression of territorial behavior are known (Pätzold, 1983). Given that Skylarks tend to select the best available habitat, fields with Skylark strips appear to offer better conditions already at the beginning of the breeding season, when conventionally sown winter cereal fields are still considered to have suitable crop architecture. Although we cannot fully resolve this here, increased prey densities and nest success in winter cereal fields altered by Skylark strips could act as positive drivers. Generally, however, increased habitat use for ground activities and territorial behavior in fields with Skylark strips compared to fields without Skylark strips suggests that the measure was well accepted by Skylarks in intensive arable areas.

From a multi-(farmland-) species perspective, it is likely that Skylarks will not be the only profiteers from an opened crop architecture of winter cereal fields, as indicated, for example, by shifts in arthropod densities. Moreover, other crop-breeding farmland birds in particular, whose niche is tied to a sparse and short crop structure (Blösch et al., 2023b), are also likely to benefit.

5 | FINAL CONSIDERATION

Opening the crop architecture in winter cereal fields with Skylark strips to mimic advantages which have been lost in the course of agricultural intensification represents a still rare example of a targeted and efficient in-crop conservation measure. Within the context of the currently reframing land-sharing/land-sparing debate, there is prominent evidence that both will be needed to preserve farmland bird biodiversity: land sparing in which land for conservation is held separate from crop production (e.g., set-asides; Henderson et al., 2012) and wildlife-friendly farming (e.g., organic farming; Smith et al., 2010; Kirk et al., 2020) that combines biodiversity conservation with agronomic production goals (Kremen, 2015). In this context, we provide an example of how wildlife-friendly farming does not have to be accompanied by yield losses, as it has previously been shown that high yields are maintained in winter wheat fields with Skylark strips (Blösch et al., 2023a). Such measures might be particularly important and best adapted for balancing biodiversity conservation and agricultural production on a large scale (Kremen, 2015). Further information on practicability and agronomy of the implementation of Skylark strips is given in the SI. For an open-land species as widespread as the Skylark, we suggest that a large-scale “matrix” of benign wild-life friendly farming with Skylark strips can represent an important and population-driving conservation component. We thus encourage the implementation of Skylark strips on a large scale (in suitable landscapes) and over multiple years in a given area to test whether benefits of such habitat improvement affect population levels.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author (SB) upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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